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Identifying regions of risk to honey bees from Zika vector control in the USA

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Managed honey bees are a crucial component of many countries' agricultural systems. Critically, it is now well established that honey bees are faced with multiple threats, and therefore, it is important that we determine and mitigate new threats. The emergence of Zika virus has introduced the new threat of insecticidal mosquito control leading to honey bee losses, with demand from beekeepers for a comprehensive risk assessment to help mitigate losses. Here, we present novel estimates of county-level honey bee colony densities across the USA and combine these new data with different projections of Zika virus suitability to assess the magnitude of this risk. We find that up to 13% of colonies can reasonably be expected to experience elevated risk of damaging pesticide exposure, according to interpretation of current Zika virus projections. We show a significant positive correlation between areas of Zika suitability and honey bee colony density. Increased risk of colony loss to pesticides are found in the South-East, Gulf Coast, Florida, and the California Central Valley. We highlight certain states which are better placed to mitigate threats, recommending other states look towards these schemes to protect apiculture from both government and commercial pesticide application.

Identificación de las regiones de riesgo para las abejas melíferas en el control de vectores de Zika en los EE.UU.

El manejo de las abejas melíferas es un componente crucial de los sistemas agrícolas de muchos países. Críticamente, ahora está bien establecido que las abejas de la miel están disminuyendo frente a múltiples amenazas, y por lo tanto, es importante que determinemos y mitiguemos las nuevas amenazas. La aparición del virus Zika ha introducido la nueva amenaza del control de los mosquitos mediante insecticidas, lo que puede provocar la pérdida de abejas melíferas, y hace que los apicultores demanden una evaluación exhaustiva de los riesgos para ayudar a mitigar las pérdidas. Aquí presentamos nuevas estimaciones de las densidades de colonias de abejas melíferas a nivel de condado en los Estados Unidos, y combinamos estos nuevos datos con diferentes proyecciones de la idoneidad del virus Zika para evaluar la magnitud de este riesgo. Encontramos que se puede esperar razonablemente que hasta un 13% de las colonias experimenten un riesgo elevado de exposición a pesticidas dañinos, de acuerdo con la interpretación de las proyecciones actuales del virus Zika. Mostramos una correlación positiva significativa entre las áreas de aptitud de Zika y la densidad de las colonias de abejas melíferas. En el sureste, la costa del Golfo, la Florida y el Valle Central de California se encuentra un mayor riesgo de pérdida de colonias a causa de los pesticidas. Destacamos ciertos estados que están en mejor posición para mitigar las amenazas, recomendando a otros estados que miren hacia estos esquemas para proteger la apicultura de la aplicación gubernamental y comercial de pesticidas.

Keywords: Zika virus; Apis mellifera; pesticide; vector control; honey bee; pollinator

Introduction

Threats to pollinators are of serious and growing concern for global agricultural systems (Potts et al., 2016) which rely on robust and diverse pollinator assemblages to provide pollination services (Garibaldi et al., 2013; Hoehn, Tscharntke, Tylianakis, & Steffan-Dewenter, 2008), especially in the context of global change (Brittain, Kremen, & Klein, 2013; Klein et al., 2007; Rader, Reilly, Bartomeus, & Winfree, 2013). Pollination services are important for both fruit quantity (Garibaldi et al., 2013) and quality (Knapp, Bartlett, & Osborne, 2017). However, a small subset of bee species are the majority providers of these

necessary pollination services (Kleijn et al., 2015), with honey bees frequently and successfully employed as supplementary pollinators (Rader, Howlett, Cunningham, Westcott, & Edwards, 2012). In the USA, managed pollinating bees (principally *Apis mellifera*) are estimated to be worth \$15bn, principally due to the demand for managed honey bee colonies to provide temporary pollination services (Calderone, 2012; Levin, 1983). However, both wild (Koh et al., 2016; Potts et al., 2010) and managed (vanEngelsdorp & Meixner, 2010) pollinating bees are declining in the USA, leading to large increases in costs of honey bee colony rental for farmers (Burgett, Daberkow,

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Rucker, & Thurman, 2010). There is a complex set of ecological literature on the variety of drivers behind these declines including disease, landscape change, and pesticide exposure (Becher, Osborne, Thorbek, Kennedy, & Grimm, 2013; Potts et al., 2010; Sánchez-Bayo et al., 2016). Although most insecticide exposure to managed honey bees is experienced via crop treatments (Johnson, Ellis, Mullin, & Frazier, 2010), an important route of exposure is insecticidal spraying to control nuisance or disease vector insects – especially mosquitos (Harriott, 2016).

