




Landscape structure and climate drive population dynamics of an insect vector within intensely managed agroecosystems

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Abstract. Characterizing factors affecting insect pest populations across variable landscapes is a major challenge for agriculture. In natural ecosystems, insect populations are strongly mediated by landscape and climatic factors. However, it has proven difficult to evaluate if similar factors predict pest dynamics in agroecosystems because control tactics exert strong confounding effects. We addressed this by assessing whether species distribution models could effectively characterize dynamics of an insect pest in intensely managed agroecosystems. Our study used a regional multi-year data set to assess landscape and climatic drivers of potato psyllid (*Bactericera cockerelli*) populations, which are often subjected to calendar-based insecticide treatments because they transmit pathogens to crops. Despite this, we show that psyllid populations were strongly affected by landscape and climatic factors. Psyllids were more abundant in landscapes with high connectivity, low crop diversity, and large natural areas. Psyllid population dynamics were also mediated by climatic factors, particularly precipitation and humidity. Our results show that many of the same factors that drive insect population dynamics in natural ecosystems can have similar effects in an intensive agroecosystem. More broadly, our study shows that models incorporating landscape and climatic factors can describe pest populations in agroecosystems and may thus promote more sustainable pest management.

Key words: ecological modeling; generalized boosted models; landscape structure; MAXENT; pest management; zebra chip disease.

INTRODUCTION

Predicting outbreaks of damaging pest populations across variable landscapes is a major challenge for agriculture (Rosenheim and Gratton 2017). Due to global change, and the increased frequency of invasions, there is also a need to predict the future distribution of pests (Worner and Gevrey 2006, Sutherst 2014, Paini et al. 2016). Identifying areas at greatest risk from pests across broad regions could form the foundation of decision support systems (Ferguson et al. 2003, Fabre et al. 2006). However, this is difficult because control tactics, such as pesticide use, strongly affect pests but are hard to quantify at landscape scales, and these tactics can confound the analysis of other factors affecting pests (Hunter 2008, Rosenheim and Gratton 2017).

Ecoinformatics (“big data”) approaches may be a method to effectively address limitations associated

with developing descriptive models for pests in agroecosystems (Rosenheim and Gratton 2017). The foundations of many pest management strategies are monitoring programs that collect data on pest abundance (Bekker et al. 2007, Krapivin et al. 2015). Ecoinformatics approaches integrate such data into models to assess how insect pest populations change across seasons, and how they affect crop yield (Rosenheim et al. 2011, Rosenheim and Meisner 2013). Moreover, it is often unclear whether ecological factors that affect insects in natural ecosystems (climate, habitat diversity, connectivity) have similar effects in agroecosystems (Marini et al. 2012, Karp et al. 2018). Moreover, ecological models in agroecosystems have most often focused on community dynamics, but have often ignored the dynamics of individual pest species (Tscharntke et al. 2005, Karp et al. 2018). This hampers the development of effective models to guide pest management on farms (Rosenheim and Gratton 2017).

Given that pest impacts on crops are correlated with abundance (Kumschick et al. 2014), it is important to

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assess factors that affect pests at local and regional scales (Halbert and Manjunath 2004, Thomas et al. 2017). Species distribution models (SDM) may be an effective tool to meet this goal, as they can depict pest occurrence and population dynamics over broad landscapes (Guisan and Thuiller 2005, Gutiérrez Illán et al. 2014, Moreno-Amat et al. 2015). SDMs developed for natural ecosystems, for example, often show that climatic variables affect large-scale population dynamics, while landscape context is often important at smaller scales (Hunter 2002, Pearson and Dawson 2003, Pearson et al. 2004, Gutiérrez Illán et al. 2010). As many pests are generalists that use multiple hosts across landscapes, developing SDMs across multiple scales could allow producers to assess how pest population dynamics will vary across regions with variable habitat availability and climate (Marini et al. 2012, Rosenheim and Gratton 2017).

Here we used SDMs to assess effects of landscape and climatic factors on potato psyllid, *Bactericera cockerelli*, populations in potato (*Solanum tuberosum*) crops of the U.S. Pacific Northwest. Potato psyllids are managed due to their ability to vector a bacterial pathogen, *Candidatus Liberibacter psyllaurus* (CLp) (Munyanza 2012). We leveraged extensive monitoring data from three states to develop SDMs for psyllids. Our results depicted spatiotemporal patterns of this pest over a period of 6 yr, and identified key landscape context and climatic drivers of psyllid distribution and population dynamics. Our study shows how developing SDMs that assess pest occurrence and abundance can provide a robust framework for determining key factors mediating pest population dynamics and guide decision-making.

METHODS

Study system

Potato psyllids are a key pest in the U.S. Pacific Northwest due to their ability to transmit CLp (Munyanza 2012). This pathogen has caused staggering economic losses that reach into the millions of dollars for individual growers (Greenway 2014). Producers have met this threat with insecticide-reliant control programs that begin in June and continue on a near-weekly basis until harvest (September). The added control costs have led to a 5–7% jump in total production costs (Patterson 2012), which jeopardizes the viability of potato production (Greenway 2014).

