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The causes and consequences of pest population variability in agricultural landscapes

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Abstract

Variability in population densities is key to the ecology of natural systems but also has great implications for agriculture. Farmers' decisions are heavily influenced by their risk aversion to pest outbreaks that result in major yield losses. However, the need for long-term pest population data across many farms has prevented researchers from exploring the drivers and implications of pest population variability (PV). Here, we demonstrate the critical importance of PV for sustainable farming by analyzing 13 years of pest densities across >1300 Spanish olive groves and vineyards. Variable populations were more likely to cause major yield losses, but also occasionally created temporal windows when densities fell below insecticide spray thresholds. Importantly, environmental factors regulating pest variability were very distinct from factors regulating mean density, suggesting variability needs to be uniquely managed. Finally, we found diversifying landscapes may be a win–win situation for conservation and farmers, as diversified landscapes promote less abundant and less variable pest populations. Therefore, we encourage agricultural stakeholders to increase the complexity of the landscapes surrounding their farms through conserving/restoring natural habitat and/or diversifying crops.

KEYWORDS
agroecology, *Bactrocera oleae*, ecoinformatics, economic injury thresholds, landscape diversification, *Lobesia botrana*, *Prays oleae*, yield losses

INTRODUCTION

Variability is inherent to natural systems in which population densities of different species naturally vary over time. For decades, ecologists studying natural ecosystems have tried to understand what causes populations and ecological processes to fluctuate (Murdoch, 1975). Variability is also of paramount importance to agricultural systems. Interannual fluctuations in crop yields can have dire consequences for the many farmers who operate at narrow profit margins and for ensuring food security for a growing human population (Tilman et al., 2011). As such, there is increasing interest in understanding what destabilizes crop yields and how farms can be better managed to increase stability (Gaudin et al., 2015; Lin, 2011). For example, as in natural systems, increasing diversity in agroecosystems may help stabilize

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food production, from local to national scales (Gaudin et al., 2015; Renard & Tilman, 2019).

Mitigating pest population variability (PV) is of particular importance to ensuring stable food production (Lin, 2011), as pest outbreaks can provoke catastrophic crop losses (Savary et al., 2019). As such, many farmers are risk averse, with fear of rare but severe pest outbreaks driving their management decisions (Gong et al., 2016; Liu & Huang, 2013). If pest populations are thought to be variable, then farmers will often prophylactically spray excessive amounts of pesticides to avoid the potential of an outbreak resulting in major yield losses, which we define here as damage that renders the crop non-profitable (Zhang et al., 2018).

In other cases, farmers are more reactive, only applying insecticides when pests exceed predefined economic injury thresholds (i.e., integrated pest management) (Stern et al., 1959). Many crops can compensate fully for low levels of herbivory, with economic losses only occurring when pests reach outbreak densities and plants' compensatory abilities are overwhelmed (Trumble et al., 1993). In this case, the effect of pest PV on farmer decision-making may depend on the tolerance for crop damage. If tolerance is high relative to equilibrium pest densities, then maintaining stable pest populations is key to preventing economically and environmentally damaging insecticide applications (Bouchard et al., 2011; Köhler & Triebskorn, 2013). However, if economic thresholds are set low, as they are for many crops that cannot tolerate even minor cosmetic damage (Higley & Peterson, 2008), then equilibrium pest densities may exceed economic injury levels, causing even the most stable pest populations to elicit heavy insecticide use. Therefore, managing for PV in agricultural systems can be quite different than in natural ecosystems because the goal is to stabilize pest densities below economically damaging levels, rather than around a natural, equilibrium density (Murdoch, 1975; Watt, 1965).

