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Museum specimen data reveal emergence of a plant disease may be linked to increases in the insect vector population

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Abstract. The emergence rate of new plant diseases is increasing due to novel introductions, climate change, and changes in vector populations, posing risks to agricultural sustainability. Assessing and managing future disease risks depends on understanding the causes of contemporary and historical emergence events. Since the mid-1990s, potato growers in the western United States, Mexico, and Central America have experienced severe yield loss from Zebra Chip disease and have responded by increasing insecticide use to suppress populations of the insect vector, the potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae). Despite the severe nature of Zebra Chip outbreaks, the causes of emergence remain unknown. We tested the hypotheses that (1) *B. cockerelli* occupancy has increased over the last century in California and (2) such increases are related to climate change, specifically warmer winters. We compiled a data set of 87,000 museum specimen occurrence records across the order Hemiptera collected between 1900 and 2014. We then analyzed changes in *B. cockerelli* distribution using a hierarchical occupancy model using changes in background species lists to correct for collecting effort. We found evidence that *B. cockerelli* occupancy has increased over the last century. However, these changes appear to be unrelated to climate changes, at least at the scale of our analysis. To the extent that species occupancy is related to abundance, our analysis provides the first quantitative support for the hypothesis that *B. cockerelli* population abundance has increased, but further work is needed to link *B. cockerelli* population dynamics to Zebra Chip epidemics. Finally, we demonstrate how this historical macro-ecological approach provides a general framework for comparative risk assessment of future pest and insect vector outbreaks.

Key words: Bayesian analysis; Candidatus *Liberibacter solanacearum*; list length analysis; NIMBLE; occupancy model; opportunistic ecological data.

Introduction

The emergence rate of novel infectious diseases of humans, wildlife, and plants has increased dramatically in recent decades (Anderson et al. 2004, Jones et al. 2008). For plant diseases, the majority of recent outbreaks have been caused by the introduction of pathogens into new areas, but climate change and agricultural change have also been implicated in recent emergence events (Anderson et al. 2004). For vector-borne plant pathogens, these same processes could also cause disease outbreaks indirectly through changes in vector populations: evolutionary, numerical, or both (Anderson et al. 2004, Canto et al. 2009, Fereres 2015). Improved understanding of the causes of disease outbreaks is critical for

managing current epidemics and for assessing risks of future ones (Garrett et al. 2011).

Climate change has the potential to exacerbate agricultural disease risk in the near future and has already caused contemporary outbreaks (Anderson et al. 2004, Garrett et al. 2011). Much of the work on agricultural pest and disease risks from climate change has relied on a combination of small-scale experiments and modeling to extrapolate experimental findings to larger scales (Juroszek and von Tiedemann 2013). However, the multiple dimensions of climate change and the multitude of biotic interactions have led to concerns about the relevance of small-scale experiments (Van Der Putten et al. 2010, Juroszek and von Tiedemann 2013). At the same time, historical macro-ecological analyses using long-term data sets can contribute critical insight into the possible role that climate change plays in contemporary outbreaks amid the complexity of climatic variation and interacting species (Jeger and Pautasso 2008).

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Beginning in the mid-1990s, potato growers in western United States, Mexico, and Central America saw widespread losses from the emergence of Zebra Chip disease, caused by infections of the bacterial pathogen *Candidatus* Liberibacter solanacearum (Lso; = *C.* L. psyllaurous) (Munyaneza et al. 2007, Hansen et al. 2008). Zebra Chip disease symptoms include plant stunting, leaf scorching, and tuber necrosis, progressing eventually to plant decline and death (Sengoda et al. 2009). Lso also causes severe losses in tomato and pepper production (Liu and Trumble 2006, Brown et al. 2010). Since its emergence, the management of Lso has primarily involved suppression of its vector, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) or potato psyllid, through insecticide use (Butler and Trumble 2012, Guenthner et al. 2012).

Despite increasing harm to agricultural production and the environment from ongoing Lso outbreaks and increasing insecticide applications (Rosson et al. 2006, Guenthner et al. 2012), the causes of Lso emergence remain largely unknown. While *B. cockerelli* is native to the western United States and Mexico, Zebra Chip disease was first described in 1994 and Lso in 2008 (Munyaneza et al. 2007, Hansen et al. 2008). And while other hypotheses warrant further investigation (see *Discussion*), one dominant hypothesis has emerged: that greater overwintering survival of northern *B. cockerelli* populations is causing Zebra Chip outbreaks.

Historically, the range of *B. cockerelli* was thought to be largely confined by its relatively narrow thermal tolerance and the availability of host plants. Pletsch (1947) and Wallis (1955) hypothesized that populations were limited in northern latitudes by cold winter temperatures, a lack of host plants during winter, or both; these regions would be subsequently colonized by populations migrating from the south in springtime. Beginning in 2011, populations of *B. cockerelli* were found overwintering in Oregon, Washington, and Idaho (Horton et al. 2015), well beyond the species' hypothesized historic northern limits (Wallis 1955), although a lack of historical monitoring leaves it unclear whether this represents a recent range expansion. Greater overwintering survival of northern populations would likely cause much greater densities in potato fields earlier in potato plant development, when plants are most susceptible to Lso infection (Gao et al. 2009). More generally, climate change is expected to increase overwintering survival of insect herbivores across temperate regions (Bale et al. 2002, Klapwijk et al. 2012).