Management of psyllids and CLp would benefit from spatial approaches, as psyllids use multiple crop (potato, tomato) and weedy (goji berry, nightshade) hosts (Yang and Liu 2009). Psyllids overwinter on weedy hosts, move into potatoes in the summer, and return to weedy hosts in fall after harvest (Swisher et al. 2013, Nelson et al. 2014, Fu et al. 2016, Thinakaran et al. 2017). Weedy hosts thus serve as reservoirs of psyllids and CLp. Moreover, CLp causes few distinct aboveground symptoms,

and can be spread even when psyllids occur at low abundance (Buchman et al. 2011, Munyanza 2012). This makes it difficult to effectively monitor psyllids or the pathogen in crop fields, causing growers to rely on prophylactic spray programs. Models that better capture the dynamics of psyllids across landscapes could thus considerably improve management programs.

Psyllid monitoring

To address factors affecting psyllids, we established a monitoring network in 2012 (Wenninger et al. 2017). This network is located in a region that encompassed 401,460 km² of Idaho, Oregon, and Washington states from 32°41' N to 60°00' N (~800 km south to north) and from 114°46' W to 138°55' W (~1,000 km east to west; Fig. 1). This region has a complex topography, ranging from sea level to 4,394 m above, and a gradient from oceanic to continental climates. Average monthly temperatures range from –25.1°C (January) to 41.5°C (July), and monthly precipitation range from 0 (July) to 524 mm (December).

Psyllids were sampled at a total of 840 sampling sites from 2012 to 2017 (36 in Oregon, 215 in Washington, 589 in Idaho). Psyllids were monitored using 15 × 10 cm yellow sticky cards (Dreistadt 1998) placed 3 m within the perimeter of potato fields (sites). Cards were collected weekly from May to October, capturing the entire potato growing season and periods where psyllids move to and from farms (Wenninger et al. 2017). We standardized the counts as average potato psyllids per trap per day.

Landscape structure

Land cover data were gathered from USGS Cropland Data Layers (NLCD 2010, Han et al. 2012) with a 500-m buffer around each site. We vectorized land cover data to produce metrics for each site, and we analyzed landscape structure using ZonalMetrics Tools (Adamczyk and Tiede 2017) and ArcMap software (ESRI 2014). The 500-m buffer distance reflected psyllid biology and the distribution of our sites. In agroecosystems, the vast majority of psyllid movement occurs over short distances (<10 m), with psyllids moving between adjacent plants (Henne et al. 2010). Mark–recapture studies at larger scales (up to 350 m) also show that over 90% of psyllids move <250 m from release sites (Cameron et al. 2013). A 500 m buffer thus captures nearly all of typical psyllid movement. Moreover, the average nearest neighbor index of our sites was 2,054 m. By setting a buffer radius of 500 m, we minimized the likelihood of overlapping buffers.

From the landscape data, we created data layers for three land cover classes: “developed,” “natural,” and “crops.” This allowed us to specifically test the “resource concentration hypothesis,” whereby increasing crop monocultures are expected to promote pest populations

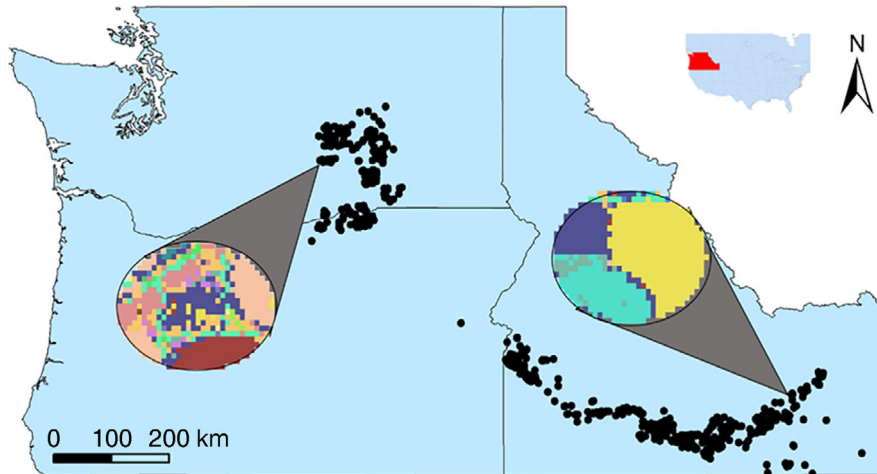


FIG 1. Map showing the geographical context of the study (upper right shows location in North America). The 840 units for analyses (500-m buffers around sampling sites) are represented as black dots. Color of pixels within the study sites represents different land use classes. Landscape structure for two exemplar sites is also shown.

(Root 1973). Second, as growers cannot typically modify their surrounding natural or developed landscape, but can adjust their crop diversity, breaking data into these classes was important for revealing strategies that growers could potentially implement to better manage psyllids. We also calculated the area of all individual habitat types (Appendix S1: Table S1). Along with the area of land cover classes, we included in our models the area of the four crops that represented at least 3% of the landscape in all years of the study (potato, alfalfa, winter wheat, and corn; Appendix S1: Table S1).

We calculated the Shannon Diversity index (*shdiv*), fragmentation index (*frag*), and largest patch index (*lpi*) for each land cover class. Landscape fragmentation was measured via the “edge metric,” which calculates the length of the edges of a selected class within each 500-m buffer. This is a common metric for fragmentation when both the shape and size of all the user-defined zones are standardized (McGarigal et al 2012, Adamczyk and Tiede 2017), as in our study. Largest patch index, *lpi*, was the area of the largest continuous patch of each class within each 500-m buffer. Finally, we calculated the variable *hidro*, which was the Euclidean distance to the nearest permanent water body. Before analyses, all layers were re-sampled to correspond to the 30 arc-sec grid cell size of the environmental variables (Merow et al. 2013).

