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The Movement of Western Honey Bees (*Apis mellifera* L.) Among U.S. States and Territories: History, Benefits, Risks, and Mitigation Strategies

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Beekeeping is a cornerstone activity that has led to the human-mediated, global spread of western honey bees (*Apis mellifera* L.) outside their native range of Europe, western Asia, and Africa. The exportation/importation of honey bees (i.e., transfer of honey bees or germplasm *between* countries) is regulated at the national level in many countries. Honey bees were first imported into the United States in the early 1600's. Today, honey bee movement (i.e., transport of honey bees *among* states and territories) is regulated within the United States at the state, territory, and federal levels. At the federal level, honey bees present in the country (in any state or territory) can be moved among states and territories without federal restriction, with the exception of movement to Hawaii. In contrast, regulations at the state and territory levels vary substantially, ranging from no additional regulations beyond those stipulated at the federal level, to strict regulations for the introduction of live colonies, packaged bees, or queens. This variability can lead to inconsistencies in the application of regulations regarding the movement of honey bees among states and territories. In November 2020, we convened a technical working group (TWG), composed of academic and USDA personnel, to review and summarize the (1) history of honey bee importation into/movement within the United States, (2) current regulations regarding honey bee movement and case studies on the application of those regulations, (3) benefits associated with moving honey bees within the United States, (4) risks associated with moving honey bees within the United States,

and (5) risk mitigation strategies. This review will be helpful for developing standardized best practices for the safe movement of honey bees between the 48 contiguous states and other states/territories within the United States.

Keywords: honey bee stock, *Apis mellifera*, human mediated movement, regulations, benefits, risks, mitigation strategies

INTRODUCTION

Honey bees, the most common pollinators across plant/pollinator networks worldwide (Hung et al., 2018), are crucial for human food production (Gallai et al., 2009). Western honey bees (*Apis mellifera* Linnaeus, 1758) are the only *Apis* species with a natural distribution that includes Europe, the Middle East, Africa, and parts of western Asia (Meixner et al., 2013). Beekeepers have transported honey bees around the world because they are easy to manage for production purposes (Crane, 1999). *Apis mellifera* now occurs on every continent except Antarctica (Hung et al., 2018) and is the dominant pollinator species used in agriculture (Williams, 1994; Aizen and Harder, 2009; Jordan et al., 2021). Globally, crop pollination and honey production services provided by managed honey bees are valued at \$182–577 billion and \$8 billion USD/year, respectively (Gallai et al., 2009; Lautenbach et al., 2012; Shahbandeh, 2021).

The human-mediated, global dispersal of western honey bees ultimately led to the development of rules and regulations created to mitigate potential negative outcomes associated with their dispersal. The exportation/importation of honey bees (i.e., transfer of honey bees *between* countries) is regulated at the national level in many countries. These measures range from outright bans on importation to the total absence of regulations. Regulatory authorities in many countries opt for structured permitting processes that, when met, allow the transportation of honey bees, or their germplasm, into a new area under strict protocols monitored by appropriate regulatory authorities. This occurs in the United States under the Honeybee Act, United States Code of Federal Regulation 7 CFR §281–§286 and §322, Subpart B—Importation of Adult Honeybees, Honeybee Germ Plasm, and Bees Other Than Honeybees From Approved Regions (Rules and Regulations, 2014). Regulations regarding the movement of other beneficial bees (i.e., bumble bees, *Bombus* spp.) are also included in this Federal Regulation. Currently, the importation of honey bees into areas where they do not exist is often prohibited worldwide, given concerns of their possible impact on native flora and fauna (Winter et al., 2006; Burgiel and Perrault, 2011).

Regulations concerning the transfer of live honey bees or germplasm *within* an area or political boundary in which they already occur (a process we term “movement” to distinguish from exportation/importation) vary within the United States. In the United States, the states and territories regulate the movement of live honey bees between themselves and other states/territories (Wehling and Flanders, 2005). At the federal level, honey bees already present in the United States (in any state or territory) are allowed to move among states and territories without federal restriction, with the exception of movement to Hawaii (see Code of Federal regulations 7 CFR Parts §319 and §322 at Rules and Regulations, 2014; Wehling and Flanders, 2005; Pernal, 2014).

In contrast, regulations at the state and territory levels vary substantially, ranging from no additional regulations beyond the federal ones to strict regulations for the introduction of live colonies, packaged bees, or queens (**Supplementary Table 1, Supplementary Figure 1** and interactive map¹). This variability leads to the inconsistent application of regulations regarding the movement of honey bees among states and territories within the United States.

In November 2020, we convened a technical working group (TWG) formed by academic and USDA personnel, to review and summarize the current status of regulations regarding the human-mediated movement of honey bees within the United States. The TWG was composed of individuals (scientists/staff/graduate students) from the United States Department of Agriculture (USDA) Agriculture Research Service (ARS), the USDA Animal and Plant Health Inspection Service (APHIS), the USDA Farm Production and Conservation (FPAC) Business Center, and Land Grant Universities (see authors and acknowledgment sections). This manuscript represents the collective output of the TWG.

Herein, we review the (1) history of honey bee importation into and movement within the United States, (2) current regulations regarding honey bee movement and case studies on the application of those regulations, (3) benefits associated with moving honey bees within the United States, (4) risks associated with moving honey bees within the United States, and (5) risk mitigation strategies for bees moving within the United States. It is not our intention with this manuscript to suggest policies related to honey bee movement within the United States. We believe that is beyond the scope of this manuscript. Furthermore, we are not proposing a change in current policies regulating movement of honey bee colonies among states/territories under current management scenarios (i.e., for commercial pollination, honey production, or similar existing activities). Instead, we hope this review will be helpful for developing best practices for the safe movement of honey bees between the 48 contiguous states and other states/territories within the United States.

HISTORY OF BEE IMPORTATION INTO/MOVEMENT WITHIN THE UNITED STATES

Historical Importations of Honey Bees Into the United States

Honey bees are not native to the Americas and were imported into the United States as early as 1622 by English settlers (**Supplementary Tables 2, 3**; Sheppard, 1989a,b). The known

¹<https://uofmd.maps.arcgis.com/apps/webappviewer/index.html?id=b01d1d7cc19d438d8a6af7ce179a4bca>

imported stocks include *A. m. mellifera* Linnaeus, a subspecies with a natural distribution across northern Europe, and *A. m. ligustica* Spinola (Italian honey bee), introduced in the mid-1800's and one of the most favored honey bee stocks (Sheppard, 1989a; Cobey et al., 2012). Other introductions occurred in the 19th century and included *A. m. carnica* Pollmann (Carniolan honey bee), *A. m. caucasica* Pollmann (Caucasian honey bee), *A. m. lamarckii* Cockerell (Egyptian honey bee), *A. m. syriaca* Skorikov (Syrian honey bee), *A. m. cypria* Pollmann (Cyprian honey bee), and *A. m. intermissa* Buttel-Reepen (a north African honey bee). See **Supplementary Tables 2, 3** for more information.