Much of the work that has been conducted on PV of pests in agroecosystems has focused on characterizing interspecific differences in mean interannual variability in densities as well as the degree to which populations exhibit cycles or display density dependence (e.g., Hassel et al., 1976; Murdoch et al., 1995; Walter et al., 2018; Lamb et al., 2019). The need for long-term data collected across many sites has largely prevented researchers from exploring intraspecific, between-population differences in PV, how environmental and/or field-management factors modulate PV, and the consequences of pest PV for farmers. The few studies that have sought to study environmental controls on pest PV have been forced to use proxies for population densities (e.g., insecticide application rates) (Larsen & Noack, 2020) or trade space for time to assess variability indirectly (Rusch et al., 2013).

In contrast, much research has focused on identifying the field, landscape, and regional contexts that influence average pest abundances (Chaplin-Kramer et al., 2011; Karp et al., 2018; Landis et al., 2000). For example, it is often hypothesized that simplified landscapes of extensive crop monocultures may allow specialist pest populations to build rapidly and spread as they exploit vast food resources (i.e., the resource concentration hypothesis) (O'Rourke & Petersen, 2017; Root, 1973). Simplified landscapes may also lack key resources (e.g., food resources or overwintering sites) to support the natural enemies of crop pests, therefore releasing pest populations from top-down control (i.e., the natural enemy hypothesis) (Chaplin-Kramer et al., 2011; Landis et al., 2000). Therefore, diversifying farming landscapes, either through planting multiple crops or retaining non-crop vegetation, may lower pest densities and reduce insecticide applications (Dainese et al., 2019; Paredes et al., 2021; but please refer to Karp et al., 2018; Tscharntke et al., 2016). It remains unclear, however, whether the factors that shape mean pest densities are also the key factors that affect pest variability, and, if so, whether they have parallel effects on mean densities and variability of densities.

Here, we used 5–13 years of pest- and field-management surveys, collected across >1300 olive groves and vineyards in Spain (18,729 field-years in all for three pests; Figure 1), to investigate the interannual variability in pest population sizes of three economically important agricultural pests: olive fly (*Bactrocera oleae*), olive moth (*Prays oleae*), and European grapevine moth (*Lobesia botrana*). Through simulations and pest population statistical modeling, we aimed to answer four guiding questions. First, is it always advisable to reduce interannual pest PV, or can variability occasionally result in preferable outcomes for farmers? Second, in what contexts would interannual pest PV provoke insecticide applications or major crop losses? Third, do the same environmental factors promote elevated mean pest densities and variable pest populations? Finally, how can farming landscapes be managed to reduce interannual pest PV?

MATERIALS AND METHODS

Database

The Andalusian Government provided us with a large database containing pest and field-management data for 13 years (2006–2018) across Andalusia, Spain (Figure 1). This is an unusually rich data resource, as it contains detailed, long-term, and well replicated pest observations. Specifically, personnel within the RAIF network (Red de Información y Alerta Fitosanitaria) monitor