Emphasis on mosquito control in the USA has increased rapidly in response to the recent emergence and rapid expansion of Zika viral disease (Schmidt, 2016). While mosquito controls are already exercised for viruses such as West-Nile or Dengue (Hadler et al., 2015; Petersen & Hayes, 2008; Rose, 2001), public concern has traditionally been low in the USA (Ho, Brossard, & Scheufele, 2007), with mosquitos viewed as a nuisance rather than a disease vector (Dickinson & Paskewitz, 2012). However, the association of Zika with severe birth defects (Mlakar et al., 2016) has led to major public health concerns (Fauci & Morens, 2016; Gulland, 2016; Petersen, Jamieson, Powers, & Honein, 2016) and widespread media attention, for example the extreme concern surrounding the 2016 Olympics in Brazil (Codeco et al., 2016). Consequently, mosquito control measures may increase at both the local and regional level in response to the emergence of Zika virus, driven by both official public health measures and private contracting. This poses a risk to US apiculture and native pollinator health (Harriott, 2016).

The proximate risk to apiculture comes from adulticidal mosquito controls (Schmidt, 2016); however, the severity of the threat depends on control approach. Control may be decided upon as in the public benefit at the county or state level but may also be undertaken on a private basis by home or land owners soliciting commercial mosquito control. In the case of county or state controls, the Centers for Disease Control and Prevention (CDC) first-line recommendation for adulticidal spraying is the organophosphate Naled (Dimethyl-1,2-dibromo-2,2-dichlorethyl phosphate) (CDC, 2016a), applied as an 'ultra-low volume' spray (Breidenbaugh & de Szalay, 2010; Mount, Biery, & Haile, 1996); however, the effectiveness of Naled spraying in controlling Aedes has been called into question following recent mixed evidence (Bouzid, Brainard, Hooper, & Hunter, 2016). Various studies have shown low risk quotients (Davis, Peterson, & Macedo, 2007), and a generally low impact on most terrestrial non-target species (Schleier & Peterson, 2010) and invertebrate biodiversity (Breidenbaugh & de Szalay, 2010), partly due to its rapid degradation (Schleier & Peterson, 2009). However, an acute risk remains for some insects exposed to Naled during its application (Hoang, Pryor, Rand, & Frakes, 2011), with high mortality in exposed honey bees leading to demonstrable impacts on colonies (Zhong, Latham, Hester, Frommer, & Brock, 2004). Furthermore, there is evidence that bees are comparatively more sensitive to stressors such as pesticides compared to other insects (Claudianos et al., 2006; Klein, Cabirol, Devaud, Barron, & Lihoreau, 2017).

Additionally, the CDC lists a variety of alternative insecticides, some of which operate as residual sprays (CDC, 2016b). A number of these control agents have been demonstrated to have negative impacts on individual honey bees or honey bee colony performance at sublethal levels (Desneux, Decourtye, & Delpuech, 2007), including the CDC-listed residual sprays imidacloprid, deltamethrin, bifenthrin, and lambda-cyhalothrin (Dai et al., 2010; Decourtye, Devillers, Cluzeau, Charreton, & Pham-Delègue, 2004; Dolezal, Carrillo-Tripp, Miller, Bonning, & Toth, 2016; Ingram, Augustin, Ellis, & Siegfried, 2015). While night-time spraying or notification of beekeepers to allow the covering of colonies can prevent exposure to rapidly degradable insecticides (Harriott, 2016), exposure to residual sprays is much harder to prevent due to their permanence in the landscape (Sánchez-Bayo & Goka, 2014). Other mosquito control approaches such as source reduction, biocontrol, larvicides (for example, hormone mimics), and the use of toxins from Bacillus thuringiensis israelensis are all viable in reducing mosquito prevalence (Floore, 2006) and do not threaten honey bees. Where adulticidal spraying is mandated, aerial, backpack, or truckmounted may all be employed based on the scale of the operation. Of these, aerial spraying is of the greatest threat to honey bees, and is routinely employed as a prevalent method of pesticide delivery (Matthews, 2011). Honey bee colony losses in response to county-mandated Zika control measures using aerial spraying have already been confirmed (Clemson University, 2016).