Landscape connectivity

Potato agroecosystems in the Pacific Northwest consist of large fields (20–60 ha) that are separated by weedy field margins and linear developed elements (e.g., roads); non-agricultural land in the region is often shrub-steppe habitat that contains weedy hosts suitable for psyllids (Swisher et al. 2013, Nelson et al. 2014, Fu et al. 2016, Wenninger et al. 2019). We expected that a

more interconnected network of landscape classes may facilitate the movement of psyllids through both crops and natural land. We thus calculated a “connectivity” metric, which was used to test whether landscape connectivity facilitated psyllid movement (McGarigal et al. 2012). We calculated connectivity for each site using the *rgeos*, *raster*, and *tidyverse* packages in R (Wickham 2017, R Core Team 2018, Bivand and Rundel 2019, Hijmans 2019). Raster layers for each site were converted into spatial points dataframes. We then calculated connectivity as the number of joinings between points of the same landscape class (McGarigal et al. 2012)

$$\text{connectivity} = \left[\frac{\sum_{j \neq k}^n c_{ijk}}{\frac{n_i(n_i-1)}{2}} \right] (100),$$

where c_{ijk} is the joining between point j and k ($0 =$ unjoined, $1 =$ joined) of the corresponding landscape class (i) and n_i is the total number of points in the landscape of the landscape class. Pairs of points were considered connected if the cartographic distance between points at cell centroids were <500 m. As potato psyllids move through both crop and non-crop habitats, we expected overall connectivity would provide a more representative measure than connectivity of any specific landscape type. Thus, values of connectivity for each class were averaged to find a site-level measure of “connectivity” (Mühlner et al. 2010). The connectivity measure was not strongly correlated with the acreage of any of the major habitat types included in the analyses (Pearson’s correlation tests, $N = 840$; R^2 values for potato, alfalfa, winter wheat, and corn were 0.095, 0.0002, 0.0005, and 0.0021, respectively; P values for each correlation were >0.10).

Environmental variables

Climatic variables for sites were generated by the Parameter Regression of Independent Slope Model (PRISM; Daly et al. 2002). This data set was created using meteorological station data, digital elevation models, and other spatial data. We used source maps at a spatial resolution of 30 arc-sec (~800 m cell size at this latitude; Daly et al. 2000). Because PRISM variables are available monthly and potato psyllids were collected weekly, but we wanted to account for conditions over the full life cycle of the insect, we calculated seasonal predictors (summer and winter). We selected four variables that were biologically meaningful and potentially associated with psyllid occurrence and abundance: temperature (maximum in summer and minimum in winter), vapor pressure deficit, dew-point temperature, and precipitation. Vapor pressure deficit (VPD) is the difference (deficit) between the amount of moisture in the air and how much moisture the air can hold when saturated. Thus, VPD is a measure of the dryness of the air. Once air is saturated, water condenses to form dew. Dew-point temperature, related to relative humidity, is the temperature to which the air would have to cool (at constant pressure and vapor content) to reach saturation. A higher dew-point temperature means more moisture in the air.

Variable selection

To account for multicollinearity, we used a backward stepwise process to calculate the variance inflation factor (VIF) for the pool of 19 predictors, and selected those with values below four (Kock and Lynn 2012). Depending on the scale of the study, some authors argue that a $VIF < 10$ may be acceptable (Hair et al., 1995), but others indicate that the maximum value should be 5 (Kock and Lynn 2012). To be conservative, we used a VIF value of 4, and discarded variables above this threshold (Appendix S1: Fig. S1). With the resulting variable set, we calculated a correlation matrix (Pearson's r) and only two variables had a coefficient above 0.5 (winter minimum temperature and winter dew-point temperature; Appendix S1: Fig. S2, S3); these variables were both retained despite the potential correlation as they described different aspects of the environment (temperature vs. air moisture; Hamilton 1987). After variable selection, the final set of explanatory variables is listed in Table 1.

Modeling and data analyses

We assessed factors affecting psyllid occurrence using Maximum Entropy (MAXENT) models, which reflect establishment in crop fields (Thomas et al. 2017). MAXENT models were chosen because they typically outperform other algorithms (e.g., GARP, CART, Random Forests) with presence-only data (Elith et al. 2006,

Phillips and Dudík 2008). MAXENT models compare presence locations with randomly selected points to find the largest spread (maximum entropy) of current conditions relative to a “background” of environmental variables. These analyses create maps of habitat suitability and assess the contribution of specific environmental variables to occurrence. Because MAXENT works with GIS raster layers, and we created user-defined units to calculate landscape structure, we only developed MAXENT models with climate data.

We assessed factors driving psyllid abundance with generalized boosted models (GBMs). GBMs are a non-parametric machine-learning technique that fits a single parsimonious model and combine strengths of regression trees and boosting (Elith et al. 2006). They are often used for SDMs as they make strong predictions, minimize overfitting, can accommodate missing data, and can model nonlinear relationships (Elith et al. 2008, Randin et al. 2009, Carvalho et al. 2010). GBMs also generally fit better than Random Forests if parameters are tuned correctly (Friedman 2002, Hastie et al. 2009). GBMs were developed with potato psyllid abundance as the response variable and either climate or landscape variables as predictors (Table 1); we ran an additional GBM with both landscape and climate predictors. We calculated the relative influence of each predictor using the *gbm* package (Greenwell et al. 2018); this provides a measure of each variable's influence on the total response and is reflected as a proportion (Elith et al. 2008). The measure is based on the number of times the variable is selected, weighted by the averaged improvement to the model in all trees. The relative influence of each variable is scaled from 1 to 100, with higher values indicating stronger influence in the model (Elith et al. 2008).