Ecological theory predicts that increases in vector density can drive outbreaks of endemic pathogens. While the relationship between vector density and host infection prevalence is complex and rarely linear, it is generally a positive relationship (Madden et al. 2000). Vector-borne pathogens that are persistently and vertically transmitted, which includes Lso (Hansen et al. 2008, Sengoda et al. 2014), should exhibit distinct epidemic thresholds across a range of vector population densities (Jeger et al. 1998), with the pathogen maintaining low prevalence in the host

population until vector populations reach very high densities (Madden et al. 2000). Early work has failed to find a relationship between adult *B. cockerelli* density and Lso infection prevalence, but has found positive relationships between late-stage nymph density, adult infection prevalence, and Zebra Chip disease prevalence (Goolsby et al. 2012, Workneh et al. 2013). Furthermore, contemporary Lso infection prevalence in *B. cockerelli* populations appears to be very low, between 0% and 8% across the midwestern and northwestern United States (Goolsby et al. 2012, Swisher et al. 2013). At such low infection rates, very large vector populations may be required to cause a disease epidemic.

While Zebra Chip disease was first described in the 1990s, there is some evidence that Lso has coexisted with *B. cockerelli* for much longer than Zebra Chip disease has been recognized (see *Discussion*). Historically, Zebra Chip may have been confused with pathological effects of *B. cockerelli* saliva, known as Psyllid Yellows disease, first described in the 1920s (Richards 1928). Given that visual foliar symptoms of Psyllid Yellows and Zebra Chip disease are quite similar (Munyaneza et al. 2007, Sengoda et al. 2009) and that Lso is unculturable, earlier researchers may have observed a combination of pathological effects from *B. cockerelli* saliva and Lso infection. As a result, it is possible that Lso is endemic to North America, has only occasionally erupted in outbreaks, such as the Psyllid Yellows outbreaks of the 1920s and 1930s and the contemporary Zebra Chip outbreaks, but remained largely undetected otherwise.

In the present paper, we tested whether numerical changes in *B. cockerelli* populations could explain the emergence of Zebra Chip disease. Specifically, we hypothesize that (1) *B. cockerelli* populations have increased over the last century in California, USA and (2) such increases are related to climate change, specifically higher winter temperatures. We tested these hypotheses by fitting museum specimen occurrence data and historical climate projections to a hierarchical occupancy model. Interest in historical ecological data, such as that from natural history collections, has increased in recent years due to their value in assessing impacts of climate change on disease dynamics and other ecological processes (Tingley and Beissinger 2009). For example, previous studies have used museum specimens to chart invasion of the Lyme's disease pathogen, *Borrelia burgdorferi,* in tick vector specimens (Persing et al. 1990), changes in pathogenic fungal populations related to air pollution in wheat specimens (Bearchell et al. 2005), and historical prevalence of chytrid fungus in amphibian populations (Ouellet et al. 2005). At the same time, museum specimens were often opportunistically collected by a diverse set of professional and citizen naturalists with different levels of expertise and effort (Isaac and Pocock 2015). They also represent presence-only occurrence data, with little or no information about where a species was searched for but not found. As a result, museum specimen occurrence data are rife with

biases, making rigorous ecological inference difficult (Newbold 2010).

Hierarchical statistical models and Bayesian analytical methods have facilitated the analysis of opportunistically collected ecological data by explicitly modeling the observation process separate from the ecological process (Isaac et al. 2014). For example, occupancy models combine an ecological sub-model, relating the presence and absence, or occupancy, of a focal species to a set of covariates, with a detection sub-model that relates detection to a distinct set of covariates. Following previous work, we generated non-detection data (i.e., absence data) for *B. cockerelli* and corrected for variation in collecting effort using list length analysis (Phillips et al. 2009, Szabo et al. 2010). List length analysis involves compiling lists of related species collected in the same time and place and using the length of these lists as a proxy for collecting effort. Some lists will contain the focal species while many others will not; these later lists constitute non-detection data. Because list length acts as a proxy for overall collecting effort (Roberts et al. 2007), incorporating list length as a covariate into a detection sub-model provides estimates of detection probability for the focal species, i.e., longer lists without the focal species are more likely than shorter lists to represent true absences. Similar analyses have been used to detect trends in bird populations (Link et al. 2006, Szabo et al. 2010, Barnes et al. 2015), butterfly and dragonfly populations (Van Strien et al. 2010, Breed et al. 2012), and changes in owl prey populations (Van Strien et al. 2015).

Here we show that the analysis of museum specimen occurrence data using Bayesian hierarchical models can provide insights into the causes of recent outbreaks of agricultural pests and disease vectors. Additionally, in the Discussion we outline how such a historical macroecological approach to the analysis of disease vector and pest outbreaks could facilitate development of risk assessment frameworks for future outbreaks.

