



Leveraging satellite observations to reveal ecological drivers of pest densities across landscapes

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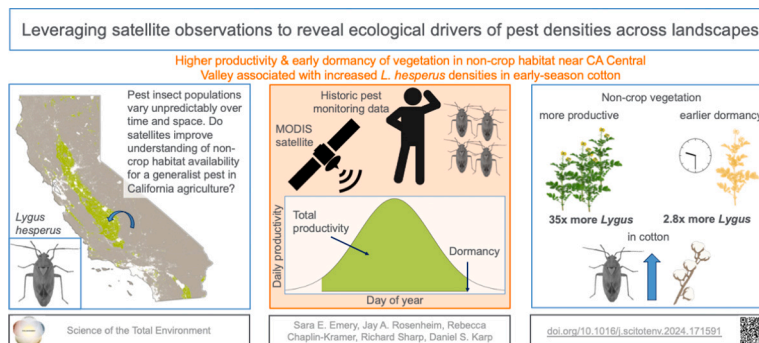
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HIGHLIGHTS

- Land cover and satellite observations may elucidate pest ecology.
- *Lygus hesperus* in CA cotton increases with non-crop habitat in N, decreases in S.
- Productive non-crop habitat with early dormancy leads to more *L. hesperus* in cotton.
- Satellite observations offer some ability to predict pest densities.

GRAPHICAL ABSTRACT



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ABSTRACT

Landscape ecologists have long suggested that pest abundances increase in simplified, monoculture landscapes. However, tests of this theory often fail to predict pest population sizes in real-world agricultural fields. These failures may arise not only from variation in pest ecology, but also from the widespread use of categorical land-use maps that do not adequately characterize habitat-availability for pests. We used 1163 field-year observations of *Lygus hesperus* (Western Tarnished Plant Bug) densities in California cotton fields to determine whether integrating remotely-sensed metrics of vegetation productivity and phenology into pest models could improve pest abundance analysis and prediction. Because *L. hesperus* often overwinters in non-crop vegetation, we predicted that pest abundances would peak on farms surrounded by more non-crop vegetation, especially when the non-crop vegetation is initially productive but then dries down early in the year, causing the pest to disperse into cotton fields. We found that the effect of non-crop habitat on pest densities varied across latitudes, with a positive relationship in the north and a negative one in the south. Aligning with our hypotheses, models predicted that *L. hesperus* densities were 35 times higher on farms surrounded by high versus low productivity non-crop vegetation (EVI area 350 vs. 50) and 2.8 times higher when dormancy occurred earlier versus later in the year (May 15 vs. June 30). Despite these strong and significant effects, we found that integrating these remote-sensing variables

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into land-use models only marginally improved pest density predictions in cotton compared to models with categorical land cover metrics alone. Together, our work suggests that the remote sensing variables analyzed here can advance our understanding of pest ecology, but not yet substantively increase the accuracy of pest abundance predictions.

1. Introduction

Despite centuries of innovations in pest management, the discovery of a diverse array of potent synthetic insecticides in the 20th century, and a continued upward trajectory in insecticide use over the past several decades, herbivorous arthropod pests still destroy 14–18 % of potential crop yield annually, constraining global food production (Oerke, 2006; Pimentel, 2009; UNEP, 2022; Shattuck et al., 2023). Predicting when and where pest outbreaks will occur is crucial, both for farmers to maintain high yields and to minimize the use of harmful insecticides (Chaplin-Kramer et al., 2019). Simplified landscapes, characterized by vast expanses of crop monocultures, have long been thought to benefit pest insects and harm their natural enemies (Root, 1973; Bernays and Graham, 1988; Landis et al., 2000). In particular, Root's classic resource concentration hypothesis posits that agricultural pests are resource limited and that pest populations should thus be able to expand rapidly and spread throughout homogenous agricultural landscapes (Root, 1973). While many pests do seem to benefit from homogenous agricultural landscapes (Rusch et al., 2016; Paredes et al., 2021; Emery et al., 2021), this response is far from universal, with a nearly equal number of studies showing that landscape simplification can reduce pest populations (Karp et al., 2018).

Pest biology may partially explain why some herbivorous pest species increase and others decline in landscapes dominated by crop monocultures (Tschamtko et al., 2016). Pest responses to landscape homogeneity depend on relative mobility, diet breadth, and host preference, with generalist pests often benefiting more from heterogeneous landscapes than specialists (Carrière et al., 2012; Dong et al., 2020; Rosenheim et al., 2022; Yang et al., 2022). Indeed, the resource concentration hypothesis was originally constructed with specialists in mind, positing that vast expanses of a specialist pests' core resource would facilitate rapid population expansion. Though more insects are specialists on a global scale (Forister et al., 2015), agricultural pests are predominantly generalist feeders (Kennedy and Storer, 2000).

Understanding what resources pests depend on, and how they are provided by different habitats at different times of the year, is key to predicting how pest populations in agriculture are likely to change across landscapes. Yet many studies characterize landscapes, and thus define habitat availability, using broad land-use categories (e.g., Thies et al., 2003; Chaplin-Kramer et al., 2011). These categories are unlikely to reflect spatial and temporal variation in key resources for generalist pests, which may explain why landscape synthesis studies often fail to detect consistent responses to landscape simplification across pest species (Karp et al., 2018). More nuanced information, characterizing the functional attributes of different ecosystems across landscapes (Fahrig et al., 2011), is needed to better understand the drivers of pest dynamics in agricultural systems.

Through long-term, frequent, and spatially continuous measurements of climate, vegetation, and other biophysical variables, satellite-based Earth observations offer opportunities to improve the spatial, temporal, and functional characterization of landscapes, beyond land use and land cover. Assessing the timing of resource availability on the landscape is important as pests are more likely to move from non-crop habitat into crop habitat early in the season just after crop emergence (Macfadyen et al., 2015) when many crops are especially vulnerable to pest damage. Satellite observations can provide accurate predictions of important vegetation phenological metrics, which often predict arthropod abundances better than rule-of-thumb calendar dates (Poyry et al., 2018; James et al., 2020), both currently and decades into the past

(depending on the satellite/sensor). Proxies for vegetation productivity, like precipitation, can provide a more accurate assessment of arthropod abundance than land-use categories alone (Campbell et al., 2023), but may not capture resource availability during a period of interest. Satellite observation imagery can directly detect vegetation productivity, which has been shown to correlate positively with arthropod densities (Perner et al., 2005; Fernández-Tizón et al., 2020).