Model evaluation

We assessed MAXENT models using area under the curve (AUC) of receiver operating characteristic plots and binary omission rates (Manel et al. 2001, McPherson et al. 2004). AUC is a common metric of model fit (Gutiérrez Illán et al. 2014, D'Amen et al. 2015) that weighs omission error (predicted absence in areas of actual presence) and commission error (predicted presence in areas of actual absence) equally. The AUC is an accuracy measure that juxtaposes correct and incorrect predictions over a range of thresholds. AUC values range from 0.5 (no better than random) to 1 (perfect fit). Useful models have AUC values of 0.7–0.9, and good discriminating models have values above 0.9 (Fielding and Bell 1997). We assessed GBMs using Spearman's nonparametric correlation coefficients between predicted and observed abundance values. We used rank correlations coefficients because observed counts were low at many sites (causing deviations from normality) and due to nonlinear relationships between predicted and observed abundance. For MAXENT models and

TABLE 1. List of final landscape and climatic variables included in the models.

Variable	Description	Mean (min-max)	Resolution	Source	Units
Landscape variables					
hidro	distance to water	17.3 (0–174.5)	250 m	USGS	m
CDL	habitat type area†	categorical	30 m ²	CropScape	NA
connect	connectivity	81.5 (46.1–98.5)	30 m ²	CropScape	%
frag	fragmentation	0.1 (0.0–0.4)	30 m ²	CropScape	km
lpi	largest patch index	17.3 (1.5–98.2)	30 m ²	CropScape	m ²
shdi	Shannon diversity	0.6 (0.1–2.2)	30 m ²	CropScape	NA
Climatic variables					
tmax	maximum temperature summer	29.5 (36.3–24.2)	30 arc-sec	PRISM	°C
tmin	minimum temperature winter	−5.7 (−16.6–−0.3)	30 arc-sec	PRISM	°C
Pptsum	precipitation in summer	11.5 (0.3–49.1)	30 arc-sec	PRISM	mm
pptwint	precipitation in winter	27.8 (3.3–93.0)	30 arc-sec	PRISM	mm
vpdsum	summer vapor pressure deficit	33.0 (24.4–44.8)	30 arc-sec	PRISM	kPa
vpdwint	winter vapor pressure deficit	0.2 (0.0–0.62)	30 arc-sec	PRISM	kPa
tdmeansum	summer dew-point temperature	6.2 (0.4–10.1)	30 arc-sec	PRISM	°C
tdmeanwint	winter dew-point temperature	−4.9 (−15.3–0.1)	30 arc-sec	PRISM	°C

†USGS national land cover database. Habitats included were potato, winter wheat, alfalfa, and corn.

GBMs, we randomly selected 70% of sites (563) to train the models and 30% (241) for validation. These evaluation tests were thus carried out on spatially and temporally independent data (Bahn and McGill 2013).

A common criticism of SDMs is failing to account for spatial autocorrelation (Betts et al. 2006, Beale et al. 2008), which can affect the reliability of spatial analyses (Algar et al. 2009). Due to the multiple factors that define the environmental conditions in the ecosystem, one would expect that populations showing similar fitness will be aggregated and models need to control for this. We tested for spatial autocorrelation in potato psyllid counts during the six years of monitoring using correlograms (Moran's I ; Moran 1950, de Oliveira et al. 2014) at increasing distances (500–50,000 m at 250-m intervals) from our sampling locations.

RESULTS

Data overview

The mean nearest-neighbor distance between sites was $2,054 \pm 40.3$ m (mean \pm standard error (SE)), and there was no strong spatial autocorrelation in psyllid abundance across sites ($N = 840$; $Z = 0.30$; $P = 0.76$; Appendix S1: Fig. S4). The Moran's I values for potato psyllid abundance were not significant at any distance (Appendix S1: Fig. S4), and we thus did not further account for spatial autocorrelation in MAXENT or GBMs.

MODEL EVALUATION

Average AUC values for MAXENT models were 0.92–0.96 (Appendix S1: Table S2), indicating they successfully discriminated presence from background locations. For the GBMs, predictive abundances were

positively correlated with observed abundance across all years. Climate models (Spearman's $\rho = 0.45$; $P < 0.001$) outperformed landscape models (Spearman's $\rho = 0.34$; $P < 0.001$), although prediction of insect abundance was strongly significant for both model types (Appendix S1: Table S2). Results of the combined model with both climate and landscape predictors showed a noticeable improvement in the prediction accuracy (Spearman's $\rho = 0.66$; $P < 0.001$), due to the extra, and complementary information provided by the two set of predictors (Appendix S1: Table S2).

Relative contribution of variables

The most important variables in the landscape models assessing psyllid abundance were landscape connectivity, crop diversity, largest natural patch index, and area of potato crops, in that order (Fig. 2). As models were non-linear, the response curves provide information on the effect of each variable (Fig. 3). Connectivity was correlated with higher psyllid abundance, with particularly strong effects above 80% connectivity (Fig. 3a). This effect supports the hypothesis that a more connected landscape increased psyllid abundance. In contrast, greater crop diversity decreased psyllid abundance (Fig. 3b), which supports the hypothesis that a highly diverse crop landscape contained many crops that were not suitable for psyllid population growth. Largest natural patch index had a positive and constant relationship with psyllid abundance (Fig. 3c), which indicates that larger patches of natural habitat facilitate greater abundance of potato psyllids. Finally, a higher amount of potato crop cover was associated with higher psyllid numbers (Fig. 3d).