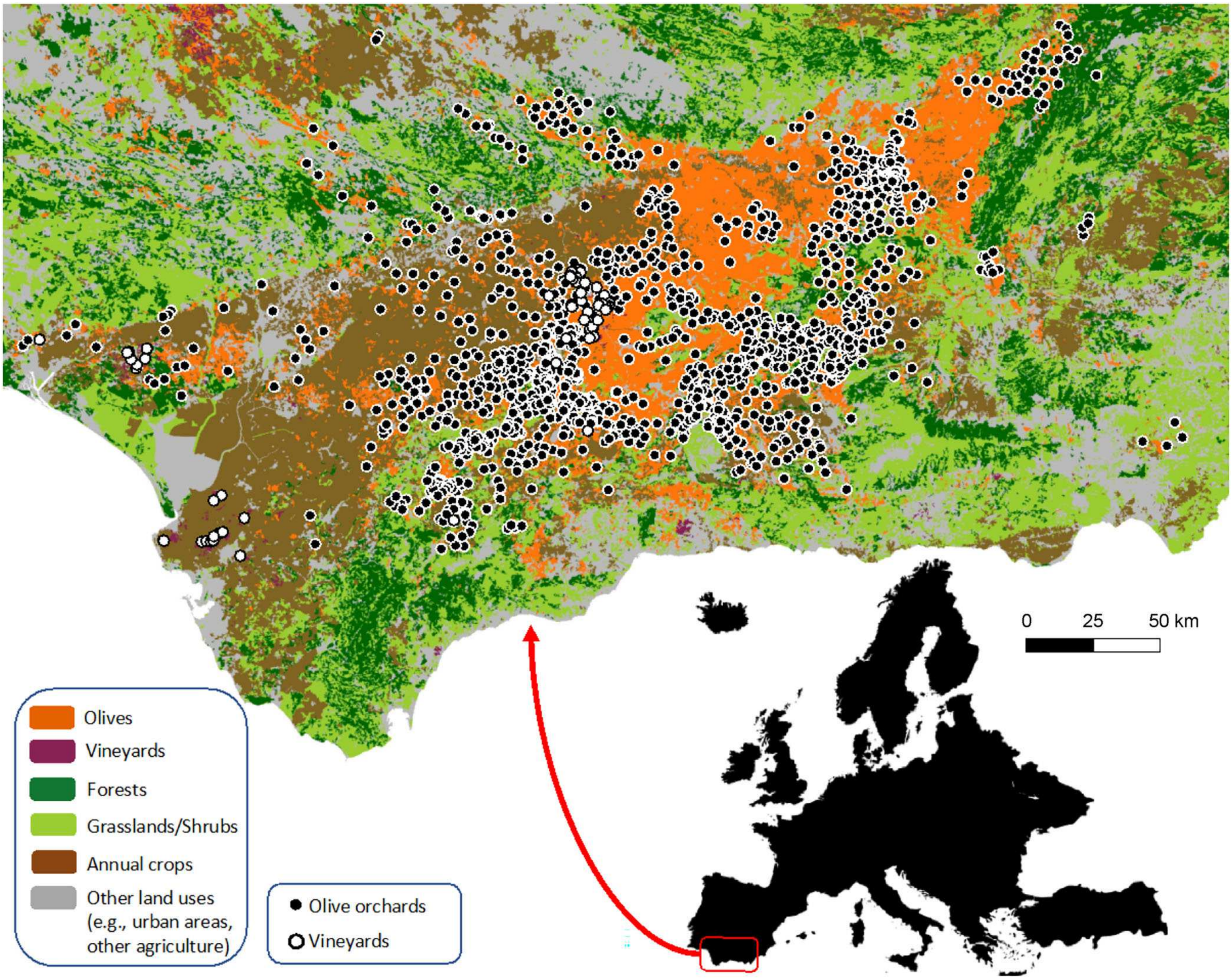

FIGURE 1 Study site map. Map depicts olive orchard and vineyard study sites in the Andalusia region of southern Spain. Inset shows study region location within Europe

pest populations on privately owned fields across the Andalusian region of Spain and advise farmers about when and how to manage pests based on economic injury thresholds and integrated pest-management rules. Farmers in the RAIF network are encouraged to use integrated management criteria, such that insecticides are only applied when pest populations exceed economic injury thresholds (as described below in the fifth paragraph of the next section). The RAIF database also records several pest-management practices, including applications of insecticides, herbicides, and fungicides, as well as tillage events. Finally, the database includes the identities of the crop cultivars, the cooperatives in which farmers are members, and the regions in which the fields are located.

We focus on the abundance of two key olive pests, the olive fly (*B. oleae*) and the olive moth (*P. oleae*), and one key vineyard pest, the European grapevine moth (*L. botrana*). The RAIF database contains information about pest abundance (i.e., the number of individuals captured in traps during a defined sampling interval) as well as other variables related to damage. Some of these metrics are used as proxies for future damage to inform decisions about insecticide applications (i.e., economic thresholds). Other variables directly measure damage to fruit at harvest but were available only for the olive fly and the grapevine moth (please refer to Appendix S1 for a detailed description pest abundance and damage metrics).