Satellite Earth observation data are now used to infer spatiotemporal trends in the distribution, abundance, and diversity of many plant and animal taxa worldwide (Pereira et al., 2013; Pettorelli et al., 2014; Skidmore et al., 2015; Reddy et al., 2021). Surprisingly, however, there has been very limited application of satellite observations (other than derived land-use products) to agricultural pests, or indeed to many ecosystem functions and services beyond carbon storage (Cord et al., 2017; Pettorelli et al., 2018; Ramirez-Reyes et al., 2019). Here we provide a case study for how advancing the use of satellite observations might allow agricultural ecologists to move beyond categorical representation of land cover and towards a more functional classification of landscapes based on resource availability.

The Western Tarnished Plant Bug, *Lygus hesperus* Knight (Heteroptera: Miridae), presents a useful model for exploring the utility of satellite observations in pest modeling. *Lygus hesperus* is a generalist herbivore and global pest of cotton, strawberries, alfalfa, and other crops (Scott, 1977; Goodell, 1988). In cotton, *L. hesperus* causes direct reductions in yield by piercing and damaging squares (the flower bud that develops into the harvestable plant part), triggering abscission from the plant (Zink and Rosenheim, 2005). In 2019, *L. hesperus* was responsible for 91 % of the insect damage in California cotton, resulting in a \$33 million economic loss from lower yields and higher management costs (Cook and Threet, 2020; Zheng and Winfree, 2021).

Critical to expectations of how landscape context might affect generalist pests like *L. hesperus* is whether the focal crop is a preferred or marginal host. In this case, cotton is a marginal host for *L. hesperus*, while many other crop and non-crop plants are important hosts, especially plants in the Asteraceae and Brassicaceae families (Mueller et al., 2005; Goodell and Ribeiro, 2006). Because *L. hesperus* uses plants growing in natural habitats and alternate crops as host plants, the resource concentration hypothesis aligns well with the long-held hypothesis that more nearby preferred habitat, whether crop or non-crop, should increase *L. hesperus* densities in cotton (Goodell, 1988; Mueller et al., 2005). While planting preferred crops (e.g. safflower) nearby has been shown to increase the risk of *L. hesperus* attack on cotton (Carrière et al., 2012; Sivakoff et al., 2013; Meisner et al., 2017), this theory has been untested with respect to non-crop habitat at larger spatial scales that extend into the California foothills (i.e., radii of tens of kilometers from sampling locations). In essence, if non-crop habitat (potentially containing preferred host plants) is highly productive, then large *L. hesperus* populations might build and spillover into the cotton crop habitat, as has been tested with variable results at smaller scales (300 m - 3 km) across the valley floor (Carrière et al., 2006, 2012; Sivakoff et al., 2013). Another possibility, however, is that non-crop habitat acts as a sink, decreasing damage in cotton fields. Indeed, the presence of nearby preferred host plants like common tarweed (*Deinandra kelloggii*) and intercropped alfalfa can act as trap crops for *L. hesperus* near cotton, and flower strips can act as trap crops for other *Lygus* species near tomatoes (Stern et al., 1969; Goodell and Ribeiro, 2006; Balzan and Moonen, 2014; Wheeler and Krimmel, 2015).

Whether a preferred non-crop host is a source or a sink of pests to crop fields likely depends on the timing of the productivity of the non-

crop host relative to the crop, which may shift from year to year depending on the climate. In Mediterranean climates with cool wet winters and warm dry summers, highly productive non-crop habitat is seasonally ephemeral; that is, most host plants are present in winter but then dry down and enter dormancy in the spring and summer. Importantly, high *L. hesperus* densities are most damaging to cotton yields in the early season (Rosenheim and Meisner, 2013). If productive non-crop habitats dry down early in the season, when cotton plants are young and vulnerable, then we might expect *Lygus* to move from non-crop habitat to cotton fields (Macfadyen et al., 2015), causing major economic damage. However, if non-crop habitats dry down after cotton plants have exited their window of vulnerability, then any migrating *L. hesperus* may generate less damage.

Here, we combine a large observational database of *L. hesperus* in California cotton fields with land cover and other vegetation-related satellite data to assess whether satellite Earth observations can both improve our understanding of *Lygus* pest ecology and facilitate more predictive modeling. We test four hypotheses:

- 1) more surrounding non-crop habitat increases *L. hesperus* spillover into cotton in the early season;
- 2) pest spillover from non-crop habitat into cotton during the early season is maximized when non-crop habitat dries down earlier in the year (i.e., dormancy is reached closer to when cotton is vulnerable to pest damage);
- 3) greater non-crop productivity during the growing season bolsters *L. hesperus* populations, resulting in higher densities in cotton;

- 4) integrating satellite observations of phenology (dormancy) and productivity (Enhanced Vegetation Index area) into pest abundance models better predicts spatiotemporal variation in *L. hesperus* densities compared to categorical land cover information alone.

2. Methods

2.1. *Lygus hesperus* field data and study region

The Central Valley of California represents a nearly contiguous landscape of crop habitat bordered on both sides by foothills dominated by non-crop habitat (Fig. 1). In the Mediterranean climate of California, *L. hesperus* overwinters in natural non-crop habitats and also in crops other than cotton. By state regulation, cotton must be plowed down by December 20 of each year, creating a cotton-host free-period. Between 6 and 8 generations of *L. hesperus* likely occur per year in Central California; though some aspects of overwintering are poorly understood, adults can survive extended host free periods with no subsequent deleterious effects on fecundity (Cooper and Spurgeon, 2015). Dispersal of winged adult *L. hesperus* might be triggered when natural areas begin to dry down and enter dormancy in late spring and/or after preferred host crops are harvested nearby (Goodell, 1988; Goodell and Ribeiro, 2006; Meisner and Rosenheim, 2014; Barlow et al., 2015).