Introductions of honey bee stocks into the United States over the past several decades are better documented and were done to benefit the beekeeping industry. Queen germplasm from the far-eastern Russian province of Primorsky was introduced into the United States after 7 months of quarantine and rigorous analyses of the biology, behavior, and pest resistance of queens and colonies from 1995 to 2000 (Danka et al., 1995; Rinderer et al., 1997, 1999, 2000, 2001a,b). The bees were reported as gentle, had high honey yields, and maintained low rates of infestation with the mite *Varroa destructor* (Anderson and Trueman, 2000; Rinderer et al., 2001a,b). Russian queen stock was made available to beekeepers in 2001 (Rinderer and Coy, 2020). Currently, a genetic stock certification protocol supports the Russian queen breeding industry (Bourgeois et al., 2020; Rinderer and Coy, 2020). However, this stock is not widely used by beekeepers (Haber et al., 2019).

Historical Movement of Honey Bees Within the United States

Beekeepers readily moved various honey bee stocks throughout the United States after initial stock importation into the country (**Supplementary Table 4**). Furthermore, many colonies swarmed, producing feral colonies that established in many locations and environments. There were no efforts to slow the movement of introduced stock once it was present in the United States. The current United States feral and managed honey bee populations are a genetic mixture of the stocks initially imported into the United States and those subsequently introduced into the United States through the permitting process (Schiff and Sheppard, 1995).

Spread of Honey Bees Into the United States

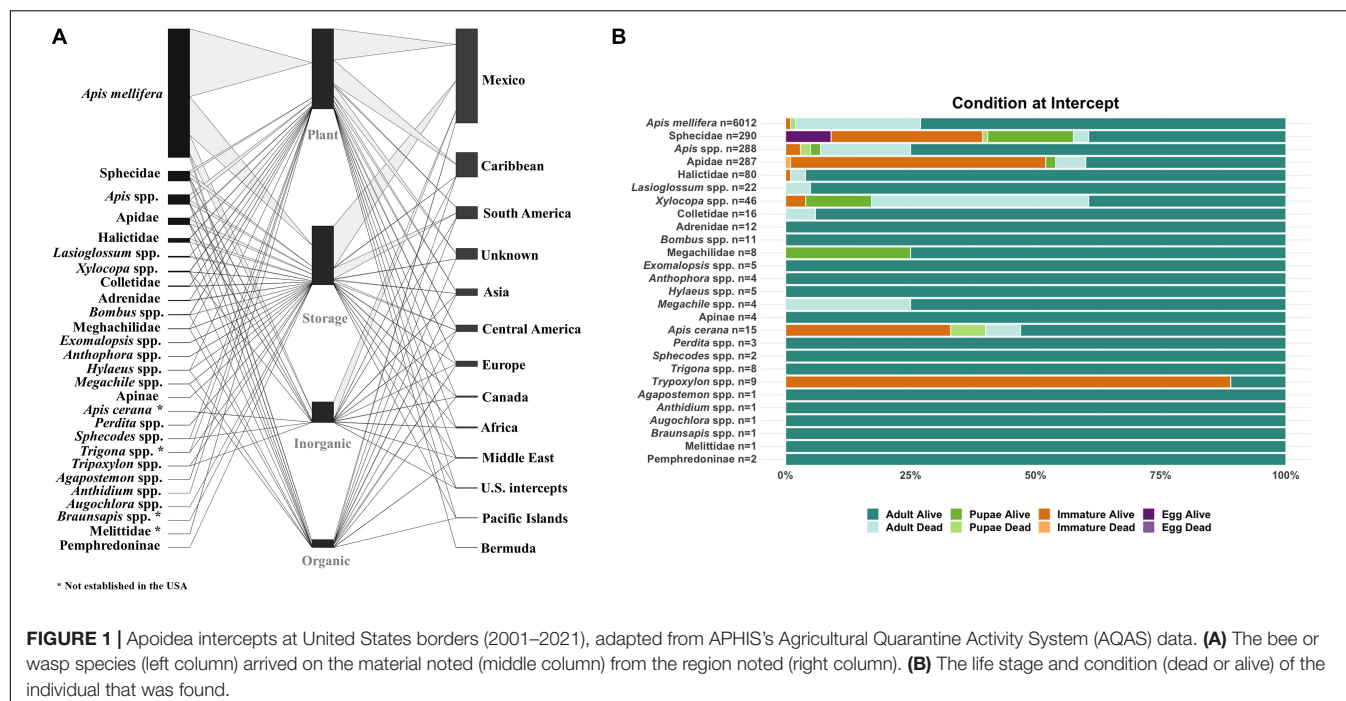
The introduction of *A. m. scutellata*, a honey bee subspecies of African origin, into Brazil in 1956 greatly impacted the distribution of honey bees in the Americas (Kerr, 1967). Imported into Brazil to increase honey production, 26 colonies of *A. m. scutellata* escaped quarantine in 1957 and hybridized with other *A. mellifera* in the region. These hybrids (Africanized honey bees—AHBs) subsequently spread (e.g., natural dispersal without further human assistance) throughout South and

Central America, the southwestern United States (Caron, 2001), and southern Florida (Hall, 1992). Hybridization is well documented across the Americas (Whitfield et al., 2006), and in the United States in particular (Calfee et al., 2020). Africanized honey bees exhibit heightened defensiveness and swarming/absconding behavior and are considered less desirable for commercial use by beekeepers in the United States. Furthermore, AHBs can outcompete and displace honey bees of European descent (EHBs) in areas where they co-occur (Breed et al., 2004; Schneider et al., 2004; Guzman-Novoa et al., 2020).

Africanized honey bee presence in an area does not always result in a negative outcome. This bee has documented resistance to *V. destructor* in Brazil (Carneiro et al., 2007) and in other areas (Strauss et al., 2015; Mondet et al., 2020). Africanized honey bees are generally the preferred honey bee among South and Central American beekeepers who value their honey production and pollination attributes (Roubik and Villanueva-Gutierrez, 2009). Africanized honey bees also occur in Puerto Rico (Puerto Rican Honey Bee or PRHB) where they are notably gentler than the Texas AHB population from which they are derived (Galindo-Cardona et al., 2013; Avalos et al., 2017, 2020; Acevedo-Gonzalez et al., 2019). This gentle demeanor has not been documented in other AHB populations in the Americas. Regulatory authorities in many states within the United States consider the AHB an “unwanted race or stock of honey bee,” and thereby prevent its movement into a given state, or its management within the state (**Supplementary Table 1**).