There is a lack of information on the prevalence of, and mitigation techniques employed by, commercial pesticide services when solicited by private home- or landowners. Minimum standards require that all applicators follow pesticide labels, but no further legal requirements exist at the federal level. States issue pesticide applicator licenses for private or commercial mosquito control, but information on what pesticides or approaches are used by commercial agents is difficult to obtain. Additionally, mitigation methods used by commercial control agents are likely very variable and another unknown. Night-time spraying may be much less likely, and information on local apiaries is not immediately accessible to private operators. Understanding the role of commercial mosquito control may be critical in protecting beekeeper's livelihoods - with beekeeping organizations already expressing concern over colony losses to commercial mosquito control operations (MABA, 2016). As efforts to verify and quantify these reports are undertaken, understanding of the prevalence of honey bee colony loss due to privately contracted mosquito control activities will improve.

This paper seeks to establish where and at what magnitudes Zika responsive mosquito control poses a risk to apiculture, and by extension pollination service provision

and therefore wider agriculture. The threat of emerging agricultural diseases is recognized (Anderson et al., 2004; Fisher et al., 2012); however, the potential indirect impact of human disease on agriculture seems unaddressed. Our identification of areas of high Zika suitability coinciding with high levels of apicultural activity will help mitigate potential conflict between apiculture and Zika control. In doing so, we hope to inform beekeepers, commercial mosquito control agents, and county or regional officials in finding the most responsible approaches to vector control while minimizing damage to apiculture.

Materials and methods

Zika suitability

For prediction of where Zika is likely to be a problem in the USA, we used published projections from independent predictions of where Zika may endogenously transmit. These published projections of Zika virus extent employ ecological niche modelling approaches, an approach to mapping disease transmission risk that has recently become highly popular in disease ecology. While some diseases are globally cosmopolitan, most vector-borne diseases do not occupy the entire range of their vectors, and ecological niche models have been increasingly employed to make these geographic delineations. We examine three separate projections generated from independent studies which sought to predict Zika-suitable regions using Zika-specific ecological niche models (others adapting dengue or Aedes data have been omitted here): Carlson, Dougherty, and Getz (2016), Messina et al. (2016), and Samy, Thomas, Wahed, Cohoon, and Peterson (2016); hereafter we refer to these projections by the name of the first author ('Carlson', 'Messina', 'Samy' respectively). The differences between these studies are subtle and often technical, but the disagreement between their results is in some regions profound (for a detailed analysis of their disagreement, see Carlson, Dougherty, Boots, Getz, & Ryan, 2018), with Carlson (the most restrictive) suggesting Zika will be confined to the southernmost tip of Florida and highly limited areas of Los Angeles county while Samy suggests isolated outbreaks of Zika are possible throughout the entire USA. For each projection, we projected US counties onto mapped suitability, and calculated the proportions of county areas which a given projection predicts to be suitable for Zika. These values are detailed in Online Supplementary Material and presented as choropleth maps in Figure 2.

Honey bee colony numbers

In order to approximate the commercial honey bee colony numbers for each county across the USA, we use the most recently available 2012 Agricultural Census data (USDA-NASS, 2012). This census data presents the number of honey bee farms (hereafter referred to as 'beekeeping operations') and number of honey bee

colonies for most counties in the USA. For some counties, no information on the number of beekeeping operations and honey bee colonies was available (Online Supplementary Material) due to no active beekeeping operations voluntary contributing to the census. We expect the numbers of commercial colonies in these counties to be small, as the total number of colonies captured in the census is in line with the total number of recognized colonies in the USA.