Materials and Methods

Compiling species occurrence records

We first collected, digitized, and georeferenced all pinned museum specimens of *B. cockerelli* from six major California natural history museums: Bohart Museum of Entomology, University of California Davis; California Academy of Science, San Francisco; California State Collection of Arthropods (CSCA), Plant Pest Diagnostics Center, California Department of Agriculture; Essig Museum of Entomology, UC Berkeley; Los Angeles County Museum of Natural History; and UC Riverside Entomology Research Museum. For each collection, we identified *B. cockerelli* specimens that had not yet been determined to the species level, housed in the "Undetermined Psyllidae" or "Undetermined Triozidae" sections of the collections. We identified undetermined specimens using the morphological description for

Paratrioza (=*Bactericera*) *cockerelli* in Tuthill (1945). We also verified identification of a random subset of specimens previously identified as *B. cockerelli*; all were confirmed correctly identified. We digitized all *B. cockerelli* specimens, and georeferenced them using the point-radius method of (Wieczorek et al. 2004) and the GEOLocate web application.[7] In addition to pinned specimens, we also included slide-mounted nymph specimens from the Bohart Museum and records of ethanol-preserved specimens from the Essig Museum. All georeferenced specimens, except for ethanol-preserved specimens, were uploaded to the Essig Museum online database.[8]

Our data set of *B. cockerelli* museum specimens represented presence-only data. To generate non-detection data, we used the target-group background approach of Phillips et al. (2009). When using presence-only data, species distribution modeling requires the selection of non-detection data, also known as background or quadrature points in the spatial statistical literature (Renner et al. 2015). Often non-detection points are selected randomly or uniformly over the geographical or environmental space of interest. However, Phillips et al. (2009) selected non-detection points by using the presence of a larger set of related taxa (i.e., target group), effectively reducing bias in the species distribution estimates compared to uniform or random non-detection selection methods.

We chose as our target group all species in the order Hemiptera, excluding families that were predominantly aquatic or carnivorous. The excluded families were Anthocoridae, Belostomatidae, Cimicidae, Corixidae, Gelastocoridae, Geocoridae, Gerridae, Hebridae, Hydrometridae, Leptopodidae, Macroveliidae, Mesoveliidae, Nabidae, Naucoridae, Nepidae, Notonectidae, Ochteridae, Phymatidae, Pieidae, Polyctenidae, Reduviidae, Saldidae, and Veliidae. The remaining families of Hemiptera are predominately (though not exclusively) composed of terrestrial piercing-sucking herbivores and are likely to be collected by entomologists in similar manners.

To generate our target group data set, we compiled digitized and georeferenced California records of our selected hemipteran families from three sources: the Global Biodiversity Information Facility (GBIF; which includes all records from the Essig Museum online database), the American Museum of Natural History (AMNH), and the CSCA database. An initial exploration of these databases returned only 25 records of *B. cockerelli*, far too few for analysis and thus requiring the digitization and georeferencing of additional specimens described above. In the CSCA database, we included only records that were opportunistically collected, excluding those that reported trap monitoring for specific pest species. The data from the CSCA were biased toward agricultural areas; however, this partially balanced biases against agricultural areas in the GBIF

[7] http://www.museum.tulane.edu/geolocate/default.html
[8] https://essigdb.berkeley.edu/

and AMNH data sets. Occurrence records were included in our data set if they were collected within California between 1900 and 2014, included the full species name, and were georeferenced.

From our compiled records, we generated lists of species collected across the same time and area of our *B. cockerelli* records. To do so, we divided California into 15 × 15 km grid cells and combined all species records collected within the same spatial cell, month, and year. This spatial resolution was similar to that previously used by Hill et al. (1999) to model changes in distribution of butterfly distribution under climate change. We included only lists with three or more species, following methods of Van Strien et al. (2013), and lists in which at least one collector had also collected a *B. cockerelli* specimen in our data set. By filtering lists to a set of common collectors, we reduced the influence of collectors focused on only a single family or other taxon, a common concern in the analysis of opportunistically collected data (Isaac and Pocock 2015).

Climate data

Our aim was to model the temporal trends in *B. cockerelli* occupancy and to test if these trends could be explained by local-scale climate change. As such, we compiled estimates of historical climate from the California Basin Characterization Model (BCM), which provides estimates of a range of temperature- and precipitation-derived climatic indices at 270 × 270 m grid resolution for much of California on a monthly basis from 1895 to 2014 (Flint et al. 2013, Flint and Flint 2014). For each species occurrence record in a list, we extracted estimates of actual evapotranspiration (AET) in the month of collection, the water-year annual minimum temperature (T_{min}, °C), and the water-year annual maximum temperature (T_{max}, °C). For annual minimum and maximum temperatures, we extracted the minimum temperature occurring in the most recent winter (December–February) and most recent summer (June–September), respectively. Because our species lists were compiled at a larger spatial cell size than the BCM cells, we extracted the climate values for each occurrence record within a list and then averaged these estimates to obtain a list-level estimate of climate. The standard deviations of these averages across lists were small for each of the three climate variables (AET mean SD = 2.08; T_{min} mean SD = 0.17; T_{max} mean SD = 0.26) relative to their standard deviations across all specimen records in the data set (AET = 35.71, T_{min} = 4.01, T_{max} = 5.86), indicating that our averaging of climate variables at the list level did not neglect significant within-list climatic variation.