Continued Threat of Honey Bee Introductions Into the United States

The possible accidental introduction of invasive honey bees and their pests/pathogens into the United States is a present and on-going threat (see section “Risks Associated With Moving Honey Bees Among United States and Territories”). APHIS personnel routinely inspect cargo and passengers entering the country for potential insect pest introductions through the Agricultural Quarantine Inspection (AQI) program. APHIS data on intercepts of individuals in the superfamily Apoidea (which includes bees and wasps) from air, maritime, and terrestrial arrivals between 2001 and 2021 show that honey bees (specifically, *A. mellifera*) compose the majority of interceptions and that most honey bee colonies and/or individuals arrive in the United States on plants and stored goods (**Figure 1A**). Furthermore, most of the intercepted honey bees arrive with materials originating from Central and South America. The volume of trade with nations in these regions may account for the number of honey bees intercepted from each country. Apart from *Trypoxylon* spp. (a crabronid wasp genus), most intercepted Apoidea arrived as live adults (**Figure 1B**). These data highlight the continued possibility of accidental or unlawful introductions of honey bees into the United States.



UNITED STATES LEGISLATION ON HONEY BEE IMPORTATION AND MOVEMENT

Federal Legislation

The United States Congress enacted the Honeybee Act (Federal Act) on 31 August 1922. Its purpose was to protect honey bees and the beekeeping industry from the tracheal mite, *Acarapis woodi*, the presumed cause of an unknown disease devastating honey bees in Europe at the time (Rennie, 1921). The Act has been promulgated multiple times (presently, 7 USCS §281-286 in effect on 3 January 2012). It has been broadened to regulate the importation of honey bee germplasm into the United States, to contain the spread of harmful diseases and parasites to honey bees within the country, and to eradicate/control undesirable species of *Apis* and subspecies of *A. mellifera* within the country and among imports (Rules and Regulations, 2014). Amendments in 1981 granted the Secretary of Agriculture the ability to approve bee-breeding stock and the release of bee germplasm. The Act now defines “honey bee” as all life stages and germplasm (with the exception of semen) of bees of the genus *Apis* (Rules and Regulations, 2014). As mentioned, there are no federal provisions to regulate honey bees currently present in the United States. This is the result of the perceived lack of risk associated with resident honey bee populations.

State/territory Legislation

Regulations regarding interstate movement of honey bees differ at the state and territory levels within the United States (Supplementary Table 1). In general, honey bee movement is

regulated by the issuance of permits from the receiving state based on certificates of bee health issued by the shipping state. Interstate movement ranges from no regulatory measures beyond those at the federal level to strict regulations for movement of live colonies, packaged bees, queens, or germplasm. This lack of uniformity has the potential to lead to the rapid spread of introduced pests, pathogens, parasites and/or deleterious honey bee subspecies across the United States, with repercussions for the beekeeping industry (Box 1).

BENEFITS OF MOVING HONEY BEES AMONG STATES AND TERRITORIES WITHIN THE UNITED STATES

There are multiple potential benefits to moving honey bees among states and territories within the United States (Russo, 2016). First, migratory beekeeping (i.e., the movement of managed honey bee colonies by beekeepers) has direct value to agriculture because the pollination services provided by bees improves fruit set, crop yield, and quality. Second, moving bees provides direct economic benefit to beekeepers who transport their bees to areas where honey is produced and/or where they are paid to use their colonies to provide crop pollination services. Third, honey bees provide ecological value through the ecosystem service of pollination. Fourth, moving bees supports stock improvement initiatives that require an influx of new genetic material from which to select. Fifth, moving bees can compensate for colony losses at a given location. We provide context for each benefit below, demonstrating that moving bees is necessary within the United States to support a healthy economy, food supply, and beekeeping industry.

BOX 1 | Case study on the spread of honey bee industry threats in the 1980s.

The lack of uniform policies and regulations among states and territories within the United States regarding honey bee movement (**Supplementary Table 1** and **Supplementary Figure 1**) has failed to stop the spread of exotic pests and pathogens introduced to the mainland, with costly and irreversible impacts on the beekeeping industry in the United States. Here, we discuss the spread of honey bee pests and pathogens in the 1980s to illustrate this point, as significant new pests and pathogens established and spread in the United States during this decade.

The United States government passed the Honeybee Act in 1922 in response to the Isle of Wight bee disease in England (Nature, 1912). This act aimed to prevent the importation of honey bees from overseas. In addition, the spread and resulting impact of American foulbrood (bee disease caused by the bacterium *Paenibacillus larvae*) catalyzed the passage of state laws and the implementation of state inspection programs in the 1930s and 1940s (Surface, 1916; Phillips, 1920; Voorhies et al., 1933). In the United States, federal and state governments have distinct roles when protecting agriculture. The federal government, acting through APHIS (United States Department of Agriculture, Animal and Plant Health Inspection Service), attempts to prevent the introduction of honey bee threats into the country, helps develop technologies to detect and monitor potential or introduced threats, and works with state governments to contain newly identified introductions. However, state governments (*via* state departments of agriculture) have regulatory authority once a pest is considered established.

The 1980's Annual Proceedings of the Apiary Inspectors of America reveals the complex and interacting factors that influenced the rate of spread within the United States of three honey bee pests during the 1980s (AIA, 1988d). These pests were honey bee tracheal mites (*Acarapis woodi*, HBTM, arrival date 1984), *Varroa destructor* (formerly *V. jacobsoni*, arrival date 1987) and Africanized honey bees (bees derived from *A.m. scutellata*, AHBs, arrival dates: feral colony intercept at FL ports in 1987 i.e., Panama City, Miami and Fort Lauderdale, followed by colonies found in Hidalgo, TX in 1990). See the timeline in this Box for more information.

For over 50 years since the passage of the Honey Bee Act (1922), the only biological threat to honey bee colonies in the United States was the fungal brood disease chalkbrood (*Ascosphaera apis*). It was first discovered in the United States in 1965, but was likely in the country prior to that time (Aronstein and Murray, 2010). At the same time, the predicted arrival of the AHB to southern states preoccupied lawmakers. The AHB quickly spread north throughout the Americas after its accidental release in Brazil in 1957 (Kerr, 1967). It is notorious for exhibiting heightened defensive responses, compared to those exhibited by *A. mellifera* of Eurasian descent managed by beekeepers in the United States. Identifying this undesirable stock was a difficult and time-consuming process. The inability to identify AHB stock efficiently and with confidence may have played some role in its dispersal. This was also true for bees infested by HBTMs. Proposals to certify stocks or bees as "HBTM free" largely failed because the mites were thought to be disseminated across the country already (AIA, 1987).