Both occurrence and abundance models had the same top three climate predictors (Fig. 4). The most

important climate factors were dew-point temperature during winter, vapor pressure deficit during winter, and summer precipitation, all of which reflect “atmospheric water” (Fig. 4). Dew-point temperature during winter had a generally positive effect on psyllids, although the relationship was unimodal, with a peak around -1.5°C (Fig. 5). As the saturation point in winter became increasingly easier to reach due to more moisture in the air, potato psyllids were more abundant. Vapor pressure deficit during winter was negatively associated with psyllid abundance (Fig. 5), which also means psyllid abundance is favored by wetter environmental conditions. In contrast, summer precipitation was negatively correlated with psyllid abundance (Fig. 5). The overall climatic suitability of the study system from the MAXENT model is shown in Appendix S1: Fig. S5.

Results of the combined models were consistent with those obtained in the climate-only and landscape-only models, and effects did not vary in direction or magnitude. Predictors were ranked in the same order, although the top three variables were all climatic variables, and overall, climatic variables had greater explanatory power than landscape variables (Fig. 6).

DISCUSSION

Our study provides strong evidence that landscape and climatic factors can effectively describe the population dynamics of a generalist pest in an intensively managed agroecosystem. Although most producers manage

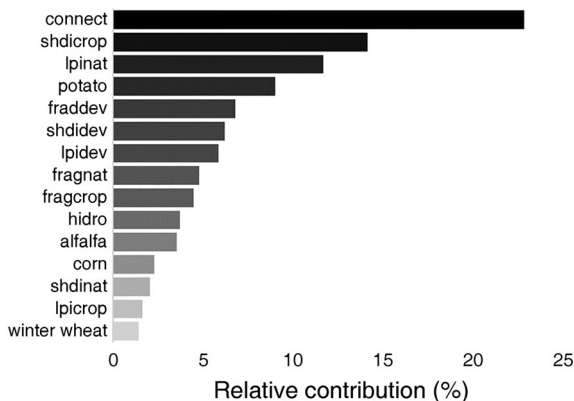


FIG 2. The relative contribution of each landscape metric in generalized boosted regression (abundance) models. Scale bars show the proportion of variance explained by each explanatory factor: (i) shdicrop, Shannon’s diversity for crop habitats; (ii) shdinat, Shannon’s diversity for natural habitats; (iii) shdidev, Shannon’s diversity for developed habitats; (iv) fragcrop, fragmentation index for crop habitats; (v) fragnat, fragmentation index for natural habitats; (vi) fragmentation index for developed habitats; (vii) lpicrop, largest patch index for crop habitats; (viii) lpinat, largest patch index for natural habitats; (ix) lpidev, largest patch index for developed habitats; (x) connect, overall landscape connectivity; (xi) hidro, distance to nearest permanent water body; (xii to xv) area of potato, alfalfa, corn, and winter wheat.

psyllids with calendar-based pesticide applications (Patterson 2012, Greenway 2014, Echegaray and Rondon 2017), collecting pesticide data from many growers is infeasible. Despite these confounding management effects, our models explained much of the variation in psyllid occurrence and abundance. While CLp is hard to sample, psyllid abundance is often strongly correlated with the incidence of CLp (Munyanza 2012). Thus, our models that describe psyllid abundance likely correlate with risk from CLp and can guide management of the vector and pathogen. Like psyllids, long-term monitoring studies exist for many agricultural pests worldwide (Rosenheim and Gratton 2017). Developing models from these data sets can provide an effective means to assess variation in pest risk across broad agricultural landscapes.

We show many of the landscape factors that affect insects in natural systems (connectivity, diversity, fragmentation) mediated psyllid populations in agroecosystems. Connectivity and crop diversity were particularly important, accounting for more than 44% of the variability in psyllid abundance. In natural ecosystems, higher connectivity facilitates dispersal of organisms (Forman and Alexander 1998, Hulme et al. 2008), and connectivity in agroecosystems can enhance the abundance of natural enemies and promote pest suppression (Aviron et al. 2018, Dominik et al. 2018). While our connectivity metric was based on the overall landscape, it is likely that crop connectivity was more important than connectivity of natural areas. This is because natural areas that may contain weedy hosts suitable for psyllids never accounted for more than 12% of the total landscape, while crops accounted for ~80%.

The response of an organism to landscape connectivity can be species-specific (Cross et al. 2012, Duflo et al. 2018). While psyllids are weak flyers, they can travel long distances on wind currents (Cameron et al. 2013). More connectivity may thus promote psyllid abundance because psyllids traveling long distances on wind currents, where movement is diffuse rather than driven by resource availability, are more likely to locate suitable habitat patches after dispersal in more connected landscapes (Cross et al. 2012). Recent studies on invasive insects have similarly found positive effects of connectivity (Carrasco et al. 2010, Thomas et al. 2017). However, ours is among the first studies to provide evidence of a positive and key role of landscape connectivity on a pest in a managed agroecosystem (see also Crossley et al. 2019). For farmers, this means reducing connectivity in agroecosystems may impede psyllid populations. However, reducing connectivity may be impractical for farmers and might inhibit predator populations (Aviron et al. 2018, Dominik et al. 2018). Rather, growers may be able to refine their management tactics to better match their specific landscape context, with reduced sprays in less connected landscapes.