We supplemented the RAIF database with regional climate and topographic (elevation, slope, and aspect) data associated with each field. Topographic data were extracted from a Digital Elevation Model (IGN, 2019). We also gathered data from 79 weather stations located across the study region and extracted climate data from the station nearest to each field. Specifically, for each surveyed field-year, we averaged mean monthly temperature and precipitation from March to December for olive pests (the olive growing season) and from March to September for grape pests (the grape growing season). In addition, we compiled data on the landscape context surrounding each field from two sources. To measure landscape simplification, we delineated a buffer of 2000 m radius centered on the focal olive orchard (or grape vineyard) within which we calculated the proportion of land that was planted with olives (or grapes) using CORINE Land Cover inventory. We also calculated landscape productivity surrounding each focal field using the normalized difference vegetation index (NDVI). using Landsat imagery. We implemented a weighting procedure such that areas located closer to the focal field were more influential than those further away (please refer to Appendix S1 for a detailed description of landscape composition and productivity calculations).

Statistical modeling

Our basic unit of replication was the individual field (i.e., an olive grove or grape vineyard). Fields were usually visited on a weekly basis; however, data gaps within growing seasons were common. To ensure that variation in the timing of field visits did not bias population size estimates, we only included data from visits during periods of peak pest population sizes (olive fly: mid-August to mid-December; olive moth: mid-March to mid-August; grapevine moth: mid-March to late September). To produce accurate mean abundance estimates for each sampling year, we only included field-years for which ≥7 weekly visits occurred within these focal temporal windows. Finally, to robustly estimate interannual pest variability, we only analyzed fields for which ≥5 years of data were available. The average numbers of years surveyed per field for the olive fly, olive moth, and grapevine moth were 7.86 ± 2.59, 8.31 ± 2.55, and 7.91 ± 1.89 years, respectively. This resulted in a final data set of 1315 fields for the olive fly, 1184 for the olive moth, and 60 for the grapevine moth. Fields were separated by more than 5 km.

To measure interannual PV, we first averaged weekly pest density estimates across all visits to a given field, in a given year. Then, we calculated the standard deviation of the log-transformed annual mean pest densities (Watt, 1965). This measure of interannual pest variability was either uncorrelated or minimally correlated with the average pest densities across years (Appendix S1: Figure S1). We also explored other metrics such as the standard deviation of annual pest densities, the coefficient of variation (CV), and the PV metric proposed by Heath (2006). However, the high number of zeros in our data set disproportionately influenced these metrics, especially when pest densities were low, eliciting very strong mean–variance relationships (Appendix S1: Figure S1). Therefore, we calculated log (mean density + 1.0) for the more abundant pests (density range for olive fly: 0–58.8 per trap per day; and olive moth: 0–572.4 per trap per day) and log (mean density + 0.01) for the much less abundant grapevine moth (density range 0–14.5 per trap per day).

Our variability measure does not differentiate between populations that have been completely extirpated from a field versus those that are present but with unchanging density over time. However, it was unusual for pests to be completely absent from a field over an entire year (i.e., 0.31% of field-years for the olive fly, 0.08% for the olive moth, and 10.74% for the grapevine moth). Importantly, we chose not to detrend variability measures, as systematic pest population increases (or decreases) would be important to farmers as key sources of population density variability.

We first explored how mean pest abundances and PV affect the likelihood of pests exceeding hypothetical pest tolerance thresholds. To do so, we simulated variation in farmers' pest tolerance levels by setting multiple hypothetical thresholds based on the abundance of each of our three focal pests. Although simulations were solely based on pest abundances, real tolerance thresholds for our focal pests are defined using fruit infestation measures (except olive fly, which includes both infestation and abundance measures). We then calculated the fraction of years during which observed pest densities exceeded the hypothetical thresholds on each field. In each case, we generated generalized linear mixed models (glmm) examining the likelihood that different pest density thresholds would be exceeded. Hypothetical thresholds were established by calculating the 1st, 25th, 50th, 75th, and 99th percentiles of mean abundance of each pest. Based on these thresholds, we then calculated response variables in two ways. First, for each field, we recorded the number of years that the threshold was exceeded at least once versus the number of years that the threshold was never exceeded, to create a proportion of counts binomial variable. Second, for each field, we recorded the total number of weekly observations that the threshold was exceeded out of the total number of weekly observations made across all years as a second binomial variable. We report the results for the first response variable in the main text, as we consider it to be the more conservative measure; however, results using the second measure were very similar Appendix (S1: Figure S2).