AET is an estimate of the water available for plant growth; it is a function of precipitation and temperature, and is more biologically relevant than raw precipitation estimates (Rapacciuolo et al. 2014). AET has been used previously to successfully model changes in herbivorous insect distributions from climate change (Hill et al.

1999). Additionally, historical descriptions of the distribution of *B. cockerelli* indicate that the species primarily occurs in arid and semiarid climates of the southwestern and Rocky Mountain regions of the United States (Wallis 1955), which would be captured by estimates of AET. We also considered incorporating estimates of climate water deficit (CWD); however, AET and CWD were highly negatively correlated within our data set and we thus opted for keeping the former only (Appendix S1: Fig. S1).

We included annual T_{min} because the prevailing hypothesis explaining the emergence of Zebra Chip Disease is that *B. cockerelli* populations at the northern limits of the species range have increased due to greater overwintering survival (Wallis 1955, Horton et al. 2015). If true, then *B. cockerelli* occupancy should be positively associated with annual T_{min}. Finally, we included annual T_{max} because of historical descriptions of *B. cockerelli* phenology suggesting that southern populations are extirpated due to high summer temperatures (Romney 1939).

Statistical analyses

We modeled *B. cockerelli* occupancy using a hierarchical occupancy model, also known as a binomial–binomial mixture model, as described in Royle and Kéry (2007). This model explicitly models the observation or detection process separately from the ecological or occupancy processes that give rise to species occupancy patterns and corrects for zero-inflation in our data set (Martin et al. 2005). Importantly, however, our data did not include repeated visits to a site. Rather, by using non-overlapping sets of covariates for the two submodels, the occupancy and detection latent states were identifiable (Sólymos et al. 2012). For the occupancy submodel, we included the year collected, AET, T_{min}, T_{max}, and a quadratic form for month collected. For the detection sub-model, we included list length and the interaction between list length and year collected. We included the interaction between list length and year to correct for changes in the relationship between list length and occupancy over time due to, e.g., changing collecting and preserving technologies and collector expertise. List length was natural-log-transformed (Szabo et al. 2010) and all continuous covariates were standardized around the mean and divided by the standard deviation. To incorporate spatial autocorrelation, we included the 15 × 15 km spatial grid cells used to construct species lists as a random effect in the occupancy sub-model. In other words, lists that originated from the same location (i.e., spatial grid cell) were assigned the same intercept. According to the simulations of Isaac et al. (2014), occupancy models with list length and a spatial random effect can be slightly conservative, but are overall more robust to bias in opportunistic occurrence data than other models.

We fit the occupancy model using the Markov chain Monte Carlo (MCMC) engine provided with the NIMBLE package (version 0.6-3) for R 3.3.2 (NIMBLE Development Team 2015, De Valpine et al. 2016, R Core

Team 2016). MCMC speed and convergence were expedited by making use of the flexibility of NIMBLE algorithms. Latent states representing true (unknown) site occupancy were analytically removed from the model formulation using a custom-specified distribution, as described in Turek et al. (2016). Block sampling was used to jointly sample the coefficients of each linear predictor term within each sub-model, since these will generally exhibit strong posterior correlation (Roberts and Sahu 1997). In addition, the standard deviation of site random effects was sampled on a logarithmic scale using the generalized Gibbs sampling framework described in Liu and Sabatti (2000). We used uninformative priors and three MCMC chains each with 150,000 iterations and a burn-in period of 50,000. Convergence was verified by calculating Gelman-Rubin diagnostic and effective sample size (Gelman and Rubin 1992, Brooks and Gelman 1998). R code for fitting models is available in DataS1.zip; additional code for compiling and filtering data and analyzing model output can be found at github.com (https://doi.org/10.5281/zenodo.555994).

Results

Our final data set of specimen records included 87,035 records of 2,840 species from 73 families; it also included 613 records of *B. cockerelli*. Specimens of all selected Hemiptera were collected throughout California, with the greatest number collected in the 1930s, 1960s, and 1970s (Fig. 1). Specimens of *B. cockerelli* were concentrated in southern California and arid interior regions of the state; the majority of specimens were collected from 1950 to 1970 with the first and last *B. cockerelli* specimen collected in 1908 and 2011, respectively (Fig. 1). From this specimen data set, we assembled 900 species lists, which ranged in length from 3 to 40 species, 36 of which contained *B. cockerelli* (Appendix S1: Fig. S2).

The MCMC chains successfully converged. Estimates of the Gelman-Rubin diagnostic for all parameters were ≤1.1 and effective sample sizes of all parameters were >1,000 (Table 1).

For the detection sub-model, list length was marginally significant and positively related to probability of detection, as was the list length × year interaction (Table 1, Fig. 2). The marginally significant interaction term was likely due to a small but significant decline in list length over time (Appendix S1: Fig. S3).

For the occupancy sub-model, the year main effect was significant and positive (Table 1). However, none of the climate variables were significant. The model predicts an increase in *B. cockerelli* probability of occupancy in the late autumn/early winter in the 1950s and increases in *B. cockerelli* throughout all seasons beginning in the 1990s, with particularly high occupancy rates in summers (Fig. 2).