High crop diversity was negatively correlated with psyllid abundance, and increasing area of potato crops

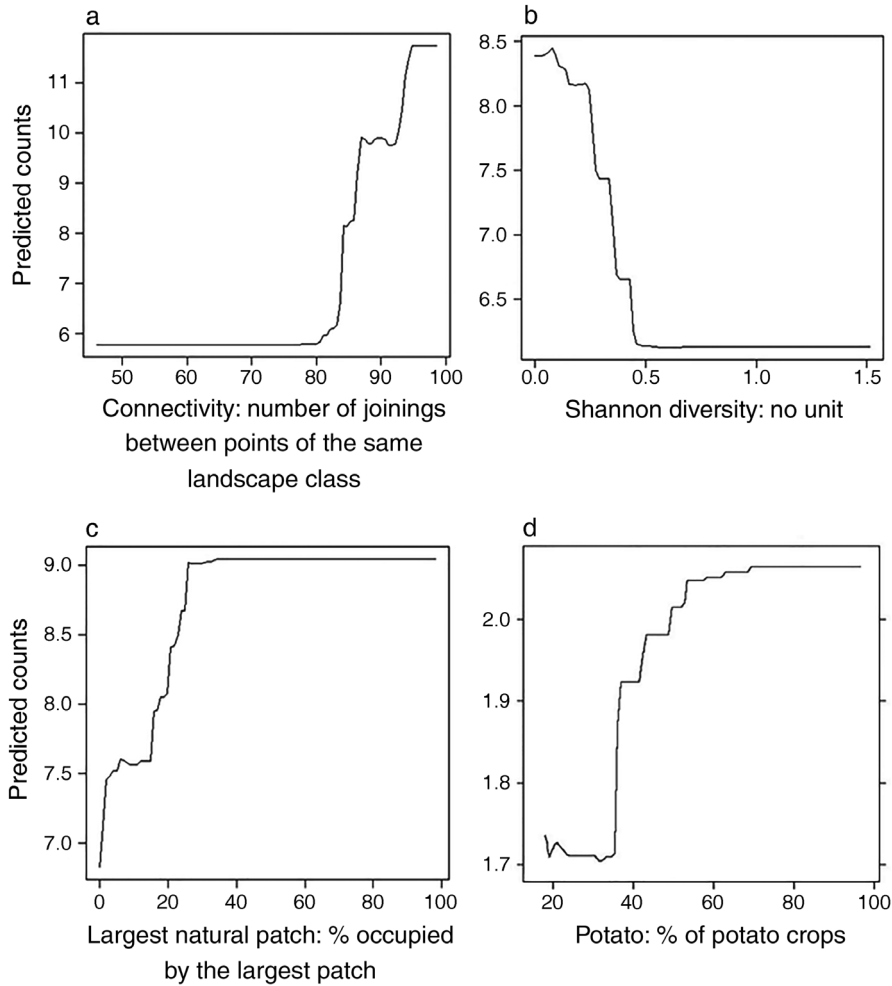


FIG 3. Response curves for the top landscape variables in the generalized boosted models that describe potato psyllid abundance: (a) connectivity, (b) crop diversity, (c) largest natural patch index, and (d) potato. Solid lines represent predicted psyllids counts in relation to each predictor.

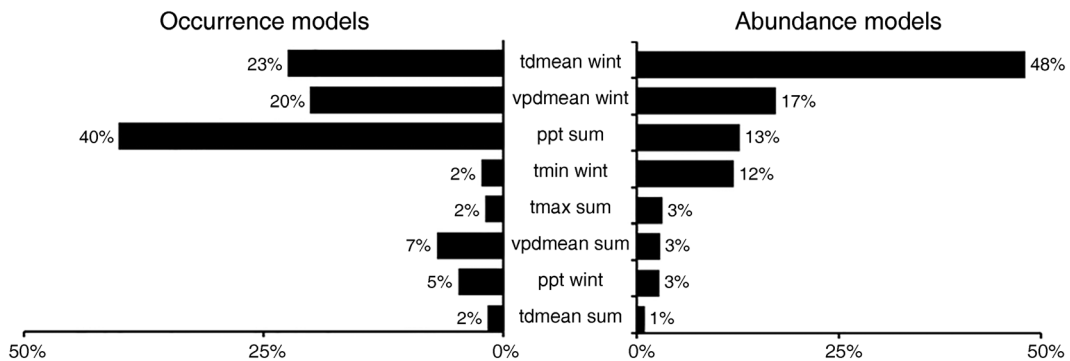


FIG 4. The relative contribution of climate factors in MAXENT (occurrence) and generalized boosted (abundance) models. Scale bars show the proportion of variance explained by each explanatory factor: (i) tdmean wint, winter dew-point temperature; (ii) tdmean sum, summer dew-point temperature; (iii) vpdmean wint, vapor pressure deficit in winter; (iv) vpdmean sum, vapor pressure deficit in summer; (v) ppt wint, precipitation in winter; (vi) ppt sum, precipitation in summer; (vii) tmin wint, minimum temperature in winter; and (viii) tmax sum, maximum temperature in summer.