Some counties had the number of colonies withheld to protect the commercial interest of beekeepers which could be identified (USDA-NASS, 2012). A bootstrapping approach was used to estimate the number of colonies present in these counties. For each state, we generated a distribution of the mean number of colonies per beekeeping operation from counties with known colony counts. In addition, we calculated the total number of unaccounted for colonies in the state by comparing the given state total against the total number of colonies in counties with known counts. We then sampled this state-wide distribution for all beekeeping operations with unknown numbers of colonies and scaled the sampled numbers to match the number of unaccounted for colonies. This was repeated 10,000 times to obtain mean and standard deviation estimates of colony numbers in these counties. Once bootstrapping had been completed for all counties with withheld numbers of colonies, we scaled our total number of colonies in the USA to match the published number of bee colonies as of January 2016 (USDA-NASS, 2017a), which includes all operations of five or more colonies as defined by the USDA. We assume the distribution of these commercial colonies across the USA is represented by the estimates we generate from the 2012 census. Estimates of commercial colony numbers for each US county are found in the Online Supplementary Material.

Assessing risk to honey bees

We examined the risk of honey bee colonies being exposed to Zika prevention measures through choropleth maps [using 'choroplethr' – (Lamstein & Johnson, 2015)] and US wide summaries.

We multiplied the density of colonies in each county by the proportion of the county area predicted to be suitable for Zika in each projection. This approach yielded density-based maps of where and total estimates of how many colonies are likely to be at risk from preventative Zika measures, according to each projection. Additionally, we assembled a county-by-county table detailing estimated number and density of colonies, and proportion of county area suitable for Zika according to each projection (Online Supplementary Material).

Finally, we examined whether there was any correlation between where a given projection predicted high Zika suitability and where high densities of honey bees could be found. We used non-parametric tests for

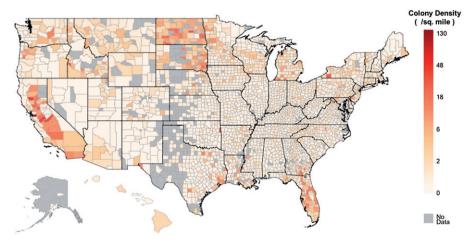


Figure 1. Choropleth map of estimated colony density for beekeeping operations with five or more hives. Calculated using data taken from USDA Agricultural Census (USDA-NASS, 2012), with withheld values estimated by bootstrapping.

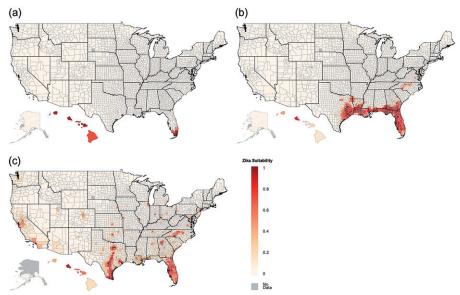


Figure 2. Choropleth maps showing proportion of County area suitable for Zika across the USA. (a) Shows data from Carlson's projection, (b) shows data from Messina's projection, and (c) shows data from Samy's projection.

correlation (Spearman's rank) to establish whether, among counties with a non-zero area of Zika suitability, counties with larger or smaller proportions of their area predicted as Zika suitable were also more likely to have higher or lower densities of honey bee colonies. Non-parametric testing was necessary due to the highly irregular distributions of the data, which rendered any parametric testing unsuitable.

Results

Our estimates of colony density across the USA revealed considerable variation, even between neighboring counties, with cross-continental densities spanning two orders of magnitude (Figure I). Notable regions of extremely high colony density included the Central Valley of California, Florida, and the Dakotas (Figure I), with expansive areas of moderately high colony density

across much of the eastern USA. This pattern is in line with traditional rhetoric on where the major beekeeping regions of the USA are (Caron & Connor, 2013). The conspicuous band of counties with no information reflects counties where no beekeepers replied to the census, and very clearly matches a notable north-sound band of the USA with extremely low population density and high rates of population emigration (US Census Bureau, 2015), suggesting that indeed very few beekeeping operations exist in these counties.