When state apiary laws were written, they were not designed to regulate the highly mobile apiary industry of the 1980s. Attempts to restrict the movement of bees, enforce quarantines, or await disease diagnosis were ineffective due to the economic and political demands of modern agriculture, i.e., the need to ship and/or truck bees, queens, and colonies across state lines to ensure the beekeeping industry's viability and human food security through plant pollinated crops. *Varroa destructor*, when first detected on the continent (1987), was already in, or on its way to, several states, and its spread paralleled migratory operations coming out of Florida (ADCP, 1987a). A year after the mites were detected in Florida, they were found in most of the contiguous states (AIA, 1988d). *Varroa destructor* is now ubiquitous across the United States except for the territory of American Samoa and some of the islands of Hawaii, i.e., Maui, Kaua'i, Moloka'i, and Lāna'i (Rusert et al., 2021).

Timeline

Notable Honey Bee Threat Introductions, Response, and Spread in the United States Over the 1980's

1979

- *Varroa destructor* scare, false positive in Maryland (AIA, 1981a).
- *Varroa destructor* response plan developed (AIA, 1981b).

1980

- United States Bee and Honey Act (1980) amended to include regulations to control the importation and interstate movement of diseases and other pests of honey bees (AIA, 1983).
- USDA initiates mite survey in Mexico, discovering the honey bee tracheal mite (*Acarapis woodi*, HBTM, Eischen et al., 1990).

1984

- HBTM first detected in Texas, and subsequently in nine states (AIA, 1985a).
- Florida rescinds all regulations on HBTM (AIA, 1985a). Regulators conclude HBTM cannot be eradicated.
- Consensus that it is best to contain HBTM until control measures are established, but now the pest is widespread, regulations controlling spread may cause more economic hardship than they would alleviate (AIA, 1985c).
- APHIS-PPQ recommends federal laws concerning HBTM be rescinded (AIA, 1985b).
- Nationwide HBTM survey discovering mites only in Florida (AIA, 1985c).

1985

- APHIS deregulates the HBTM (AIA, 1987). They are assumed widespread as migratory beekeepers and package producers continue to ship from Florida (AIA, 1987).

1986

- Each state implements its own protocols for HBTM detection and permitting for the shipment of packages, queens, and movement of colonies (AIA, 1986a).
- Florida queen and package industry "eliminated" by quarantine procedures by other states, halting movement of bees for pollination services and honey production in northern states (AIA, 1986b).

(Continued)

Box 1 | (Continued)

1987

- *Varroa destructor* found in Wisconsin, from packaged bees from Florida (ADCP, 1987a).
- *Varroa destructor* in New York State, in migratory beekeeping from Florida (ADCP, 1987a).
- Concluded that restricting migratory movement is impossible to enforce (ADCP, 1987b).
- Canadian border closed to United States queen and package imports, devastating the queen and package industry in the United States (AIA, 1988b).
- Africanized honey bee intercepted at Florida ports (Hall, 1992).

1988

- USDA Action Plans-*Varroa* and Africanized Bees (AIA, 1988c).

1989

- Reaction to USDA action plan largely negative and meets resistance as too restrictive, or not restrictive enough, by different states (AIA, 1988e).

1990

- Feral Africanized honey bee colonies found in mainland United States, at Hidalgo, TX (Visscher et al., 1997).
- *Varroa destructor* arrives in Canada (AIA, 1990).

Benefits of Honey Bee Movement to United States Agriculture

The United States agricultural sector is dependent on insect-mediated pollination for crop yield and/or quality (Jordan et al., 2021). Migratory beekeeping ensures that crop pollination demands are met (Rucker et al., 2012; Ferrier et al., 2018). In the last 50 years, the global demand for pollinator-dependent crops has increased by 300% (Aizen and Harder, 2009; Jordan et al., 2021). The estimated pollination services provided by honey bees to crop production in the United States averages \$12–50 billion USD/year (Bauer and Wing, 2010; Calderone, 2012). To preempt pollination deficits, beekeepers move colonies to blooming crops that rely on insect-mediated pollination for fruit, vegetable, and nut production. Those colonies may originate from outside a state if an insufficient number of colonies exists within the state to provide the pollination services needed by the crops grown in that state.

Almond production in California requires a greater number of pollinating colonies than does any other single crop in the United States (Bond et al., 2021). Honey bee pollination of almonds contributed ~\$9.2 billion USD to the California's gross state product (GSP) in the 2017/18 crop year (Matthews et al., 2020), and an estimated direct value of \$6.09 billion USD in 2020 (Sumner et al., 2014; NASS, 2020). These are not marginal values; yet they account for a fraction of all marketable services and service fees that honey bees provide through migratory beekeeping. Almonds bloom in California in February, making this crop the starting point of an annual migratory route for many commercial beekeepers (Figure 2). Approximately 1.8 million managed honey bee colonies (~60–75% of all United States commercial colonies) are moved to California each year to provide pollination services for almonds (Perez and Plattner, 2014; Goodrich et al., 2019).

From almonds, beekeepers move these colonies across the country to provide pollination services for additional crops