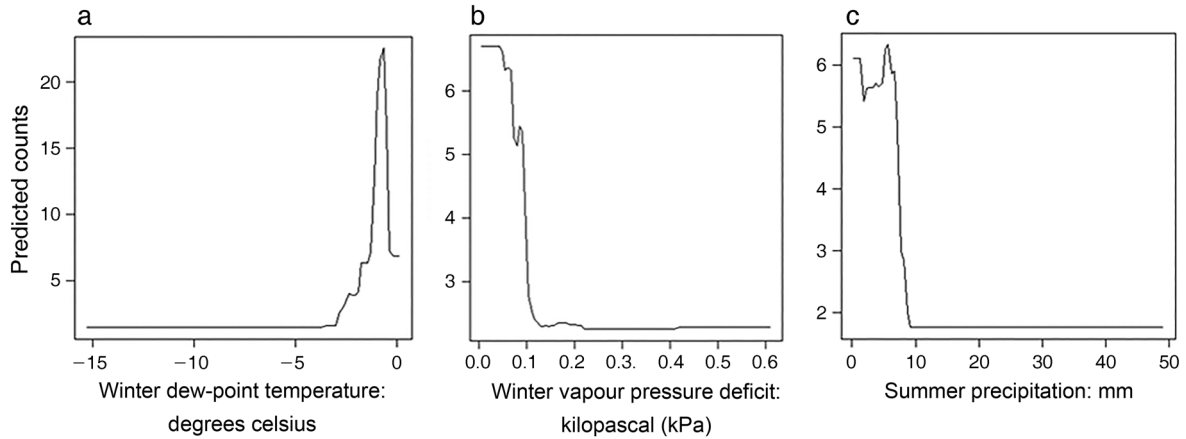


FIG 5. Response curves for the top three climate factors in the generalized boosted models used to describe abundance of potato psyllids: (a) winter dew-point temperature, (b) vapor pressure deficit in winter, and (c) precipitation in summer. Solid lines represent the predicted psyllids counts in relation to each predictor.

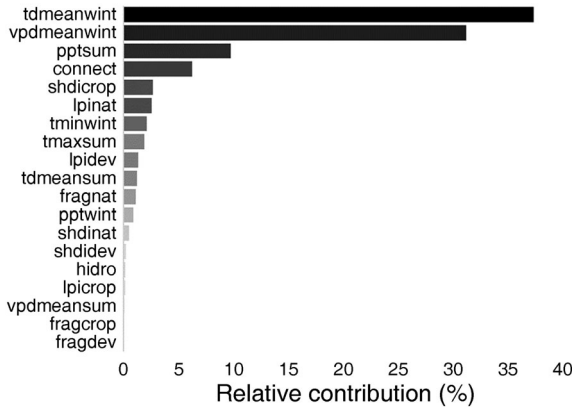


FIG 6. The relative contribution of each predictor in generalized boosted regression combined models. Scale bars show the proportion of variance explained by each explanatory factor: (i) shdicrop, Shannon’s diversity for crop habitats; (ii) shdinat, Shannon’s diversity for natural habitats; (iii) shdidev, Shannon’s diversity for developed habitats; (iv) fragcrop, fragmentation index for crop habitats; (v) fragnat, fragmentation index for natural habitats; (vi) fragnat, fragmentation index for developed habitats; (vii) lpicrop, largest patch index for crop habitats; (viii) lpinat, largest patch index for natural habitats; (ix) lpidev, largest patch index for developed habitats; (x) connect, overall landscape connectivity; (xi) hidro, distance to nearest permanent water body; (xii) tdmean wint, winter dew-point temperature; (xiii) tdmean sum, summer dew-point temperature; (xiv) vpdmean wint, vapor pressure deficit in winter; (xv) vpdmean sum, vapor pressure deficit in summer; (xvi) ppt wint, precipitation in winter; (xvii) ppt sum, precipitation in summer; (xviii) tmin wint, minimum temperature in winter; and (xix) tmax sum, maximum temperature in summer.

was positively associated with psyllids. This is consistent with the “resource concentration hypothesis” (Root 1973), where increasing concentration of a single crop benefits herbivores because they are more likely to locate and persist in monocultures. Although potato psyllids are generalists, potatoes are the only major solanaceous

crop grown in the study region. Increasing crop diversity thus represents greater acreage and diversity of non-solanaceous crops unsuitable for potato psyllid feeding. While growers have little control over their surrounding landscape, they may be able to limit psyllid populations by diversifying their farms.

Unlike crop diversity, increasing area of natural patches was associated with more psyllids, possibly because natural habitats support weedy hosts used for overwintering (Knowlton and Thomas 1934, Burckhardt et al. 2014). Understanding the role of such habitats in pest dynamics can aid growers in making proactive management decisions. Moreover, many studies report that conservation of natural habitats enhances biological pest control and bolsters yields, although this is not always a general trend (Karp et al. 2018). In our study, any potential positive effects of natural habitats on biological control appeared to be outweighed by positive direct effects on psyllids, resulting in the positive correlation between natural habitats and psyllid abundance.

Climatic models also effectively described psyllid occurrence and abundance across the heterogeneous U.S. Pacific Northwest region, and climatic factors appeared to mediate psyllid abundance more strongly than landscape structure. The most important climate factors were associated with air moisture and precipitation. Similar climatic factors are key drivers of populations for other western U.S. taxa including butterflies (McLaughlin et al. 2002) and birds (Gutiérrez Illán et al. 2014). Water availability may impact psyllids, and other pests, by altering the suitability of crop and weedy host plants. For example, potato psyllids overwinter on non-crop hosts, move into irrigated crops in the summer, and return to non-crop hosts in fall after harvest (Swisher et al. 2013, Murphy et al. 2013, Thinakaran et al. 2017). Winter humidity may make overwintering hosts more abundant and more suitable, increasing psyllid abundance and their potential to establish in crops the

following season. For example, higher values of VPD indicate more water stress, and this can translate to lower number of insects on the host plant. This may explain why lower VPD in winter, and greater dew-point temperature, both of which reflect greater air moisture, were associated with increased abundance of psyllids the following season in potato crops. Our results are similar to those reported for the citrus psyllid, *Diaphorina citri*, which is sensitive to variation in atmospheric moisture and is negatively impacted by low winter precipitation (Narouei-Khandan et al. 2016, Thomas et al. 2017). Growers may thus be able to use winter conditions, particularly related to precipitation, to better predict the potential risk from psyllids in the following year and make more proactive management decisions.