We generated maps of the estimated occupancy probability over three different time periods: 1920–1945, 1950–1975, and 1990–2015 (Fig. 3), covering the
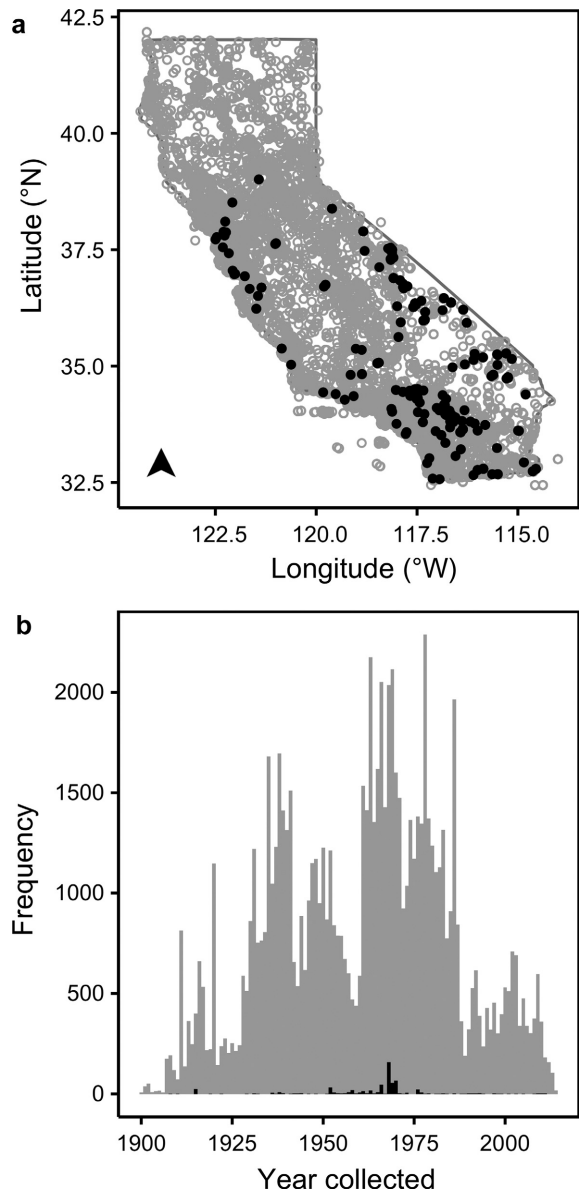

Fig. 1. (a) Spatial and (b) temporal distribution of all museum records (gray points and bars) and of *Bactericera cockerelli* museum records (black points and bars).

historical Psyllid Yellows outbreak, a non-outbreak period, and the contemporary outbreak period, respectively. Although recent data are sparse, the model predicts an overall increase in occupancy probability in southern California in more recent years, with greater variation in occupancy in early time periods.

Discussion

Since emergence in the early 1990s, Zebra Chip disease has devastated potato production in epidemic areas of the United States, Mexico, and Central America (Secor and Rivera-Varas 2004, Rosson et al. 2006, Horton et al.

TABLE 1. Estimates of the Gelman-Rubin diagnostic, $\hat{r}$ (with 97.5% credible intervals, CI), effective sample size (ESS), and posterior mean (with 95% CI) for linear coefficients for *Bactericera cockerelli* occupancy model.

Model term	$\hat{r}$ (97.5% CI)	ESS	Mean [2.5% CI, 97.5% CI]
Year	1 (1)	2,268.39	50.4 [16.1, 95.4] ‡
Month	1 (1)	2,976.61	1.88 [−48.7, 53.9]
Month^2	1 (1)	3,536.05	9.12 [−40.9, 57.9]
AET	1 (1)	3,068.94	−22.7 [−73, 31.3]
T_{min}	1 (1)	2,470.83	−13.6 [−62.7, 35.2]
T_{max}	1 (1)	2,579.5	−11.6 [−62.9, 41.5]
Detection sub-model intercept	1 (1)	7,144.72	−2.41 [−2.86, −1.97] ‡
List length	1 (1)	24,529.71	0.283 [−0.0478, 0.595] †
List length × year	1 (1)	24,186.37	0.332 [−0.0172, 0.701] †
μ_α	1 (1)	5,088.08	−11 [−65.6, 48.1]
σ_α	1 (1.01)	1,219.42	271 [57.4, 868]

Notes: AET, actual evapotranspiration; T_{min}, water-year annual minimum temperature; T_{max}, water-year annual maximum temperature; μ_α, mean of the spatial cell random effect; σ_α, variance of the spatial cell random effect.
 † Significant at 90% CI; ‡ significant at 95% CI.

2015). For example, whereas Texas potato growers traditionally used few or no insecticides, growers currently average over seven applications annually as a direct result of Zebra Chip emergence (Goolsby et al. 2012, Guenthner et al. 2012). Yet the causes of these outbreaks remain unknown. Using museum specimen occurrence data and a Bayesian occupancy model, we showed that occupancy probability of the vector, *B. cockerelli*, has increased in California over the last century.

Our analysis showed increasing occupancy probability over the last century through a significant and positive year main effect. However, sparse data weaken further inference. Despite our initial large data set (>87,000 hemipteran records and >600 *B. cockerelli* records), our final data set consisted of 900 total species lists with only 36 containing *B. cockerelli*. The sharp reduction in data when constructing the lists was due to a large number of single species lists and to a large number of duplicate records, which in each case reduces to a single detection event.