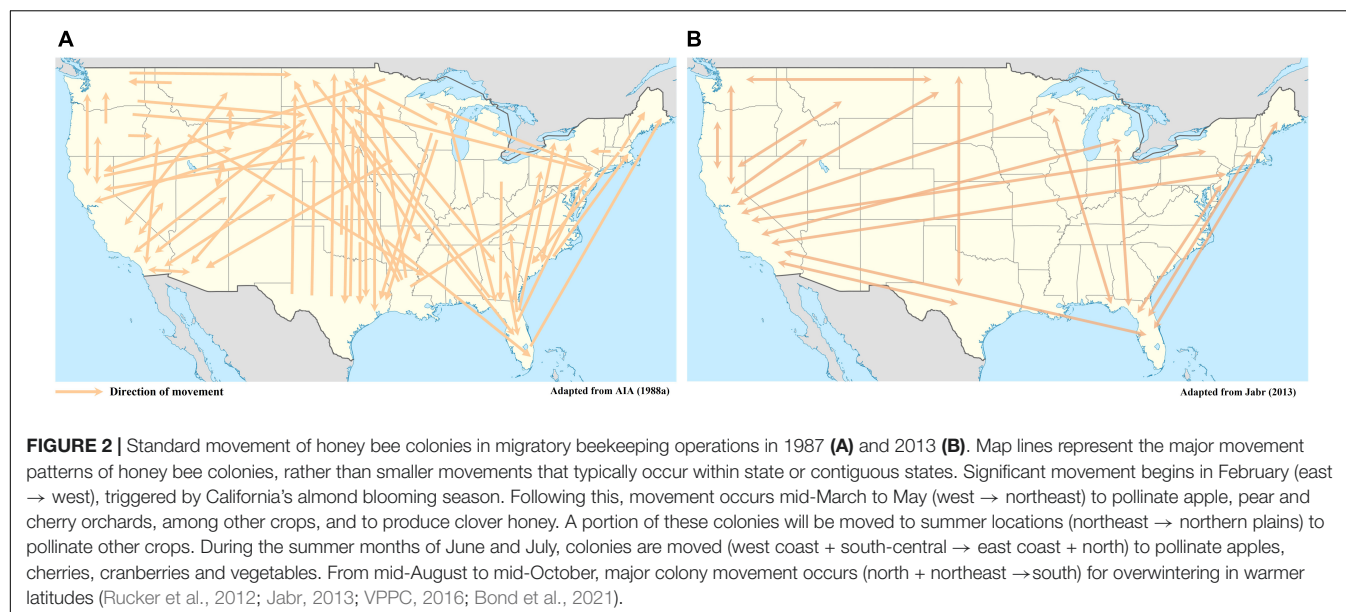
or to major nectar flows around the United States for honey production purposes. Additional colony movements occur during the fall season to allocate hives to warmer latitudes (e.g., Texas, Florida, etc.) for overwintering (Rucker et al., 2012; Jabr, 2013; VPPC, 2016; Bond et al., 2021). Only a subset of beekeepers are migratory. Many provide pollination services only within their region or state.

Commercial Value of Bee Movement for Beekeepers

The movement of honey bees results in direct economic benefit to beekeepers. The revenue generated by providing honey bees for pollination services [rental fees ranging from \$70–210 USD per colony, depending on the crop (USDA, 2020)] was estimated at \$254.3 million USD in 2020 (NASS, 2021). This value was close to the \$299.6 million USD generated from the production of honey in 2020 (NASS, 2021). Wax, pollen, queen, package, and nucleus (nuc) production represent additional value-added products originating from the hive and all generate income for beekeepers.

Ecological Value

Non-marketable ecosystem services are provided *via* the movement of honey bees. These include the improvement of ecosystem function and stability (Losey and Vaughan, 2006). Honey bees are the most frequent visitor of non-crop plants worldwide, being present in about 89% of plant pollination networks (Hung et al., 2018). As a generalist species, honey bees visit a wide variety of flowering plants, while more specialized pollinators only visit a few species or families. Abundant pollination of native and wild vegetation increases the availability of plant resources which, in turn, benefit surrounding wildlife through the production of seeds, berries, nuts, and fruits (Pilati and Prestamburgo, 2016; Klein et al., 2017). In addition, honey bees are often used as bioindicators as they are exposed to trace contaminants such as pesticides and airborne heavy



metals derived from anthropogenic industrial activities while foraging (Conti and Botrè, 2001; Van der Steen et al., 2011; Kennedy et al., 2013; Pilati and Prestamburgo, 2016; Goretti et al., 2020; Traynor et al., 2021). These contaminants can be traced in nectar/honey, wax, propolis and pollen samples, and can be used as indicators of environmental pollution for a given location (Conti and Botrè, 2001; Finger et al., 2014).

Stock Improvement

The movement of honey bees supports stock improvement programs that advance disease resistance and productivity in a managed stock (Spivak and Reuter, 2001; Traniello et al., 2002; Sadd et al., 2005; Blacquièrre and Panziera, 2018). Queen breeders and researchers monitor colonies for vigor and health. In response, they can select for traits such as productivity, gentleness and resistance to pests and pathogens (Ferrier et al., 2018). The movement of the selected stocks among states allows beekeepers in other states to incorporate the stocks into their beekeeping operations. As an example, scientists and queen breeders inseminated breeder queens in Hilo, Hawaii with drone germplasm from the USDA *Varroa* sensitive hygiene (VSH) stock (Harbo and Harris, 1999a,b; Ibrahim and Spivak, 2006). Movement of queens from this new stock, the Hilo bee, to the mainland United States is not restricted, but movement of honey bees to Hawaii is regulated.

Disease/pest resistant strains of honey bees can develop as a result of natural selection, making the movement of these bees of potential value to beekeepers. As an example, research suggests that the PRHB provides an opportunity to improve disease and pest resistance in the managed honey bee population in the United States (Rivera-Marchand et al., 2012; Avalos et al., 2017) by their inclusion in selective breeding programs.

Replacement for Colony Losses

Bee movement allows for the replacement of dead colonies. The individual, additive, and synergistic effects of colony stressors are responsible for annual gross colony loss rates averaging 45.5% (Steinhauer et al., 2020; BIP, 2021). Beekeepers mitigate these losses by splitting and/or purchasing colonies or queens of a preferred stock.

RISKS ASSOCIATED WITH MOVING HONEY BEES AMONG STATES AND TERRITORIES WITHIN THE UNITED STATES

There are inherent risks associated with the movement of honey bees among states and territories within the United States. These include the dissemination of honey bee pathogens and pests, spread of resistance genes in a pest/pathogen population, trait dissemination or loss, impacts on other local flora/fauna, and others. It is important to recognize the risks associated with moving honey bees so that appropriate risk mitigation strategies can be developed.

Dissemination of Honey Bee Pests and Pathogens

The movement of a honey bee subspecies or stock risks introducing pests and pathogens that may impact the resident honey bee population (Ji et al., 2003; Moritz et al., 2005; Neumann, 2006; Cavigli et al., 2016; Owen, 2017). The reciprocal is likewise possible, with the introduced stock being naïve to a pest/pathogen endemic in an area, possibly being highly susceptible to it. The United States honey bee population harbors many of the major pests and pathogens known to impact honey bee colonies (Boncristiani et al., 2021), but their distribution

and levels differ among states and territories within the United States. Puerto Rico and Hawaii can be used as examples of this difference. Deformed Wing Virus-A (DWV-A) and Acute Bee Paralysis Virus (ABPV) are the most prevalent honey bee viruses in Puerto Rico (APHIS, 2018), while Chronic Bee Paralysis Virus (CBPV), Israeli Acute Paralysis Virus (IAPV), and Slow Bee Paralysis Virus (SBPV) have not been detected there (APHIS, 2018). The movement of honey bees between the continental United States and Puerto Rico could result in the spread of these viruses from the continent to managed honey bees on the island (Grozinger and Flenniken, 2019). In Hawaii, *V. destructor* occurs in honey bee colonies on some islands but not on others (Ramadan et al., 2019; Beaurepaire et al., 2020; Boncristiani et al., 2021; Rusert et al., 2021). Moving bees among islands could spread *V. destructor* to islands where it does not occur.