In contrast, greater summer precipitation was negatively associated with psyllid abundance in potatoes. This result may occur because one of the major weedy hosts of psyllids, *Lycium* spp., loses its leaves during dry summer periods, which can drive psyllid movement into potatoes (Thinakaran et al. 2017). If summer precipitation is high, *Lycium* spp. will retain their leaves, and even small amounts of precipitation can cause a leaf flush. Thus, when summer precipitation is relatively high, psyllids have less incentive to disperse from weedy hosts into irrigated potato fields, which may reduce psyllid numbers in potato crop systems. Second, as potato fields are irrigated heavily during summer, a decrease in rainfall would consequently trigger an increase in artificial irrigation in potato crops, which has been shown to negatively impact psyllid populations compared to drier crop conditions (Huot and Tamborindéguy 2017). As with winter conditions, these data may be used within seasons for growers to fine tune their management programs. During periods of drought, psyllid movement into potatoes may increase, and more proactive management measures may be warranted than during periods with rainfall.

Atmospheric water conditions may also affect psyllids, and other sap-feeding insects, at smaller spatial scales within fields. There is considerable evidence that phytophagous insects, especially sap feeders, are affected by moisture (Huberty and Denno 2004). For psyllids, moderate levels of drought stress can affect nymphal survival (Huot and Tamborindéguy 2017). Our results showing that psyllid abundance increased as summer precipitation decreased may reflect, at least in part, such positive effects of water stress on psyllid population growth rates within fields. This can have important implications for the expansion and control of insect pests under a changing environment, where insects will be forced to track favorable conditions at a rapid pace, and more adaptable species might be more likely to cope with climate change (Root et al., 2003, Hoffman and Sgro 2011). However, more research is needed to identify the potential mechanisms by which water availability affects psyllid populations, especially given that potato fields are typically irrigated.

Although our climatic and landscape models accurately described potato psyllid occurrence and abundance, substantial variation remained unexplained. There are numerous climatic and non-climatic factors capable of driving insect population dynamics, and most of them remain unincorporated in ecological models. A first source of variation may arise from the nature of the environmental variables. Due to the availability of predictors, most niche models are developed at a coarser scale than the scale of perception by many insects (Gillingham et al. 2012). Recent studies have reported that finer scale microclimates can provide refugia against regional climates (Moritz and Agudo 2013). Second, many species show a lag in response adapting to climatic and land use changes, and thus insect population dynamics will likely not be fully captured by niche models (Jetz et al. 2007). Additional sources of variation are anthropogenic factors such as the use of fertilizer and pesticides, and biotic relationships such as competition, mutualism, and predation (Blois et al. 2013, Gaba et al. 2014). Unfortunately, fine scale data sets capable of incorporating local dispersal behavior and physiological tolerances are extremely rare, particularly in field studies.

Many ecological models consider landscape and climatic variables as independent factors, but there are reasons to expect that they can interact synergistically to affect insect populations. This may be particularly true in agroecosystems, where anthropogenic factors cause more rapid turnover in land use and environmental conditions than in most natural systems. We hypothesize that there are several crucial ways in which landscape and climatic factors could interact over longer time scales than were investigated in our study. For example, pest populations that are already in expansion due to land use change may be more likely to behaviorally adapt to climate change, and thus have increased potential for colonizing newly available landscapes at the expanding edge. In contrast, landscape fragmentation may reduce functional connectivity of landscapes, thereby limiting the potential for population persistence and range shifts due to climate change. A critical next step will be to design approaches capable of assessing interactive effects of landscape and climatic factors on pest populations, but this has proven difficult to date for observational studies.

While many conservation studies in natural ecosystems focus on the role of landscape and climatic factors in supporting insect populations (Hodgson et al. 2011, Oliver et al. 2015, Papanikolaou et al. 2017), within managed systems the goal is to limit pests. In other words, when conservation is the goal, promoting connectivity and large patches of undisturbed natural areas is a strategy to maintain or increase population of the target species (Rayfield et al. 2011, Luque et al. 2012, Rubio et al. 2015). On the contrary, results presented here suggest that, when the primary objective is to control pests, promoting low connectivity and high crop diversity can be an effective approach. Similarly, favorable

environmental conditions can promote populations of threatened species in natural systems (Hoffmann and Sgro 2011, Sánchez-Fernández et al. 2013). In contrast, producers must be aware of how climatic factors promote pests to effectively gauge risk in managed agroecosystems (Rosenzweig et al. 2014, Altieri et al. 2015). Our study shows that “big-data” ecoinformatics approaches can effectively integrate landscape and climatic data with data from monitoring networks to guide pest management decisions.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2109/full>

DATA AVAILABILITY

Data are available from Figshare: <https://doi.org/10.6084/m9.figshare.11764539.v1>.