We assembled a large dataset of *L. hesperus* densities in commercial cotton fields in California's Central Valley from pest control advisors between 1997 and 2008 (Fig. 1). Observational datasets like these can be powerful tools to understand variation in pest abundance and

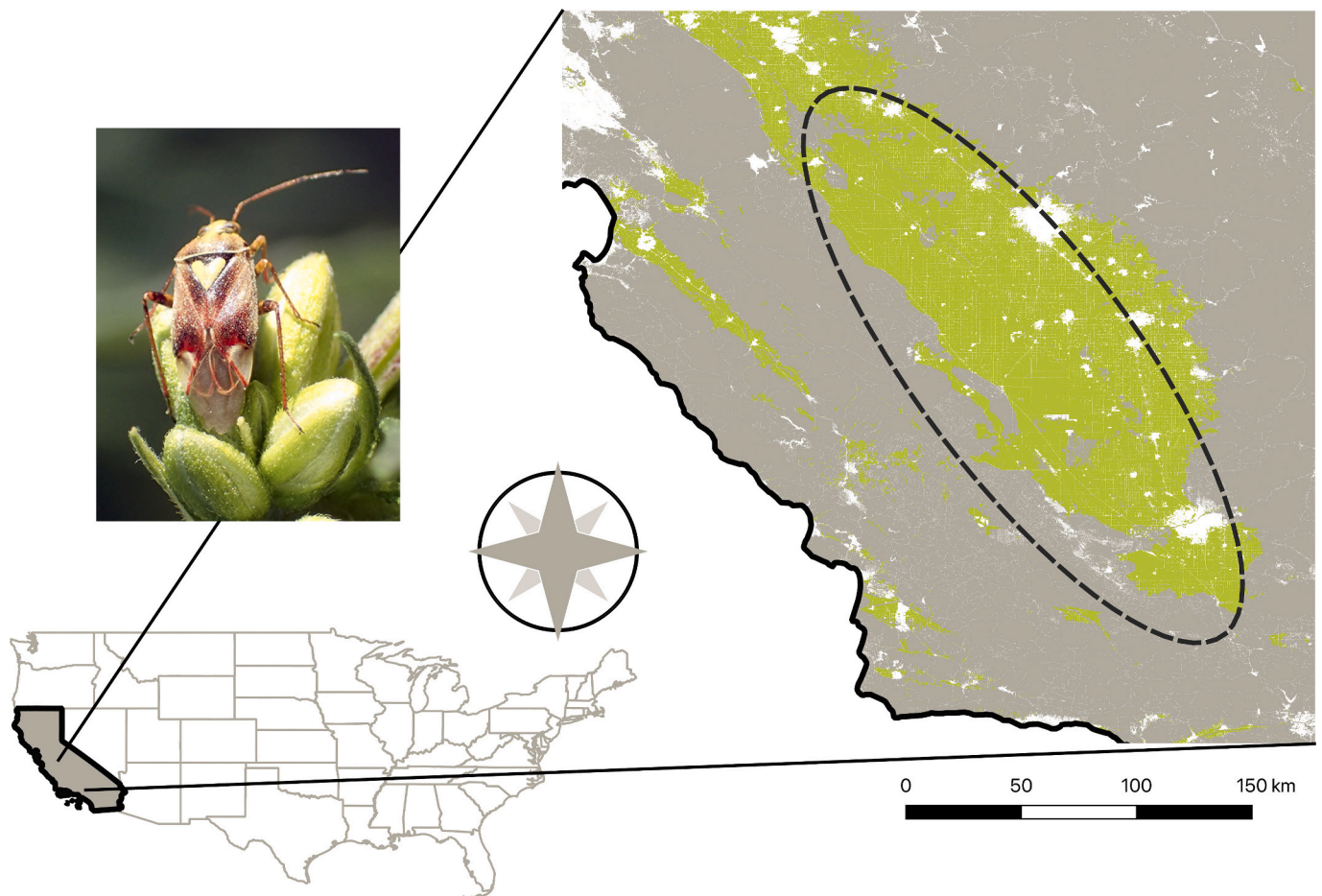


Fig. 1. Study region shown as an inset map in California. Inset map shows California's Central Valley with a dotted ellipse showing the latitudinal gradient along which early season field-replicate *L. hesperus* densities were assessed between 1997 and 2008 ($N = 1487$ field years). Green, grey, and white indicate crop areas, non-crop vegetated areas, and developed areas, respectively. Photo credit for *L. hesperus* adult: Whitney Crenshaw.

population patterns across the landscape and over time that smaller datasets would be unlikely to capture (De Valpine and Rosenheim, 2008; Martín-Vertedor et al., 2010; Emery and Mills, 2019; Paredes et al., 2021; Emery et al., 2023). This “ecoinformatics” approach, capitalizing on data gathered by professional pest consultants, pest control advisors and growers, allows us to build larger datasets that compensate for any reduction in measurement precision (Rosenheim, 2021). Our cotton dataset encompassed 1487 field-year replicates of *L. hesperus* observations across 565 conventionally-managed irrigated cotton fields located within 18 ranches (i.e., fields managed by the same organization or grower that may or may not be spatially contiguous). The study site network spanned ~280 km of California’s Central Valley, with fields in different ranches separated by an average of 100 km (Interquartile range 31 km). Cotton was usually planted in April ($N = 630/872$ for which planting date was known). Pesticides were regularly applied to target *L. hesperus*, most often at peak trap capture (July) and not in the early season studied here (see below). Latitude, longitude, year, and the ranch name were available for all fields. *Lygus hesperus* densities were sampled in *Gossypium hirsutum* (“upland cotton”) and *Gossypium barbadense* (“Pima cotton”) (Rosenheim and Meisner, 2013).

Although pest data were collected throughout the growing season, we focus on early season pest abundances as they had been reported to have the greatest negative effect on yield. Indeed, mean *L. hesperus* densities collected between mid-May through the end of June exhibited a strong negative relationship with cotton yield, such that if only 0.1 *L. hesperus* are found in 50 sweeps of early-season cotton, then the yield is expected to be 2068 kg/ha, while if 7.4 *L. hesperus* are found then the yield is expected to be 1274 kg/ha (Fig. 2). Pest densities were calculated from aggregating 50 swings of a sweep net across the top of the plant canopy. Usually 6–12 sweep samples were taken for a given field on a given date. Pests were typically surveyed 3–8 times during this early season period (range 1–13) and reflect all motile stages combined. Linear interpolation was used to transform successive samples into mean density estimates by calculating the area under the curve of *L. hesperus* density by time and dividing by the number of days between sampling intervals (Rosenheim and Meisner, 2013). Cotton lint yield was measured and reported once per field-year in bales/acre, which was