We found some significant correlations of county area suitability for Zika and density of honey bee colonies. Due to the large number of counties with no projected Zika suitability, we limited this rank correlation analysis to include only counties with some area predicted suitable for Zika. For each projection, we assessed whether counties with higher proportional areas of predicted Zika suitability also had higher honey

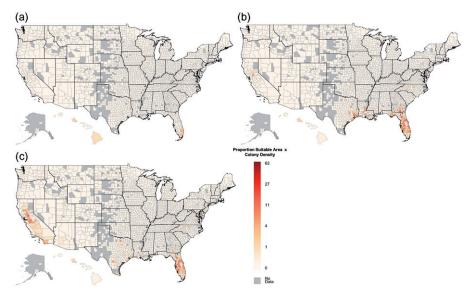


Figure 3. Choropleth maps of estimated colony density for beekeeping operations with five or more colonies across the USA multiplied by proportion of county area suitable for Zika. (a) Uses suitabilities from Carlson's projection, (b) uses suitabilities from Messina's projection, and (c) uses suitabilities from Samy's projection.

Table 1. Percent of colonies in the USA estimated to geographically coincide with Zika preventative or responsive measures under different published projections.

Zika suitability projection	Percent of colonies in USA geographically coinciding with response
Carlson	0.75 ± 0.01
Messina	9.44 ± 0.30
Samy	13.03 ± 0.20

Note: Uncertainties are standard errors associated from the bootstrapping used when gauging honey bee colony densities.

bee colony densities. We found no correlation for the Carlson projection ($\rho=$ -0.316, p=0.216), which may be limited by the low number of counties included. However significant correlations were found for the Messina ($\rho=$ 0.138, p=0.004), Samy ($\rho=$ 0.168, p<0.001) projections.

Our risk maps (Figure 3) quantitatively account for the area of a county suitable for Zika, and colony density, and show large difference between projections as would be expected [see Figure 2 and Carlson et al. (2018)]. Carlson's projection shows the least worrying projection. Overall, we expect less than 1% of colonies will coincide with autochthonous Zika transmission according to Carlson's data set (Table 1). The Messina projection shows a pattern of coincidence with colonies now confined principally to Florida, South Georgia, and the Gulf Coast (Figure 3b). However, the high density of colonies in these regions combined with expansive areas of Zika suitability leads to an expectation that around 9.4% of colonies in the USA may coincide with established Zika, over 10-times the estimate from the Carlson projection (Table 1). For the Samy projection (Figure 3c) the Californian Central Valley appears as a large area of high colony density and extensive Zika suitability, coupled with Florida and parts of the Gulf Coast. Under the Samy projection, 13% of colonies in the USA may be expected to coincide with potential for Zika outbreaks (Table I). The data underpinning the choropleth maps can be examined in full detail in the Online Supplementary Material and should be consulted for information about individual counties.

Discussion

Our analysis shows the potential for regional exposure of honey bee colonies to mosquito-controlling insecticides, as well as scope for mitigating this threat. The risk of exposure could be most pronounced in areas of the USA where agriculture heavily relies on pollination services for good yields and profitable farming, potentially exacerbating the overall risk posed to apiculture. However, the degree of uncertainty between our analyses illustrates a difficult challenge for officials to navigate. The magnitude of differences between projections, and therefore uncertainty in the numbers of colonies which may be exposed to insecticidal spraying, is a problem which must be addressed if responsible Zika control is to be achieved. Additionally, the challenges of interpreting these projection differences is as profound if our analysis is to be extended to native pollinators.

Should spraying be confined only to the specific areas within counties which are considered Zika suitable, differences in colony exposure between published projections span over an order of magnitude (Table I), reflected by

the regions identified as potential hotspots of colony losses in the choropleth maps (Figure 3). For the Messina and Samy projections, proportions of colonies at risk across the USA are of magnitudes relevant to or comparable with summer losses of colonies across the entire USA (Steinhauer et al., 2014). While it is difficult to say what the proportional loss or reduction in productivity of colonies would be following spraying, pesticide kills are cited as the third most common cause of colony loss by American beekeepers [Bee Informed Partnership (Connell et al., 2012), accessed May 2017]. This magnitude of exposure highlights that the potential economic loss to agriculture discussed here is of industry relevance even if only very targeted spraying is carried out.