Next, we related pest PV to real-world outcomes of direct importance to farmers (e.g., major losses of either harvest quantity or quality) using similar GLMMs. Specifically, we used established thresholds for economic injury (when the cost of control is less than the value of the prevented crop injury) for harvested fruit quality and for major yield losses as established by the Andalusian Government's rules for integrated pest management (BOJA, 2005, 2010). As for the hypothetical thresholds, the response variable that we analyzed was a binomial proportion of counts (years exceeding the threshold versus years not exceeding it). For the olive fly, the economic injury threshold is set at three flies captured per trap per day and 3% of olives 'stung' (i.e., oviposited into) per week. This is the only pest for which the economic threshold is jointly defined by two criteria. For olive moth and grapevine moth, thresholds are set at 2% of olives and 8% of grapes with visible signs of oviposition, respectively.

Our prior work using the same data set has already documented that insecticide applications increase in vineyards when the grapevine moth exceeds economic spray thresholds (Paredes et al., 2021). To determine whether exceeding economic thresholds also results in a higher probability of applying insecticides in olive groves, we modeled whether or not insecticides were sprayed in a given field and in a given year as a function of the fraction of field visits for which economic thresholds were exceeded. Importantly, reporting of management practices in the RAIF database appeared to be less uniform than other key variables, with some RAIF technicians frequently failing to report on field management. Therefore, we omitted from our analyses all field-years in which no insecticide, herbicide, or fungicide applications were reported, assuming that these were not true absences but instead represented failures to report. We then implemented generalized additive mixed models (GAMM) with a binomial error distribution, a logit link function, and random effects of year, observer identity (i.e., the technician collecting the data), and olive cultivar ($N = 15$ cultivars).

Higher pest densities and variability may lead to worse economic outcomes for farmers beyond simply eliciting insecticide applications. For olive flies, a fruit quality threshold of 10% of fruits with olive fly exit holes has been established, as this level of infestation causes olive oil to be downgraded from extra-virgin to virgin (Mraicha et al., 2010). No comparable fruit quality thresholds have been established for the olive moth or European grapevine moth. Nonetheless, we also defined major yield losses for the olive fly and grapevine moth at 20% crop loss; other yield loss thresholds (10%, 15%, and 30% for the grapevine moth and 30% and 50% for the olive fly) are shown in the Appendix S1. Because olive and grape damage accumulates over the growing season, thresholds were considered to have been exceeded if any of the last three samples prior to harvest showed above-threshold levels of damage, and we included fields with any number of within-season damage estimates. Similarly, as the response variable that we analyze is a binomial proportion of counts (years exceeding the threshold versus years not exceeding it), we relaxed the requirement for a minimum number of annual observations, as the number of annual observations was already accounted for in the response variable. Fruit damage data were not collected as regularly as abundance data; the final data set included 1270 observations for the olive fly and 39 observations for the grapevine moth.