The reduced spatial coverage and total number of lists in more recent decades, particularly in northern California, prevented us from testing for a potential northward range expansion of *B. cockerelli* (Fig. 3). However, we do not expect this decline in the number of records to have influenced our main result of an overall increase in occupancy probability for *B. cockerelli* over time. Despite there being fewer lists in recent decades, the proportion of those lists containing *B. cockerelli*, the species' reporting rate (Szabo et al. 2010), increased markedly (Appendix S1: Fig. S4). This trend persists after correcting for overall collecting effort and changes in collecting effort over time, which we accounted for by including a list length main effect and a list-length × year interaction effect in the detection sub-model.

In epidemiology of vector-borne pathogens, patterns of vector occupancy are less relevant than patterns of vector population dynamics for determining pathogen spread. Nonetheless, occupancy probability over large spatial scales is positively related to abundance (Gaston et al.

2000, Oliver et al. 2012, Gutiérrez et al. 2013) except when species exhibit very low colonization ability (Freckleton et al. 2005). Evidence suggests that *B. cockerelli* exhibits high colonization ability (Nelson et al. 2014). Thus, a positive occupancy–abundance relationship should hold and the increases in occupancy probability that we detected should generally be associated with increases in vector abundance. In future analyses, it may be possible to treat duplicate species records as count data and directly model abundance within a list length analysis framework. However, theory relating species list lengths to count data has not been developed and would likely require additional statistical assumptions.

We had hypothesized that occupancy should be positively related to T_{min} based on the previous literature (Wallis 1955). While we found no evidence for an association between T_{min} and *B. cockerelli* occupancy, climate change could influence *B. cockerelli* populations and Lso emergence through processes beyond our present analysis. Changes in degree-days are often more relevant for insect development rates than annual minimum or maximum temperatures (Bale et al. 2002). Recently, Tran et al. (2012) showed that nymphs of *B. cockerelli* ceased development and ~90% of individuals died at a constant 8°C under laboratory conditions. In our data set, T_{min} reached below 8°C in 98% of all lists and 97% of lists containing *B. cockerelli*. This apparent discrepancy may be because the duration of cold temperatures or the temperatures experienced over the entire developmental period, as captured in degree-days, are more important than the minimum temperature experienced at a single point in time. We hope to incorporate degree-days into future analyses.

Climate change could also influence *B. cockerelli* populations indirectly. We hypothesized that any relationship between AET and *B. cockerelli* occupancy would be mediated through changes in host plant populations. However, we found no evidence of a relationship between AET and *B. cockerelli* occupancy. Explicitly
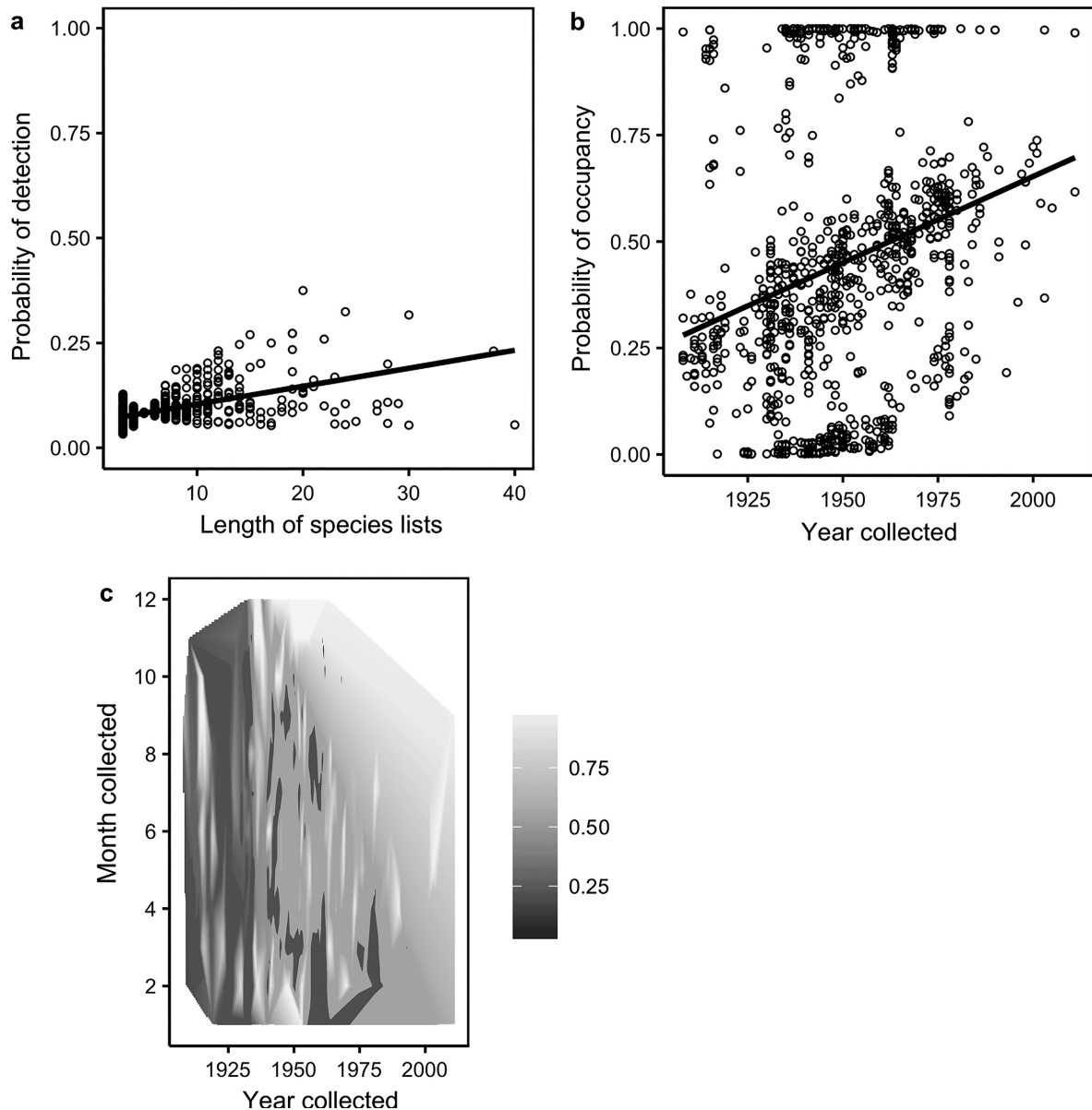
Fig. 2.   Occupancy model results. (a) Relationships between occupancy model-predicted probability of detection and list length, (b) between model-predicted probability of *B. cockerelli* occupancy and year collected, and (c) the relationships of occupancy probability, year collected, and month collected. Trend lines on scatterplots are linear model fits to model-predicted probabilities. For the contour plot (c), grayscale values indicate probability of occupancy.