We therefore stress our capability to reduce impact on colonies to insignificant levels through thorough warning procedures, and through mosquito control approaches which do not pose an acute threat to honey bees. As previously discussed, the principal routes of impact on honey bees from Zika control are from adulticidal approaches. Non-residual 'space sprays' (CDC, 2016b) are only a threat to adult honey bees outside the hive, and are therefore preferably applied at night time (when no bees are outside the hive), eliminating risk of exposure. The greatest threat occurs during day time hot weather when most adult bees are 'bearding' outside the entrance to their hive in order to thermoregulate (Caron & Connor, 2013). Notably, warm weather in much the USA aligns with when mosquito vectors are most abundant. Notifying beekeepers in such conditions (day time spraying in warm weather), and reducing space spray drift, is critical in preventing further losses. In the case of residual sprays, permanence in the landscape inevitably means some exposure to honey bees, as pesticides will be brought into the hives in both flower pollen and nectar, where honey bee larvae are then exposed (Rumkee, Becher, Thorbek, & Osborne, 2017). In these cases, reducing the quantities of pesticide used is paramount. In both of these instances (reducing pesticide volumes and reducing drift during application) ensuring the use of effective modern application technologies is of great benefit (Matthews, 2008; Matthews & Hamey, 2003; Matthews & Thomas, 2000).

It is immediately apparent from our choropleth maps (Figure 2) that there is currently limited consensus on where in the USA we might expect areas of autochthanous Zika transmission (Carlson et al., 2018). This, in part, reflects the different approaches used by these studies, and the challenges posed by a recently emerging infectious disease. For example, Carlson uses exclusively Old World Zika occurrence across the last half century (Carlson et al., 2016) so as to avoid the confound of the outbreaks coinciding with an El Niño year (Paz & Semenza, 2016). This, however, presents a much more limited projection and may miss ecological differences between Old World and New World strains. Messina does include the much more expansive New World projection, but parameterizes much of their ecological

niche model with assumptions taken from knowledge of dengue virus (Messina et al., 2016). Samy differs from both by including socioeconomic factors as a semi-separate driver of autochthonous Zika transmission, additional to environmental suitability (Samy et al., 2016). This understandably leads to a much more expansive Zika range and highlights areas of high population density, which if not interpreted correctly could incite alarm. These critical but nuanced differences between projections are impractical for consideration by most officials, but as our analysis demonstrates, could lead to very different economic impacts as Zika responses mount.

We believe that some of the differences between projections may however be useful in assessing the more challenging question of where mosquito control poses most threat to honey bee colonies. For example, in the case of colonies being lost to spraying in Dorchester County, South Carolina in September 2016 (Clemson University, 2016), our county-level data shows that two of the three projections predict no areas of suitability for Zika in this region, with the third projection (Samy) showing about 20% of the county area is classified as suitable. This case of seemingly low Zika suitability demonstrates how many counties across the USA may be sites of future spraying.

The Samy projection's inclusion of socioeconomic factors - including population density - is a likely driver of the strong statistical correlation between Zika suitability and colony density for this projection (Carlson et al., 2018). Honey bee colonies are unsurprisingly associated with higher population densities (Figure 1), and it is likely that many of the colonies missed by this analysis (operations with <5 colonies) are found in urban or sub-urban areas. Pressure on officials to take action against Zika will be influenced by population densities and likelihood of travel cases - and therefore could be considered partly accounted for in the Samy projection, regardless of the veracity of its autochthonous Zika transmission predictions. Additionally, solicitation of commercial mosquito control agents will pose threat to honey bee colonies only where homes are close enough together for substantial pesticide drift or exposure to foragers - again tightly aligned with population density. We therefore take the opinion that combining our colony density map with the Samy projection may inherently capture additional factors contributing to the likelihood of conflict between Zika abatement and managed honey bees.