Finally, we explored the determinants of population densities and variability using GAMMs. Predictors included mean values of the following variables, calculated across all years the fields were visited: landscape productivity (i.e., NDVI), landscape composition (i.e., percentage land cover of the focal crop), elevation, aspect, and weather (i.e., growing season temperature and precipitation). We also included mean population density in models examining determinants of pest PV to provide statistical control for any residual correlation between mean density and variability of density that remained after the log transformation of population size (Appendix S1: Figure S1). The topographic variable slope was highly correlated with altitude, and therefore was not included as a predictor. We also included year-to-year variation in some of these variables as predictors, measured as the standard deviation of the log-transformed values: precipitation (log[value +0.01]), temperature (log[value +1.0]), and NDVI (log[value +1.0]). We could not include across-year variability in land cover measures, because we did not have independent yearly measurements. All continuous predictor variables were allocated a maximum of three knots to avoid overfitting (Taylan et al., 2007).

Importantly, we opted for another approach for the grapevine moth because the low number of observations ($N = 60$) prevented us from fitting the same models that were fit for the olive fly and moth. Instead, we fit a linear model containing the same predictors that were included in the GAMMs, but excluding all random effects from the model (please refer to the last paragraph of the section). Including random effects resulted in model overparameterization and non-convergence. Even after removing the random effects, no environmental variables were identified as significant predictors of grapevine moth PV (Appendix S1: Table S1).

Spatial variation in field management could possibly confound insights into the environmental drivers of mean pest density and variability. We therefore calculated a single index of management intensity by summing the aggregated per field scaled numbers of herbicide and fungicide applications and tillage events. The two sets of analyses, with management intensity excluded and included, produced very similar results. Therefore, because technicians frequently failed to report information on field management (as noted four paragraphs above), we present analyses without management intensity in the main text and with management intensity in the supplement (please refer to Appendix S1: Tables S2 and S3).

In all cases, mean pest population densities and variability in population densities were modeled with Gaussian error distributions. For olive pests, we included random effects for plant cultivar and for the cooperative through which the farmer marketed their crops ($N = 290$ cooperatives). By including random effects for cooperative identity, we accounted for any potentially unmeasured but important management practices that might vary across cooperatives. For example, members of each cooperative may tend to share the same pest-management practices. Moreover, as cooperatives were spatially clustered, the variable also helped account for spatial autocorrelation in mean pest abundance and pest variability. Nonetheless, we still detected residual spatial autocorrelation in the models of mean pest abundance. We therefore also included a random effect of geographic region in abundance models ($N = 63$ regions). This variable was included in the RAIF database and delineates regions with similar crop and pest characteristics. Residuals from models including random effects of geographic region displayed no further evidence of spatial autocorrelation ($p > 0.05$ for Moran's I tests). To account for the variable number of years of survey effort per field and produce robust estimates of our response variables, all observations of mean pest density and variability were weighted by the number of years that contributed to a particular estimate. GLMMs used to assess the likelihood of pests exceeding hypothetical or real threshold values (detailed in the fourth paragraph of this section) shared similar mixed effects structures as GAMMs, with cooperative and cultivar as random factors. Response variables for the GAMMs were log-transformed to satisfy the assumption of normality. Finally, we verified that all analyses conformed to model assumptions regarding normality (when appropriate) and heteroscedasticity. All analyses were conducted in R (R Development Core Team, 2018), with GLMMs implemented in the *lme4* package (Bates et al., 2015) and GAMMs implemented in the *mgcv* package (Wood, 2011).

RESULTS

Context-dependent effects of pest population variability

We found that the effects of pest PV were complex, depending on whether the average pest population