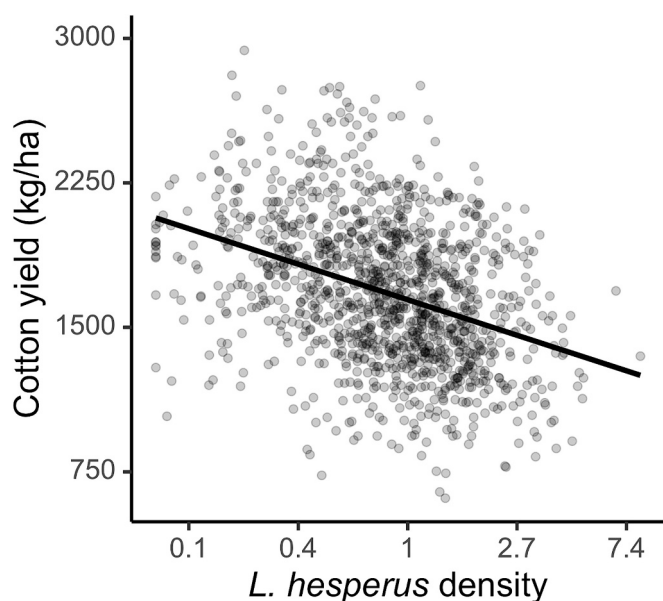


Fig. 2. Relationship between early season (May and June) mean *L. hesperus* densities (number per 50 sweeps) and cotton lint yield (kg/ha). Linear regression suggests a significant negative effect of *L. hesperus* on cotton yields ($R^2 = 0.14$, $F_{1,1233} = 197.4$, $P < 0.001$, $n = 1235$ replicate field-years between 1997 and 2008 for which yield data were available). *L. hesperus* density is plotted on a natural log scale such that $y = -184.5 * \ln(L. hesperus \text{ density}) + 1643.3$.

converted to kilograms/ha for this analysis. Yield data were available for 1235 of the 1487 field-year replicates.

2.2. Land cover, precipitation and remote sensing data

The fractions of crop and non-crop habitat around each focal field were extracted from the National Land Cover Database (NLCD) (Dewitz and Geological Survey, 2021) by quantifying the fraction of 30m² pixels in each of the two cover classes within three buffer radii around each pest sampling site (see below). Since NLCD data were not available each year, data were matched with the closest year for which data were available (crop years 1997–2002: NLCD 2001, 2003–2005: NLCD 2004, 2006–2007: NLCD 2006, 2008: NLCD 2008). Crop area was defined as either pasture/hay or cultivated crops (NLCD classes 81 and 82). Non-crop vegetation was defined as grasslands (71), shrub/scrub (52), forests (41, 42, 43), or wetlands (90, 95). The composition of vegetation in the non-crop habitat surrounding cotton fields varied latitudinally across our study region (Fig. S1). Moreover, the fraction of surrounding non-crop habitat varied not only between ranches, but also within them (Fig. S2).

Next, we extracted satellite-based climate and vegetation variables within the non-crop habitat. For precipitation in the non-crop habitat, we averaged the total annual precipitation reported from Daymet across all 1 km pixels within both the non-crop habitat and relevant buffer radius. Daymet data estimate near-surface meteorological conditions where no instrumentation exists using statistically interpolated weather variables (Thornton et al., 2020). For information on vegetation productivity throughout the growing season (Enhanced Vegetation Index [EVI] area) and vegetation phenology (dormancy day of year), we acquired MODIS satellite products (MCD12Q2, Version 6) using the Land Cover Type 2 band (Friedl and Sulla-Menashe, 2019). MODIS data are available at a 500 m resolution from 2001 to 2019; therefore, earlier pest density data (1997–2000) were not analyzed. EVI area reflects the sum of daily estimates of EVI amplitude between green-up and dormancy. The days on which green-up and dormancy are reached was estimated as the days of the year that the EVI amplitude first (green-up) and last (dormancy) crossed 15 % of the maximum EVI amplitude (Fig. 3). For both EVI area and dormancy of vegetation, values were averaged across all 500 m pixels within the non-crop habitat and the relevant buffer radius. To account for the seasonal nature of precipitation in the California Mediterranean climate, both metrics of productivity (precipitation in non-crop habitat, and EVI area), and phenology (day of year on which dormancy was reached in the non-crop habitat) were estimated using a start date of September 1 in the previous year (i.e., the beginning of the rainy season; see Fig. S3 for a visual depiction of the non-crop vegetation, crop, and pest phenology in this system).

All landscape, precipitation, and satellite observation data were extracted at multiple spatial scales (10 km, 20 km, and 30 km). These relatively large scales were chosen to ensure that the non-crop habitat within the adjacent California foothills was included in analyses (see Fig. 1), allowing us to test hypotheses regarding long-distance spatial movements of *L. hesperus* from the foothills to valley agriculture. Indeed, *Lygus* show evidence for both long distance movements (Maccreeary, 1965; Fleischer et al., 1988; Sivakoff et al., 2012), supporting the hypothesis that they move from the natural foothill habitats that abut California’s Central Valley growing region, as well as shorter distance movements to crop fields from small remnant non-crop habitats nearby (Bancroft, 2005).

To ensure that landscape productivity (precipitation and EVI area) and phenology (dormancy) were accurately estimated in non-crop habitats, we filtered the dataset to include only sites with at least 10 % surrounding non-crop habitat at each radius, and for which MODIS pixels were available for at least 25 % of that coverage (see Supplementary methods 1.1, Fig. S4). Filtering steps reduced the sample size from 1487 (full data set) to 1163 field-year replicates used for model comparisons at the 30 km scale. Substantial variation remained among