Some honey bee stocks may harbor new pests/pathogens not broadly distributed in the United States. For example, an in-depth genetic analysis of United States mainland and Hawaiian honey bee samples collected during the 2015 APHIS National Honey Bee Pest and Diseases Survey found new viruses not linked to any reported clinical signs (Ray et al., 2020). The detection of these new viruses raises concerns that other undetected pests and pathogens exist, leading to their possible transmission when honey bee colonies are moved.

Honey bee movement may lead to the future dissemination of organisms likely to prove harmful to the beekeeping industry (see **Box 1**). These include *Tropilaelaps* spp., a genus of mites with members that are pests of honey bees in Asia (Anderson and Morgan, 2007), and *Nosema neumannii*, a new species of *Nosema* recently discovered in Africa (Chemurot et al., 2017). This list also includes *A. mellifera* species of concern, such as *A. m. capensis* (the Cape honey bee), known to be social parasite of managed honey bee colonies in South Africa (Neumann and Moritz, 2002).

Spread of Resistance Genes in a Pest/pathogen Population

Honey bee movement can result in the spread of resistance genes in pest/pathogen populations. As an example, some populations of *V. destructor* have documented resistance to amitraz, fluvalinate, and coumaphos in different areas within the United States (Kast et al., 2020; Rinkevich, 2020; Millán-Leiva et al., 2021). Correspondingly, moving honey bees that host miticide-resistant *V. destructor* could spread the resistance trait to miticide-susceptible *V. destructor* populations (Benito-Murcia et al., 2021).

Trait Dissemination or Loss

The movement of honey bees could lead to the spread of negative traits from the introduced population to the resident managed population and *vice versa*. For example, introduced AHBs express heightened defensive behavior, absconding tendencies, etc. and these can be incorporated, *via* hybridization, into the managed honey bee population in areas where AHBs spread (Caron, 2001; Schneider et al., 2004).

Bee movement can impact heritable traits in other ways as well. A selected stock that exhibits beneficial traits can lose those traits when moved into a new area. This occurs because of open mating, i.e., newly produced queens leaving their hives to mate with multiple drones from different colonies among the local population (Koeniger et al., 2014). As an example, selected breeding stock could lose some of its desirable traits, e.g., gentleness and resistance to *V. destructor*, when moved into an area with established honey bee colonies. This may occur even when the original intent of the proposed move was to introduce selected traits into resident managed populations.

Honey bees (resident or introduced) may lose or lack adaptations that improve their health, productivity, and survival in a specific area. Multiple research teams have demonstrated that honey bees in a selection program can fail to perform as expected when moved to a different environment with different climatic conditions (Costa et al., 2012; Hatjina et al., 2014; Kovačević et al., 2020). For example, a pan-European evaluation on behavioral traits across 16 genotypes of five honey bee subspecies in various environmental conditions across Europe showed that genotype and location can impact traits such as defensiveness and swarming behavior (Uzunov et al., 2014). The widespread movement of a large percentage of the managed honey bee population in the United States may limit the development of locally adapted honey bee stocks.

Impacts on Other Local Flora/Fauna

Honey bee colonies, shipped packages, and bees may harbor other arthropods, pests, and pathogens that can impact local bees, other animals, and plant communities (Graystock et al., 2016). Furthermore, plant communities can change when honey bees are moved into an area. This occurs when honey bees pollinate a variety of flowering species, resulting in increased weed species (Goulson and Derwent, 2004) or reduced ranges of range-restricted plants (Norfolk et al., 2018). Moved honey bees may also impact local pollinator communities through competition and displacement (Torné-Noguera et al., 2016; Cane and Tepedino, 2017). The placement of honey bee colonies in high densities at a given location reduces the connectedness of plant-pollinator networks, and in some cases may lead to a decline in ecosystem resilience (Goulson, 2003; Guimarães, Jordano and Thompson, 2011; Geslin et al., 2017; Valido et al., 2019). Additionally, there is evidence for population-level changes with native bee and flora decline in areas where honey bees are the dominant pollinator. This results in the homogenization of honey bee pollinated fauna (Thomson, 2004, 2016; Paini and Roberts, 2005; McKinney and La Sorte, 2007; Balfour et al., 2015; Goulson et al., 2015; Guzman-Novoa et al., 2020).

It is noteworthy that most of these studies document the potential for large-scale impacts on resident native pollinator populations from introduced non-native bees such as honey bees, and not empirical evidence of direct effects on native bee fitness, abundance, and diversity in response to honey bee competition. Usually, negative impacts are predicated on the assumption that natural communities are at capacity and all plants are pollinated efficiently. However, this is not always the case as has been shown

in neotropical communities (Ackerman, 2021). Investigators, through long-term studies on the impact of AHBs on native solitary bees in Central and South America, failed to identify impacts of AHB introductions on native orchid bees. In fact, they found that orchid bee populations increased in numbers after AHBs became established. This finding may be explained by increased foraging resources resulting from pollinator services provided by honey bees (Roubik, 2009; Roubik and Villanueva-Gutierrez, 2009). If honey bees do negatively impact non-*Apis* bee communities in the United States, it is likely to be concentrated around apiaries, and the roadways that give beekeepers access to them, and influenced by local environmental characteristics. The magnitude of honey bee impacts on native pollinators and plant communities depends on local parameters such as foraging bloom density and patchiness, distance from forage, hive density and host specificity of the native pollinators (Cane and Tepedino, 2017; Mallinger et al., 2017).

Other Risks

Every year, beekeepers move more than 1.8 million honey bee colonies around the United States to provide good forage sources for their bees, manage them in more favorable climates/environments, and gain profit by making honey and/or providing pollination services (Ferrier et al., 2018; Goodrich et al., 2019; Bond et al., 2021). There is always a risk of accidents when moving bees on large trucks that typically hold *ca.* 400 colonies. An overturned trailer may contain 1.2 million or more bees and they pose significant risk to people involved in the accident, those passing it, and the first responders addressing it. Sensationalized press coverage of such events, including AHBs or “killer” bees as often called by the press, can harm the reputation of the industry, and may make the public more cautious about bees and beekeepers.