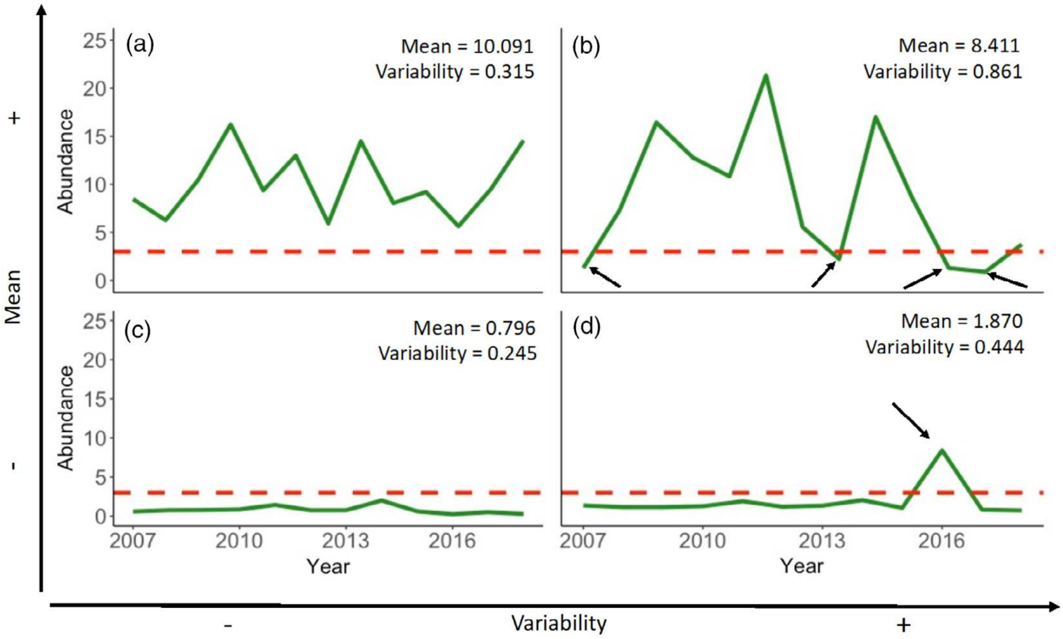

FIGURE 2 (a–d) Temporal dynamics of olive fly abundances across four actual farm fields, exhibiting distinct combinations of low versus high mean population densities and variabilities. Red dashed lines represent the economic threshold for the olive fly. Arrows indicate years in which the threshold was exceeded (d) or years in which population densities fell below the threshold (b)