The correlative association between apparent Zika suitability and honey bee colony density is cause for concern. While this correlation is not apparent for the limited area of the Carlson projection, for the Messina and Samy projections, counties with more Zika suitable area have higher densities of colonies. The potential population-density driver behind this for the Samy projection is discussed above. However, in the case of the Messina projection, Zika suitability is evaluated on purely environmental (principally climatic) grounds. The significant

correlation in this case supports a hypothesis that, at smaller scales, environmental conditions which attract high colony densities (areas which are good for beekeeping) are also environmental conditions associated with supporting Zika transmission. Speculatively, one potential environmental driver behind this is that neither Zika vectors nor honey bees fare well in very arid environments.

Some specific regions of the USA stand out as areas of concern in this analysis. Two regions are consistently identifiable across all projections: southern Florida and parts of Hawaii (Figure 3). While Zika risk in Hawaii is high (Figure 2), and apiculture prevalent at moderate densities on the islands (Figure 1), insecticidal responses for mosquito control are more likely to be assessed based on threats to native fauna. This is especially likely given the recent listing of several endemic Hawaiian bees on the USA endangered species listing (FWS, 2016). Our presentation of projected environmental suitability estimates for Zika virus (Supporting Information 1) may be relevant when considering the threat to endemic insects.

In the case of Florida, the South-East, and the Gulf Coast, Carlson's projection limits Zika to southernmost Florida where there are only moderate estimated colony densities (Figure 3a); but both Messina and Samy predict greater environmental suitability in northern Florida where colony densities are higher (Figure 3b-d). Similarly, both projections predict an appreciable degree of Zika suitability coinciding with moderate to high colony densities across parts of the gulf and south-east. The need for immediate review of Aedes control processes and protection of apiculture likely varies across this region. Florida, for example, already exercises considerable mosquito control programs (Duprey et al., 2008), which are already implicated in the successful control of Zika (Dinh, Chowell, Mizumoto, & Nishiura, 2016), and therefore may be better equipped with processes and policies to protect apiculture, agriculture, and the environment. Additionally, beekeepers in this region may already have measures in place to mitigate losses due to aerial drift from commercial mosquito control agents. However, other states or counties across this region, and beekeepers operating in them, may not have robust processes in place. States such as Louisiana legally require registration of every apiary in the state; however, this information is not publicly available, in order to protect commercial interests and to prevent opportunistic theft or vandalism of apiaries. Requiring commercial or county-mandated pesticide application to account for nearby apiaries in mitigating unintended pesticide damage would be very beneficial and could be a sensible model for other states in the region to adopt. The prevalence of commercial mosquito control in this region makes due process particularly important as public concern over Zika grows: for example, in Georgia, there are 994 active mosquito control licenses as of May 2017.

The Californian Central Valley is another important region our analysis highlights. There is stark

disagreement between suitability projections for Zika across California (Figure 2). Considering the large area, high agricultural value (Schoups et al., 2005), high colony density (Figure 1), and large population (US Census Bureau, 2015) present across California's Central Valley, these mixed predictions are liable to pose a considerable challenge. However, California law already specifies the requirement of licensed mosquito control agents to notify beekeepers, with exceptions only granted for commercial control agents who are part of the Department of Health Services 'Cooperative Agreement'. This model may be a useful example for other states when navigating conflict between mosquito control and the apicultural industry.

There is additional concern that Florida and the Central Valley of California are areas of identifiable risk. Our estimation of colony densities in these areas is likely conservative due to the number of transient colonies which pass into these areas as part of migratory beekeeping operations. Both Florida and the Californian Central Valley draw large numbers of migratory colonies (Hodges, Mulkey, Philippakos, & Sanford, 2001; Simone-Finstrom et al., 2016), either for overwintering, or due to the high demand of pollination services required for the agricultural industries in these areas (Potts et al., 2016). Of particular note are the almond orchards in the Central Californian Valley (Brittain, Williams, Kremen, & Klein, 2013) and the citrus industry in Florida (Albrigo & Russ, 2002; Russ, 1999). The potential risk of new or heightened mosquito control measures in these regions may pose a threat to migratory colonies; however, the phenology of major pollination demand periods may not necessarily overlap with periods requiring abundant mosquito control.