Transporting bees can harm them directly. Repetitive relocation of bees during migratory beekeeping seasons can induce oxidative stress, lead to overheating, and decrease the lifespan of a colony (Ahn et al., 2012; Simone-Finstrom et al., 2016). Multiple relocations, and travel itself, also leads to higher exposure to pesticides and other agrochemicals, which can affect colony survival (Mullin et al., 2010; vanEngelsdorp and Meixner, 2010; Doublet et al., 2015). In addition, high colony densities on moving trucks can lead to pest and pathogen transmission and intensify disease outbreaks. A stress response is also triggered by the need for foraging bees to reassess their changing environment continuously (Simone-Finstrom et al., 2016). vanEngelsdorp et al. (2012) inspected colonies in three migratory beekeeping operations in the eastern United States, quantifying survivorship and prevalence of pests and pathogens. The team identified two risk factors that were predictive of colony mortality in migratory operations, idiopathic brood disease syndrome (IBDS), where brood of different ages appears molten on the bottom of their cells, and queen replacement or failure. In addition, Zhu et al. (2014) reported that transportation increases the abundance and prevalence of *N. ceranae* in honey bees. Moving bees to better forage may counter these effects and ultimately improve the growth and survival of colonies.

RISK MITIGATION STRATEGIES FOR HONEY BEE MOVEMENT AMONG STATES AND TERRITORIES WITHIN THE UNITED STATES

There are means to mitigate the risks associated with moving honey bees. A successful risk mitigation approach integrates multiple risk reduction strategies. Here, we review risk mitigation strategies associated with bee movement and discuss their feasibility of adoption, which may depend on individual state regulations already in place (Supplementary Table 1).

Timely Detection of Pests, Pathogens, and Negative Behavioral Traits

An important risk mitigation strategy could include screening the honey bee stock/life stage (i.e., adult bees, immature bees, and germplasm) proposed for movement between the contiguous 48 states and outlying states/territories for pests and pathogens they may harbor, or undesirable behavioral traits they may display. The APHIS National Honey Bee Pests and Diseases Survey has expanded to screen for additional agents of concern (Traynor et al., 2016; Fahey et al., 2018, 2019; Ray et al., 2020). These types of surveys can target the detection of specific pathogens or pests present in the country (e.g., *V. destructor*, *Nosema* spp., etc.), or of major concern if they were introduced (e.g., *Tropilaelaps* spp., *N. neumannii*, SBPV).

High-throughput sequencing and additional molecular technologies can detect viruses and other microbes infecting honey bees (Cox-Foster et al., 2007). Novel and inexpensive metagenomic screening tools exist and are used to detect viruses in bee communities (Galbraith et al., 2018). These are also used for detection of viruses in honey bees (Runckel et al., 2011; Granberg et al., 2013; Beaurepaire et al., 2020). Environmental DNA (eDNA) has been used to screen for pathogens and pests in honey (Ribani et al., 2020), while shotgun sequencing of honey can identify traces of organisms that bees encounter while foraging (Bovo et al., 2020).

There are also techniques for screening for unwanted species/subspecies of honey bees, though they vary in degree of accuracy. For example, the African honey bee, *A. m. scutellata*, and its hybrids can be identified using a reduced set of single nucleotide polymorphisms (SNPs), a real-time qPCR assay, or combinations of morphological features (Pinto et al., 2014; Harpur et al., 2015; Munoz et al., 2015; Eimanifar et al., 2018, 2020; Boardman et al., 2021; Momeni et al., 2021). Geo-morphometric analyses of honey bee wings coupled with SNP data (Calfee et al., 2020; Henriques et al., 2020), or geo-morphometrics alone (Nawrocka et al., 2018; Bustamante et al., 2020) have been used to identify *A. m. scutellata* populations as well. However, there are problems with relying on the output from some of these screening techniques. For example, morphometric methods can fail to assign hybrid populations accurately (Guzman-Novoa et al., 1994). Furthermore, methods that rely on mitochondrial DNA

are limited as they do not account for paternal contributions (Meusel and Moritz, 1993).

Colonies can also be screened for visible signs of infection/infestation by pathogens/pests and for the presence of undesirable traits using standard protocols (e.g., Shimanuki and Knox, 2000; Dietemann et al., 2013; Spivak and Reuter, 2016). Some behavioral traits could be screened for using molecular technologies (Avalos et al., 2020) or in the field (Giray et al., 2000; Avalos et al., 2014). There are caveats to these trait screening tools when genes governing a phenotype are not yet known, making a molecular screen impossible, or when a phenotype does not manifest in colony-based assays, as in the case of heightened absconding behavior.

A comprehensive monitoring program that profiled the microbiome and behavioral traits of honey bee stocks proposed for movement would be beneficial on a regional/country wide level. These activities could be considered as an integral component of the decision-making process for the inter-regional movement of honey bee stock to a new area.

Phased Movement Within United States Land

Phased movement includes the movement of a honey bee stock into an area after being quarantined. Phased imports serve as an example of how phased movement within the United States could be implemented. APHIS developed procedures for phased imports to mitigate the spread of pests or pathogens from foreign stock to the United States. Similar procedures could be implemented when proposing the movement of honey bees from United States island territories to the mainland and *vice versa*. Here, we provide two examples of phased imports, the first for honey bee queens and the second for germplasm.

USDA scientists implemented a phased import strategy for the Russian honey bee (or Primorsky bee). Briefly, they imported 100 Russian honey bee queens and quarantined them on Grand Terre Island, USDA-ARS Honey Bee Quarantine Station, Louisiana, United States in 1997. The scientists requeened colonies of local stock with the Russian queens and monitored the colonies for pest and disease resistance, behavior, offspring vigor and resistance to *V. destructor*. The quarantine lasted seven months until the new stock was certified free of notifiable pests and pathogens (Rinderer et al., 1999). A Russian queen commercialization and stock certification protocol is now established in the United States *via* the Russian Honey Bee Breeders Association (Bourgeois et al., 2020; Rinderer and Coy, 2020).

Phased movements of germplasm can follow the strategy implemented for phased imports of germplasm, which include the importation of germplasm into a quarantined stock before its release. Sheppard (2012) documented the importation of honey bee semen from managed stocks of *A. m. ligustica* (from Bologna, Italy, 2008, 2009), *A. m. carnica* (from Kirchhain, Germany, 2008, 2009) and *A. m. caucasica* (from the Tblisi and other locations, Republic of Georgia, 2010) to quarantine sites located in the wheat growing Palouse region of eastern

Washington (Bald Butte and Smoot Hill, Whitman County). The imported semen was used to inseminate unmated queens for stock improvement purposes in the United States (Sheppard, 2012). The wheat fields consisted of several hundred hectares with restricted access and were surrounded by hectares of crops that do not provide resources to honey bees (e.g., lentils, barley, etc.). This experimental plan minimized interactions between the research stock and colonies managed by beekeepers in the area. The semen was screened for viruses prior to its use for the insemination of clipped queens. The queens were maintained in nucleus colonies under quarantine until approval was received from APHIS for their release.