modeling changes in host plant occupancy in relation to climatic variation and then relating host plant occupancy to *B. cockerelli* occupancy, perhaps through a joint distribution model, would be a more robust test. Finally, beyond any effects on *B. cockerelli*, climate change could contribute to Lso outbreaks by directly influencing Lso populations or the interactions between host plant, vector, and pathogen (Garrett et al. 2006).

Separate from climate change, *B. cockerelli* population abundances may have increased through other mechanisms. Horton et al. (2015) have hypothesized that the outbreaks in the northwestern United States are

caused by invasion of a nonnative host plant, *Solanum dulcamara* (Solanaceae), and concomitant adaptation by *B. cockerelli* populations. More broadly, the role of wild host plants in *B. cockerelli* population dynamics and distribution remains an important area for future research. Additionally, population or genetic differences in *B. cockerelli* reproduction, development, and insecticide resistance have been described by previous authors, any of which could contribute to Zebra Chip emergence (Liu and Trumble 2007, Mustafa et al. 2015a, b).

In a review of plant disease emergence events by Anderson et al. (2004), pathogen introduction was the
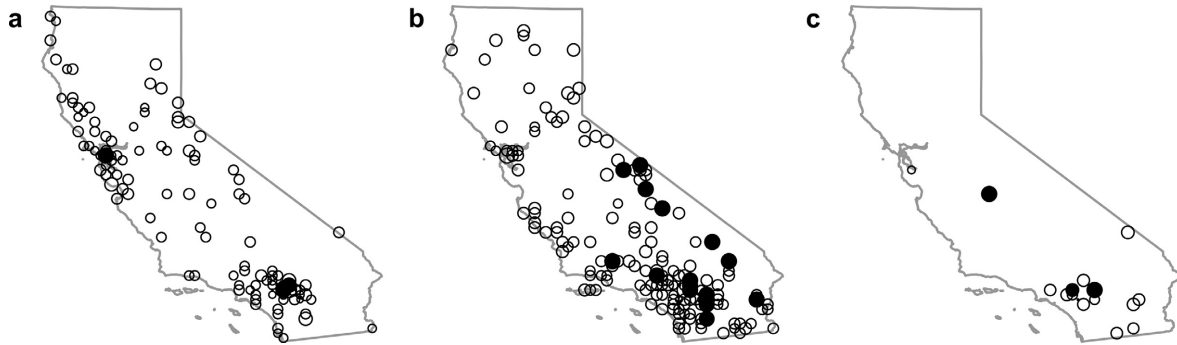
Fig. 3.   Maps of estimated *B. cockerelli* occupancy across California, USA for three selected time periods, (a) 1920–1945, (b) 1950–1975, and (c) 1990–2015. Solid circles indicate species lists containing *B. cockerelli* (i.e., detection events); open circles indicate non-detection events. The size of the circle indicates the estimated probability of occupancy, with larger circles representing greater probabilities. Occupancy probabilities were averaged over years for each site. Map coordinates are the same as in Fig. 1a.

most common cause of emergence. For Zebra Chip disease, introduction of Lso into North America remains a possible but unlikely explanation. Lso has recently been detected in Europe and is associated with the triozid species *Bactericera trigonica* and *Trioza apicalis* (Munyaneza et al. 2010, Teresani et al. 2014). However, the European isolates appear to be genetically distinct from the North American isolates and infect primarily non-solanaceous host plants (Nelson et al. 2011, Lin and Civerolo 2014). We also constructed a cladogram of available 16S rDNA sequences that supports previous assertions that an introduction of Lso from Europe to North America has not occurred recently (Appendix S2). Future genetic analyses of historical and contemporary samples would provide critical insight into the origins of Lso. Importantly, none of the above possible causes are mutually exclusive. Rather, multiple factors may be contributing to the emergence of Lso-associated diseases and may differ in relative importance in different epidemic areas.