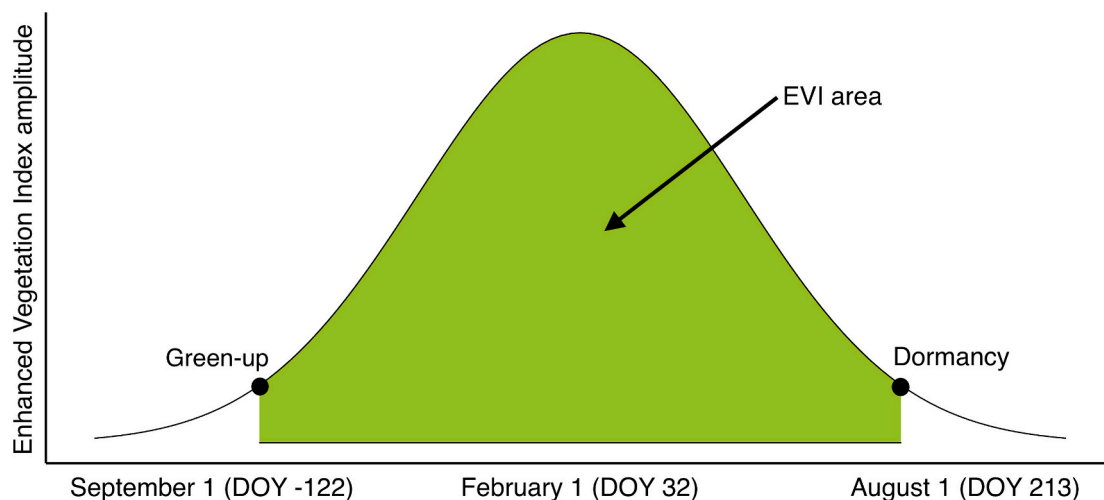


Fig. 3. A conceptual figure showing how green-up, dormancy and Enhanced Vegetation Index (EVI) area are calculated from MODIS satellite observations. Green-up is defined as the day of the year (DOY) that EVI amplitude first crosses 15 % of the maximum EVI amplitude. Dormancy is similarly defined as the day of the year that the EVI amplitude last crosses 15 % of the maximum EVI amplitude. Since California has a Mediterranean climate, phenological variables are calculated from the beginning of the rainy season, identified here as September 1 (or – 122 days relative to January 1). EVI area is the sum of the daily interpolated EVI amplitude values from green-up to dormancy.

field-year replicates across all the variables of interest (Fig. S5). For the 20 km and 10 km analyses, 1016 and 502 field-year replicates remained after filtering, respectively.

2.3. Statistical analysis

We implemented generalized additive models (GAMs) to assess landscape effects on *L. hesperus* densities because they flexibly estimate nonlinear relationships. All analyses were completed in R version 4.3.0 (R Core Team, 2023). Generalized additive models were developed using the mgcv package version 1.8–42 and plotted with the gratia package (Wood, 2023, 2024). Since *L. hesperus* densities were continuous and positively skewed with many 0 values, models were implemented with a Tweedie distribution (power variance = 1.6) and log link to fit model assumptions. Models fit with a Tweedie distribution exhibited better fit than did models using log transformed densities and a Gaussian distribution, consistent with other findings (Xue et al., 2018; Lawton et al., 2022). In all models, we included year as a random effect and ranch identity as a fixed effect to account for variation in management practices (pesticide use, fertilization regimes, etc.) and multiple fields located in the same ranch.

First, to assess the hypothesis that vegetation in non-crop habitat bolsters *L. hesperus* densities in cotton fields, we built a model including an interactive spline for latitude and non-crop habitat within 30 km of a focal cotton field. Latitude and non-crop habitat were allowed to interact because the composition of non-crop habitat varied latitudinally (Fig. S1), meaning important host plants may be more abundant in non-crop habitat at some latitudes than at others. This model was applied to both the full data set (1997–2008; $N = 1487$ field-years) and the filtered dataset used for remote sensing analyses (2001–2008; $N = 1163$ field-years; see supplementary methods 1.1). Next, to evaluate the effects of non-crop habitat phenology, we built a second model that included not only the interactive effect of latitude and non-crop habitat but also the dormancy date (phenology) associated with the vegetation in the surrounding non-crop habitat. Finally, we built models with the interactive effect of latitude and non-crop habitat, phenology, and either of the two metrics of productivity; specifically, the total seasonal precipitation in the non-crop habitat as a proxy for productivity (Daymet) or the direct measure of productivity of vegetation in the non-crop habitat (EVI area; MODIS). These two metrics were highly correlated and could not be included in the same model (Fig. S6). All models were compared using

likelihood ratio tests and AIC (see Supplementary methods 1.2). To evaluate consistency across spatial scales, we repeated this process using 20 km and 10 km radius buffers around sampling sites.

Despite including a latitudinal spline and a fixed effect of ranch, all models exhibited evidence of residual spatial auto-correlation (P -values associated with Moran's $I < 0.01$; Tables S1, S2). To evaluate whether results were robust to spatial autocorrelation, models were refitted with a spatial spline (Tables S1, S3). Doing so demonstrated a tradeoff between spatial autocorrelation and concavity (Tables S1, S2, S3). Because high levels of concavity (> 0.5), the equivalent of collinearity in a GAM-based framework, can cause variance inflation and unstable predictions (Ramsay et al., 2003; Salazar et al., 2021), and results were robust to addressing spatial auto-correlation (see Results), we proceeded with models that did not include spatial splines.

Finally, to evaluate predictive capacity (hypothesis 4), we compared two models. The first model only included latitude interacting with the proportion of non-crop habitat within 30 km, but no ranch or satellite covariates. The second model included latitude interacting with the proportion of non-crop habitat within 30 km, as well as dormancy (phenology) and EVI area (productivity) of the vegetation in the non-crop habitat. Year and ranch covariates were excluded from these models because we were interested in assessing the predictive capacity of land cover and satellite observation information in contexts for which additional covariates might not be available. For each model, we implemented a cross validation procedure 1000 times, training models from a randomly selected 70 % of the field-year replicates ($N = 814$) and then testing them against the remaining 30 % ($N = 349$ field-year replicates). Specifically, parameters estimated in each training model were used to predict early-season *L. hesperus* densities in the corresponding validation dataset. The Root Mean Square Error (RMSE) between the predictions and the true observations in the validation dataset (i.e., the spread of the residuals around 0) was calculated using the Metrics package (Hamner and Frasco, 2017). RMSE is reported in the same units of measurement as the response variable and is scale-dependent, with smaller values reflecting lower error and thus better prediction ability.

Finally, we implemented two additional analyses to evaluate prediction performance and robustness. First, we tested whether models could predict *L. hesperus* densities in novel time periods by using data from either 2001–2003 or 2006–2008 as validation data (and training the models on data from the other years). Second, we tested whether models could predict *L. hesperus* densities in novel spatial contexts by

holding back data at five groupings along the latitudinal gradient as validation data. In both cases, models were sometimes subsequently tested with parameter values absent in the training data (Fig. S5). For example, holding back years 2006–2008 resulted in the model occasionally being forced to predict at extreme dormancy dates not present in the training model dataset.