Regulate Interstate and Territory Movement

Another mitigation strategy involves regulating interstate/territory movement following a standard protocol, similar to the one used at the national level for stock importation (Regulation 7 C.F.R. §322 at Rules and Regulations, 2014). In this case, bee movement is permitted when the honey bee stock or germplasm is accompanied by a permit or certificate that states the bees are free of pests, pathogens, and/or harmful phenotypes. This would trigger federal and state reviews of the risks and benefits of moving the bees. Such protocols exist but are not applied consistently across states (**Supplementary Table 1**).

Admittedly, regulating movement at the state level through inspections, certifications, and permits can be arduous and time-consuming. However, a vetted and implemented permitting process, triggered by notifying APHIS personnel with a request to move bees, could remove some of the inconsistencies between state and territory regulations regarding the movement of honey bees (Mailander and Grant, 2019). The adoption of a standardized permitting process across all states and territories may translate into a more uniform and judicious regulation of bee stock movement.

Instrumental Insemination and the Introduction of Germplasm Into an Existing Honey Bee Population

The movement of germplasm, rather than actual bees, can mitigate some risks associated with moving honey bees. Safeguards can be implemented to ensure pest-free germplasm. The movement of drone semen, for example, does not carry the risk of moving *Varroa* spp., *Tropilaelaps* spp., or other arthropod pests. Semen can be screened for pathogens using molecular tools and discarded at low cost if pathogens are discovered (Sheppard, 2012). Furthermore, germplasm is easier to transport, does not carry the risk of bee escape, and can be introduced into resident populations of honey bees through instrumental insemination (Hopkins and Herr, 2010; Hopkins et al., 2012; Sheppard, 2012). Due to these advantages, it was the protocol chosen for the introduction of Russian honey bees, *A. m. ligustica*, *A. m. carnica*, and *A. m. caucasica* germplasm into the United States (Sheppard, 2012). This method was also used for the Hilo and Pol-line stocks kept in Hawaii in closed mating systems for

queen releases to commercial beekeepers (Danka et al., 2016; Bilodeau et al., 2020).

Stock Certification Program

A stock certification program can include multiple risk mitigation strategies. First, a stock can be defined per its attributes, such as possessing a selected trait (i.e., *Varroa* Sensitive Hygiene) or combination of traits that make it resistant to a pest or pathogen. The latter happened in the case of the Russian honey bee, with its origin and general resistance to *V. destructor* being integral to the stock's defined attributes (Bourgeois et al., 2020). Second, a certification program can include routine screening for pests, pathogens, and undesirable traits. If the stock is derived from an "unwanted race or subspecies" of honey bee (language often used at the state regulatory level), a demonstration that the stock is free of the "unwanted" trait could be included as part of the stock's definition.

It is important to demonstrate that the genetic stock will not re-acquire, or revert to, undesirable phenotypes. It is also necessary to develop a maintenance plan for the stock. This could include a strategy to maintain and monitor the stock's purity, along with a demonstration that it is not prone to broad geographic dissemination and competition with resident populations. The classic example of a failure to contain invasive bees is the introduction of the AHB into Brazil in 1956 (Kerr, 1967). Multiple AHB queens escaped from research colonies before adequate safeguards were put in place, leading to the establishment of one of the most successful invasive insects in the Americas (Smith, 1991; Visscher et al., 1997; Caron, 2001; Moritz et al., 2005).

Prohibit Movement of Honey Bee Stock Into an Area in Which It Is Not Already Present

Another risk mitigation strategy involves the prohibition of movement of honey bee stocks to areas they are not present. This represents the most extreme mitigation strategy and is employed only if the risk is so great that a negative outcome is almost ensured. It is necessary to ensure that a prohibition of this type would not affect the normal movement of honey bees for typical beekeeping purposes. In most cases, this mitigation strategy is probably not practical.

Additional Considerations

There are additional variables to consider when developing appropriate mitigation strategies. First, the level of mitigation can vary depending on what is being moved (i.e., queens, packages, colonies, germplasm, etc.). Second, certification requirements for a given move request would depend on its specific characteristics (e.g., island setting vs. mainland setting, variable regulatory frameworks between states, etc.). Third, a testing framework and appropriate certification process would be required for genetic, pest, and pathogen testing that ascribes to specific standards, such as the Good Laboratory Practices (GLP). Adherence to accepted standards could be demonstrated by private and federal laboratories that may conduct such tests. Fourth, it is important

to consider the regulatory costs for monitoring movement. Consistency on movement policies and risk mitigation strategies at federal and state levels is needed for a country-wide regulatory framework to function in an efficient manner. The serious consideration of the issues presented in this manuscript can serve as the basis upon which to build a framework that will lead to a fair, economic, equitable and beneficial process for moving honey bees between states and territories within the United States, especially between the 48 contiguous states and the outlying states/territories.

GENERAL CONCLUSION

Honey bees are vitally important to agriculture in the United States, ensuring a significant portion of the nation's food supply through the pollination services they provide. Beekeepers move colonies to provide pollination services, produce honey, recover colony losses, improve stocks *via* new genetic material, and recuperate costs. The movement of honey bees is a necessary and critical component of agriculture in the United States and it supports the beekeepers whose incomes rely on healthy bees. Although necessary, the movement of honey bees is not without risk. This risk has led state and territory officials to develop a variety of rules and regulations imposed to ensure honey bee health and sustainability of the beekeeping industry.

The issues associated with the regulatory process and regulations regarding the movement of honey bees among states and territories within the United States led to this review. We believe bee movement remains a necessary and critical component of agriculture and the beekeeping industry in the United States. The information we present herein can inform future efforts designed to create standardized best practices for moving honey bees among states and territories within the United States.

AUTHOR CONTRIBUTIONS

JM and JEl conceived and developed the review. JEv, ToG, TuG, EN, RR, WS, and DvE provided empirical knowledge and scientific expertise regarding the application of current state and federal regulations on bee movement, present status of the bee industry and beekeeping in states and territories within the United States, and risks and mitigation strategies associated with moving honey bees within the United States. KC, AN, and CB performed data analysis, figure preparation, and interactive map assembly. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.850600/full#supplementary-material>

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