Understanding the causes of plant disease outbreaks is critical for integrated management of pathogens and vectors (Garrett et al. 2011). Our analysis has been the first to show an increase in *B. cockerelli* occupancy over

relatively large spatial and temporal scales. However, more work is needed to link *B. cockerelli* population dynamics and distribution to Lso spread, especially given the difficulty of detecting a relationship at smaller scales (Goolsby et al. 2012, Workneh et al. 2013). Just as importantly, future work on the underlying causes of *B. cockerelli* population expansion will aid in identifying conditions that generate the greatest risk of future epidemics.

The potential that climate change could reduce agricultural sustainability through pests and disease outbreaks, and resulting increases in pesticide use, has become an increasing concern for growers, scholars, and other stakeholders. As with ecological risk assessment of other stressors, a key challenge in the analysis of outbreak risks from climate change remains to identify which pest or pathogen species are most likely to become more problematic and through which risk pathways (USEPA 1998, Garrett et al. 2011). Most work to date has approached the problem mechanistically, focused on predicting outbreak risks by testing for changes in particular biotic interactions or responses from species with different life history traits under a subset of predicted climatic changes (Juroszek and von Tiedemann 2013). However, the

TABLE 2.   Estimated posterior means (with 95% credible intervals) of linear coefficients for occupancy model of *Lygus hesperus*, *Myzus persicae*, and *Rhopalosiphum padi* occurrence using the same model and data set as for *B. cockerelli* occupancy.

Model term	*Lygus hesperus*	*Myzus persicae*	*Rhopalosiphum padi*
Year	−52.8 [−81.7, −23.1]‡	−7.91 [−66.9, 54.3]	−13.2 [−54.9, 37.2]
Month	8.91 [−4.72, 29.5]	−24.1 [−77, 32.1]	−20.8 [−67, 31.3]
Month^2	−11.2 [−29.2, 8.53]	−7.34 [−49.8, 38.8]	38.1 [−12.9, 82.9]
AET	15.7 [−0.0975, 36.8]†	28.3 [−28.2, 81.3]	21.4 [−20.1, 72.2]
T_{min}	−21.7 [−53.4, 1.39]†	1.6 [−57.3, 58.5]	−8.37 [−57.8, 42.1]
T_{max}	13.9 [−8.16, 33.9]	−1.94 [−54.1, 49.2]	−3.02 [−56.4, 57]
Detection intercept	−1.44 [−1.63, −1.24]‡	5.79 [−1.79, 22.2]	−2.13 [−2.59, −1.71]‡
List length	0.29 [0.124, 0.456]‡	24.2 [0.611, 64.7]‡	0.299 [−0.0439, 0.641]†
List length × year	−0.0424 [−0.188, 0.102]	−19.7 [−55.4, 0.753]	0.0141 [−0.32, 0.35]
μ_α	65.2 [33.1, 99.5]	−16.4 [−76.1, 49.2]	17.9 [−42.6, 74.3]
σ_α	63.5 [26, 121]	352 [79.7, 920]	362 [38, 944]

Note: MCMC convergence diagnostics showed similarly good convergence as for the *B. cockerelli* occupancy model.
† Significant at 90% CI; ‡ significant at 95% CI.

complexity of biological responses to climate change limits the realism of small-scale mechanistic studies.

Our analysis points to an additional, complementary approach. Modeling changes in occupancy for a range of pest and vector species within our data set may provide valuable comparative insights into which species pose the greatest risk. As an example, we applied the same occupancy model to detection and non-detection data for three pest species that were well represented in the data set: *Lygus hesperus* (Hemiptera: Miridae), a pest of strawberries and cotton; *Myzus persicae* (Hemiptera: Aphididae), a vector of potato leafroll virus; and *Rhopalosiphum padi* (Hemiptera: Aphididae), a vector of barley yellow dwarf virus. Our analysis indicates that *L. hesperus* occupancy probability has significantly decreased in California over the last century, and is marginally related to changes in AET and T_{min}. In contrast, occupancy probabilities of *M. persicae* and *R. padi* have shown no clear pattern of change (Table 2). Our results for *R. padi* are in line with those of the analysis of Davis et al. (2014) for populations in the northwestern United States; in both cases, *R. padi* distribution showed little temporal trend and no relationship to climatic variation.

Although our analysis is spatially and temporally coarse and ignores the roles of biotic interactions and agricultural change, comparisons among species, using a common data set and model, could facilitate more fine-grain investigations into the specific mechanisms that underlie large-scale differences among pest species and their relationships to climatic variation. Linking fine-scale studies of biotic interactions and life history traits to macro-ecological analyses will be necessary to develop rigorous assessment frameworks for the future risks of pest and pathogen outbreaks caused by climate change.

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SUPPORTING INFORMATION

DATA AVAILABILITY