3. Results

For the full data set ($N = 1487$), we found that the higher proportions of surrounding non-crop habitat are strongly correlated with higher early-season *L. hesperus* densities, but only in fields located at the northern end of the Central Valley. In fact, the opposite trend was found in the south (Fig. S7). In the reduced and filtered dataset ($N = 1163$), there was also a strong interaction between the proportion of non-crop habitat and latitude (Figs. 4A, S8A; Table S2; $P = 0.003$).

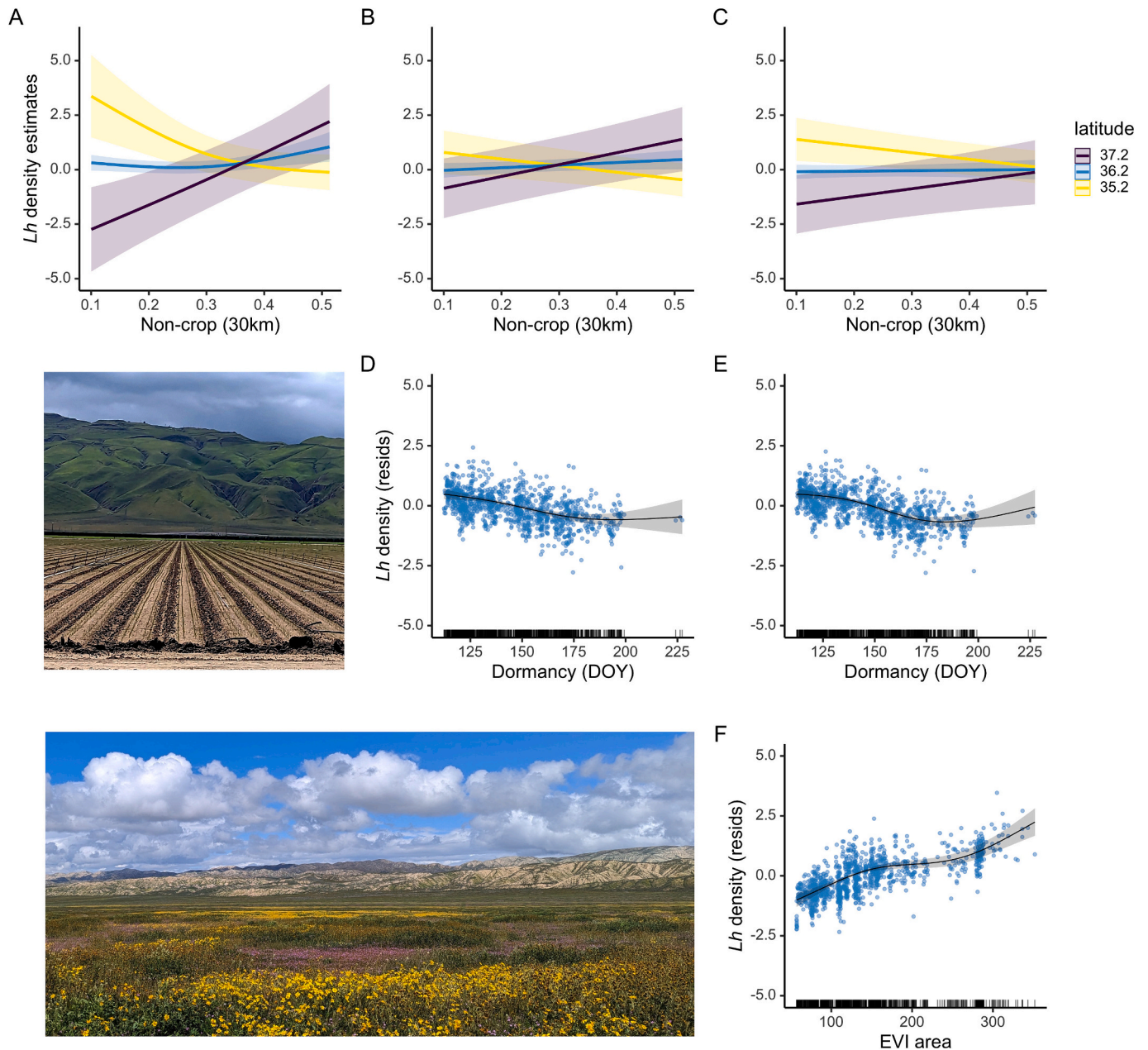


Fig. 4. Estimated smooths (A, B C) and partial effect plots with 95 % confidence intervals and rug plots along the x-axis (D, E, F) from GAMs assessing the relationship between *L. hesperus* density residuals and landscape variables in cotton fields ($N = 1163$, see Methods). Columns correspond to three models of increasing complexity (Panel A: just latitude interacting with non-crop habitat; Panels B/D: latitude interacting with non-crop habitat as well as dormancy; Panels C/E/F: latitude interacting with non-crop habitat, dormancy, and productivity). Models showed that pest densities increased with higher surrounding natural area in the north, but the opposite trend was observed at more southerly sites (Panel A; edf = 4.5, $P < 0.001$, Panel B; edf = 3, $P < 0.001$ and Panel C; edf = 3, $P < 0.001$). Models including the day of year (DOY) on which dormancy was reached for vegetation in the non-crop habitat (Panels D and E; edf = 4, $P < 0.001$) showed a negative relationship between later dormancy and *L. hesperus* densities in early season cotton. Finally, the model with all variables additionally indicated that non-crop vegetation productivity was positively related with higher *L. hesperus* densities in early season cotton (Panel F; edf = 4, $P < 0.001$). The two images show California Central Valley agricultural habitat bordered by foothills to the west (middle, left) and non-crop grassland within adjacent foothill habitats (bottom left). Photo credits: Daniel Karp.

Aligning with our second hypothesis, early vegetative dormancy within the non-crop habitat resulted in greater early-season *L. hesperus* densities in cotton fields ($P = 0.0001$, Fig. 4D). In line with our third hypothesis, both metrics of non-crop productivity (precipitation and EVI area; Fig. 4F) correlated positively with early season *L. hesperus* densities in cotton ($P < 0.001$). Likelihood ratio tests suggested including either productivity metric (i.e., precipitation or EVI area) explained more variation in *L. hesperus* densities relative to the models with only non-crop habitat and dormancy. The model including precipitation, however, had unacceptably high concurvity, limiting confident interpretation of results (Table S2). Including a spatial spline eliminated spatial autocorrelation and yielded very similar effects of remote-sensing variables on pest densities (Fig. S9), but resulted in high levels of concurvity and unstable effects of non-crop habitat (Table S3).