This study presents what we believe to be the first honey bee colony density map of the USA resolved to county level, and the limitations of this require some appraisal. The patterns presented in Figure I, as described in the results, are in good agreement with population densities and areas traditionally understood to be important for US apiculture. One caveat of our approach is the difficulty in accounting for migratory beekeeping, which underpins much of US apiculture (Brosi, Delaplane, Boots, & de Roode, 2017; Rucker, Thurman, & Burgett, 2012). To our knowledge, no suitable quantitative data on seasonal variation in honey bee colony densities due to migratory practices is available, and so could not be included in the analysis. However, as discussed above, regions known to be destinations of large numbers of migratory operations can still be assessed. Additionally, beekeeping operations (regardless of their location) can refer to the data presented here to make their own assessments of how likely they are to encounter Zika preventative measures during their migratory movements.

Our approach is based on the 2012 Agricultural Census data, which is part of a voluntary program; it is

therefore difficult to establish what the uptake among beekeepers is. For some states, beekeeper registers are maintained, and can therefore be tested against. In Louisiana, as of 2016 there were 679 registered beekeepers in the state - more than twice the 323 beekeeping operations accounted for by our analysis. While the census may therefore miss many beekeepers, the scale of these missed operations appears small. The agricultural census, and most USDA records, exclude operations with fewer than five colonies. Across the country the census accounts for 3,282,570 colonies in the USA in 2012. The most recently available total for the USA is annual peak honey bee colony number for July 2015 of 3,132,880 colonies (USDA-NASS, 2017a). Unfortunately, equivalent data do not exist for 2012. Instead, records for specifically honey producing colonies do exist. Honey producing colonies in 2015 peaked at 2,660,000 colonies (USDA-NASS, 2017b), 85% of the previously stated total. The equivalent figure in 2012 is 2,624,000 (USDA-NASS, 2013); if we assume that 85% of US colonies are listed as honey producing, as previously derived, we can estimate that in 2012 colony number peaked at approximately 3,080,000 colonies. This is fewer colonies than accounted for in the census, suggesting that while many beekeepers may not take part in the census, it accounts for a large majority of colonies in the USA captures more colonies than other quoted sources, and that uncounted beekeepers represent small operations. We therefore consider the density map of honey bee colonies across the USA to be defensible and accurate in its portrayal of US apiculture.

In addition to identifying broad regions where conflict between Zika control measures and apiculture is likely, we present county-level data for practitioners to consult (Online Supplementary Material). We hope these data, showing estimated colony numbers and Zika suitability, will allow officials to more easily assess the case for protecting apiculture. Additionally, beekeepers who are in counties with few colonies may not fall in an identified 'high risk' region, but still require knowledge of likelihood of insecticidal spraying. We therefore present the county-level data for all beekeepers to assess the case for their own county and hope that it will help beekeepers in preventing losses. It is apparent that beekeepers are already engaging with mosquito control following the Zika virus pandemic and providing this information should assist in these efforts.

In summary, we conclude that the greatest risk to apiculture from Zika abatement mosquito controls is likely to be in the South-East and the Gulf Coast. Notably, we provide evidence that environmental conditions thought to be conducive to Zika virus are also associated with higher densities of honey bee colonies. California, Florida, and Hawaii appear as other notable regions but appear to have schemes already in place to mitigate impacts from necessary pesticidal control. We believe there is potential for effective preventative action in the South-East and

Gulf, noting Louisiana as an example where registration of apiaries with the state may allow for easy preventative measures to be introduced. We strongly encourage officials and beekeepers to use the data available and address protecting honey bee colonies. Cases can be made for wider mandatory registering of beekeeping activities if commercial mosquito control agents must consult this information via official channels. Additionally, these regions of the USA should be targeted for increased monitoring of colony losses due to pesticides and should be considered for initiatives to encourage beekeepers to report such losses to the authorities.

Author contributions

LJB and MB initiated the idea for the study. LJB and CJC designed methodology and gathered data. LJB performed analysis and drafted the paper with significant contributions of specific sections from all authors. All authors critically revised the manuscript and gave approval of the final version for submission.

Data accessibility

All novel data presented in this analysis is made available in the Supporting Information. Zika suitability projections used are available in association with their original publication.

Supplementary material

Supplemental data for this article can be accessed at: https://doi.org/10.1080/00218839.2018.1494914

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No potential conflict of interest was reported by the authors.

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