The effect sizes associated with the interactive effect of proportion non-crop habitat and latitude, non-crop vegetation dormancy, and non-crop vegetation productivity in the multivariate model were substantial. The model predicted that *L. hesperus* densities increased over 4-fold at northern latitudes when fields were surrounded by 10 % versus 50 % non-crop habitat within 30 km. In the south, over the same range of non-crop habitat, pest densities decreased 3.5 fold. Models predicted that fields would have 2.8 times higher *Lygus* densities (1.4 versus 0.5 *Lygus* per 50 sweeps) if dormancy was reached early in the cotton susceptibility period, on May 15 (day 135) versus June 30 (day 181). Finally, models predicted that fields surrounded by low, moderate, and high productivity natural habitat (EVI areas of 50, 200, and 350) would host 0.3, 1.7, and 10.9 *L. hesperus* per 50 sweeps, representing a 35-fold increase from the least to most productive habitats.

Results were broadly consistent across spatial scales. At 20 km and 10 km, integrating phenology and productivity metrics with land classification data resulted in better models than those with land classification data alone (Figs. S10 and S11, Tables S4 and S5). However, coverage of non-crop habitat across latitudes was markedly lower, especially at 10 km, reducing confidence in extrapolated smooths (Figs. S8E, S11A).

Partially aligning with our fourth hypothesis, integrating satellite observations of non-crop vegetation phenology (dormancy) and productivity (EVI area) at 30 km improved our ability to predict spatiotemporal variation in early-season *L. hesperus* densities over a model with the proportion of non-crop habitat interacting with latitude alone, but only marginally (Figs. S12A and S12B). Indeed, cross validation indicated that models with non-crop habitat interacting with latitude, dormancy, and productivity (EVI area) offered significantly higher predictive capacity when applied to the novel validation data set (mean RMSE of 0.69) compared to models that included non-crop habitat interacting with latitude alone (mean RMSE of 0.72; difference of +0.03 RMSE between models; $P = 0.03$; Fig. S12). Unlike the cross validation exercise, however, adding phenology and productivity variables (dormancy and EVI area) to the model with a proportion non-crop habitat and latitude spline did not consistently improve predictive performance across novel time periods (a subset of years held back and used for model validation) or in novel regions (fields located in one of five regions along the latitudinal gradient iteratively held back and used for model validation) (Table S6).

4. Discussion

Only partially aligning with our first hypothesis, we detected a strong and significant interaction between latitude and the proportion of non-crop habitat on the density of *L. hesperus* in early season cotton, with non-crop habitat benefiting *Lygus* in the north but not in the south. However, we did show support for our second and third hypotheses that the phenology and productivity of the non-crop habitat affect *L. hesperus* densities in cotton fields. Specifically, earlier dry down of the non-crop habitat was associated with higher *L. hesperus* densities in the early-season period of cotton vulnerability. We also found that more

productive non-crop habitat was associated with greater *L. hesperus* densities in early season cotton. Finally, our analyses suggest that integrating satellite observations of phenology (dormancy) and productivity (EVI area) into pest abundance models better explains spatiotemporal variation in *L. hesperus* densities and results in greater predictive accuracy within the time and spatial ranges used for estimation compared to traditional approaches relying solely on broad land cover classifications. However, the increase in predictive accuracy was marginal for cross-validation and absent when predicting in novel time periods or spatial contexts.

4.1. Landscape ecology of *Lygus hesperus*

Lygus hesperus densities were higher in landscapes with more non-crop habitat and lower in simplified agricultural landscapes at the northern, but not the southern end, of the California Central Valley. This trend bucks conventional wisdom and the original interpretation of Root's resource concentration hypothesis which predicted that more complex landscapes should host lower pest abundances (Root, 1973). Nonetheless, we had predicted higher pest abundances would exist in more complex landscapes given the ecology of *L. hesperus* as a native, mobile, and generalist herbivore (Tamburini et al., 2020). Indeed, *L. hesperus* is native to the patchy and temporally dynamic ecosystems of the western United States, and was likely pre-adapted to disperse and thrive across multiple habitat types (Skoracka et al., 2022). Exactly why *L. hesperus* seemingly benefitted from non-crop habitat in the north, but not the south, is unclear, but could reflect latitudinal differences in plant communities (Fig. S1). If key non-crop host plants are only abundant in the north, then this may explain why surrounding non-crop habitat did not elicit higher on-field *L. hesperus* densities in the south.

Because other host plants are preferred to cotton, it was alternatively possible that vegetation in the non-crop habitat could act as a trap crop, drawing *L. hesperus* out of cotton fields (Balzan and Moonen, 2014). However, the typical phenological patterns of non-crop vegetation in a Mediterranean climate, coupled with the timing of when cotton is young and vulnerable, make this scenario less likely. Specifically, when non-crop vegetation senesces and enters dormancy earlier in the year, *L. hesperus* may be forced to disperse out of non-crop natural habitats and into more productive, irrigated agriculture. For fields surrounded by non-crop habitat in which the vegetation enters dormancy especially late, this poses less of a problem, since the period of cotton crop vulnerability would have passed.

Another consideration regarding landscape effects on pests is the response of their natural enemies, which are often assumed to benefit from complex, heterogeneous landscapes (Bianchi et al., 2006; Gardiner et al., 2009). Most of the predators of *L. hesperus* in California are also generalists, predominantly *Orius tristicolor* and *Geocoris* spp. (Zink and Rosenheim, 2008; Hagler et al., 2018), making it hard to predict their responses to heterogeneous landscapes. Generalist predator responses to the landscape also depend on diet breadth, habitat preference, and relative mobility (Caballero-López et al., 2012; Tamburini et al., 2020). In this case, it appears that, even if natural enemies benefit from landscapes with more non-crop habitat in the northern Central Valley, increased top-down regulation in more complex landscapes does not override the resource benefits of such landscapes for *L. hesperus*.

Finally, it is worth noting that the large spatial scale of this analysis stands in contrast to much of the agroecology literature, which often focuses on characterizing landscapes at a 1–3 km scale (Karp et al., 2018; Martin et al., 2019, but see Thies et al., 2003). That said, prior work suggests that landscapes may influence generalist pests, like *L. hesperus*, at significantly larger scales than specialist pests or natural enemies (Bennett, 1971; Tschardt et al., 2005; Chaplin-Kramer et al., 2011). There is evidence that *Lygus* spp. in particular may disperse great distances and thus interact with landscapes at large spatial scales (Maccreeary, 1965; Fleischer et al., 1988; Sivakoff et al., 2012). Moreover, *L. hesperus* has been found flying in the evening and early morning

between 1 and 3 m off the ground (Butler, 1972), making it more likely that the Diablo and Santa Ana winds (i.e., prevailing hot, dry winds blowing through the foothills and mountains from the East to West across California) could be significant dispersal forces (Reynolds et al., 2013). These observations in addition to the strength of our findings at the 30 km scale lend credence to the idea that herbivorous insects may be interacting with the landscapes at much larger scales than previously tested.

4.2. Limitations

Our current application of satellite Earth observations is not without limitations. First, MODIS productivity and phenology variables only became available beginning in 2001, meaning we were unable to make use of earlier data. Moreover, because MODIS variables are reported at a 500 m scale, vegetated field margins and riparian habitats at smaller scales within the agriculture-dominated valley floor could not be identified, let alone monitored for productivity and phenology. Nonetheless, such habitats can influence *Lygus* abundances in crop fields (Goodell, 1988; Mueller et al., 2005). Further, though *L. hesperus* are generalists, they do not make use of all vegetation resources in non-crop habitat equally. Current tools cannot yet be used to identify spatiotemporal trends in productivity of specific host plant species. These limitations may partially explain why integrating satellite observations into our models only marginally improved our ability to predict *L. hesperus* abundances within the study system and not at all in novel contexts (i.e., different regions and different years). Predicting pest abundance in novel landscapes may require finer-grained data on spatiotemporal patterns in host plant productivity and plant functional group.

4.3. The future of integrating satellite observations into landscape pest modeling

Landscape ecology has evolved rapidly as a discipline over the last 40 years (Wu, 2017). The field was initially dominated by island biogeography theory and the idea that organisms interact with their environment in a simple patch/non-patch framework (MacArthur and Wilson, 1967; Strong et al., 1984). With time, the field moved towards an understanding that many mobile organisms utilize multiple habitats across the landscape (Ricketts et al., 2001; Perfecto and Vandermeer, 2002). Indeed, landscape management plans have been developed in the California Central Valley, based on this understanding, for a similarly broad herbivorous generalist, the beet leafhopper, *Circulifer tenellus* (Davis et al., 1998; California Department of Food and Agriculture, 2019). With the knowledge of organism movement across habitats came a need to quantify and categorize land cover types based on the degree to which they could provide resources for the organism of interest (Fahrig et al., 2011). This knowledge, coupled with the emergence of publicly available landcover databases, represented a huge step forward in our ability to understand resource availability on the landscape scale. Nonetheless, land cover maps still often require laborious ground-truthing and regularly classify landscapes into categories that are too broad to adequately characterize organisms' habitat and/or resource needs (Foody and Boyd, 1999; Shalaby and Tateishi, 2007).

Satellite-based remote-sensing is now being used to develop highly derived products that describe the environment more accurately and over smaller time scales than ever before, thus providing time-bounded estimates of habitat productivity and phenology. This rich source of information is proving extremely useful for modeling species distributions and abundances across heterogeneous landscapes (Pettorelli et al., 2014; Anderson, 2018). For pests, satellite products beyond land cover have been underutilized (Cord et al., 2017; Pettorelli et al., 2018). In this case study satellite products provided great insights into the ecology of *L. hesperus* populations in agricultural landscapes, but failed to deliver large increases in our ability to predict *L. hesperus* population densities across space and time.

Looking forward, metrics on the productivity and phenology of specific host plant species within non-crop habitats may be needed to truly quantify resource concentration and accurately predict pest population dynamics. Such information may soon be within reach. Hyperspectral data has been used to generate much more granular information, from mapping grass and forb species across a prairie (Pau and Dee, 2016) to providing early warning systems for pest and disease outbreaks (Nansen et al., 2021; Sapes et al., 2022). But satellite data need to be easily accessible and further integrated with ecological data sets by end users to realize their full potential for informing management decisions (Cavender-Bares et al., 2022). Hyperspectral data will likely soon be available on a global scale, allowing exploration of community composition measurements to assess availability of preferred plant hosts, more taxon-specific estimates of plant productivity and phenology, and an array of diversity metrics to test relationships between niche breadth and diversity at different scales (Dronova and Taddeo, 2022). In the meantime, advances in mapping crop composition, health, and yields from satellite data (Burke et al., 2021; Tommaso et al., 2021; Wang et al., 2023) could be utilized to explore what features in the agricultural system best predict pest distributions, which have until now been similarly limited to broad categories of "crop" or occasionally the crop mosaic (Sivakoff et al., 2013; Vasseur et al., 2013; Meisner et al., 2017). Since the majority of pest species are generalists, understanding how the location and extent of other crops (and non-crop host species in natural habitats) supports their populations and what functional attributes contribute to outbreaks could provide a major leap forward for integrated pest management.

4.4. Conclusions

Despite centuries of pest management, current warming trends have been hypothesized to promote increased pest population growth, crop consumption rates, and range expansion in temperate regions, ultimately decreasing potential crop yields. To test these hypotheses long term monitoring is needed on a broad scale. There is an opportunity, using an ecoinformatics approach, to utilize existing datasets collected by pest control advisors to monitor future changes in pest populations. These data provide an important source of replicated surveys over time and space and are often available decades into the past. Because they are collected to help growers make within-year management decisions, they suffer from fewer of the continuity issues that plague field-work from non-commercial monitoring efforts. Our work demonstrates that combining these broad, replicated data sets with satellite-based Earth observations creates unique opportunities to better understand the ecology of agricultural pests and, with the future advances in remote sensing technology, potentially develops new pathways for predicting pest outbreaks across agricultural landscapes.

CRedit authorship contribution statement

Sara E. Emery: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Jay A. Rosenheim:** Writing – review & editing, Supervision, Resources, Methodology, Data curation. **Rebecca Chaplin-Kramer:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition. **Richard Sharp:** Writing – review & editing, Software, Resources, Methodology, Data curation. **Daniel S. Karp:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data (except latitude) and code used to run models available on DRYAD <https://doi.org/10.5061/dryad.r4gxd2mz>.

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Appendix A. Supplementary data

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