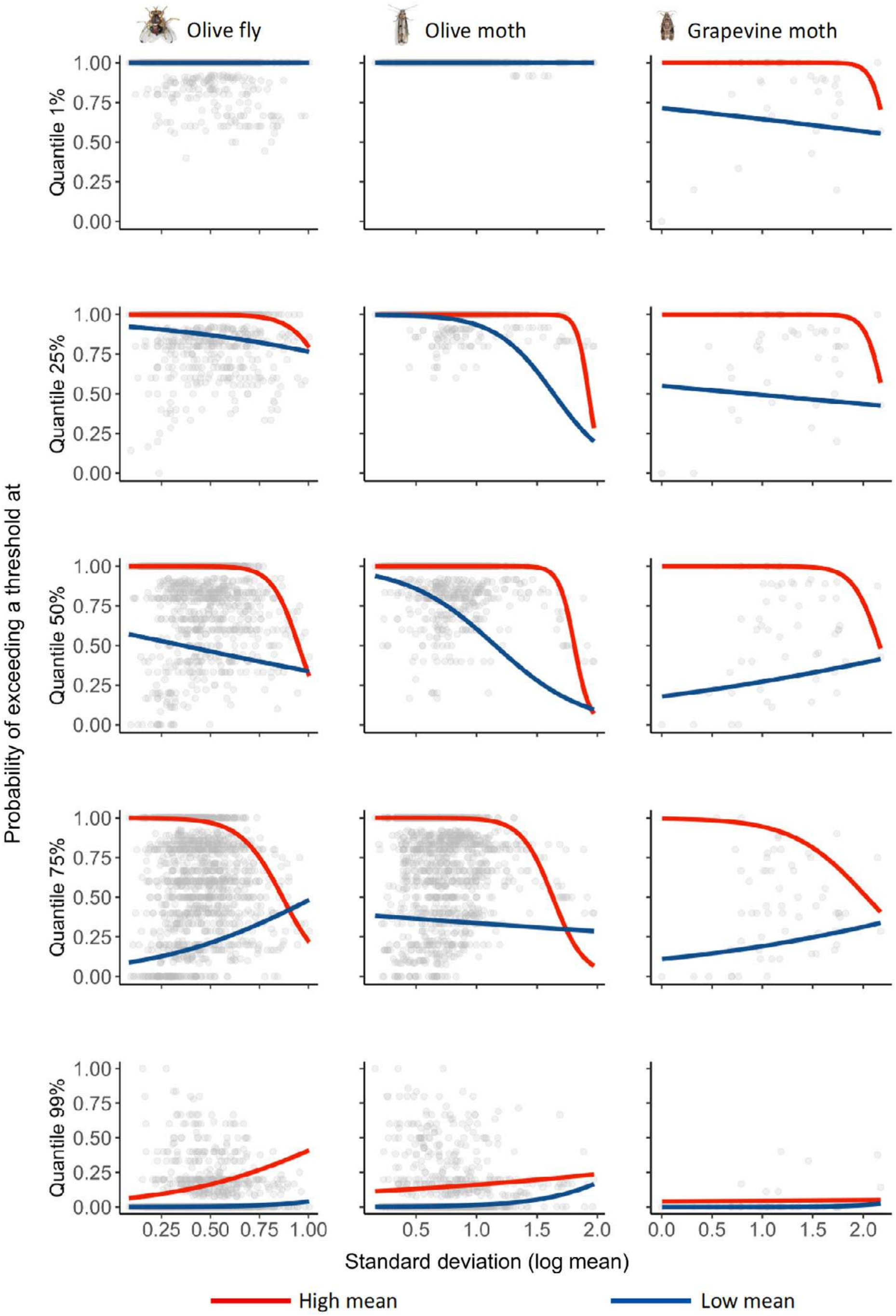

FIGURE 3 Effects of pest population variability depend on pest abundances and tolerance levels. Hypothetical pest tolerance thresholds were set at the 1%, 25%, 50%, 75%, and 99% quantiles of pest numbers trapped per week (olive fly: 0.07, 1.00, 2.70, 5.95, and 28.1 individuals/week; olive moth: 0.14, 2.57, 10.2, 34.3, and 400 individuals/week; grapevine moth 0.07, 0.21, 0.57, 1.70, and 21.7 individuals/week, respectively). At high tolerance levels (99% quantile), more variable pest populations are always more likely to exceed thresholds. At low tolerance levels (1% and 25% quantiles), pest densities are almost always above-threshold levels, except when variable pest populations drop to unusually low densities. At intermediate tolerances (50% and 75%), variability in pest populations may increase, decrease, or have little effect on the risk of exceeding thresholds. Lines are predicted effects of pest variability (standard deviation of interannual log mean abundances) on the likelihood of exceeding thresholds from generalized linear mixed models. Red and blue lines represent fields with high mean pest densities (top 10% pest abundance quantile) and low mean pest densities (bottom 10% quantile), respectively ($N_{\mathrm{olivefly}} = 1315$ fields, $N_{\mathrm{olivemoth}} = 1184$ fields, $N_{\mathrm{grapevinemoth}} = 60$ fields)

densities were above or below the threshold for economic pest damage. Pest PV always increased the likelihood that pests would exceed economic thresholds that were higher than the mean population density (i.e., panels (c) and (d) in Figures 2 and 3; Appendix S1: Table S4). However, if economic thresholds were below mean pest densities (i.e., panels (a) and (b) in Figure 2), then pest PV paradoxically decreased the likelihood of pests exceeding thresholds. Finally, if economic thresholds were set very near the mean pest population density, then global effects of variability were predicted to be neutral, and effects registered at any particular field depended on that field's average pest abundance. For fields in which pests tend to be abundant, variability increased the likelihood that densities occasionally dropped beneath threshold levels. However, for fields where pests tended to be rare, variability increased the likelihood of occasional outbreaks that exceeded threshold levels (Figure 3; Appendix S1: Table S4).

Pest population variability effects on real-world outcomes

We found that more variable olive fly and grapevine moth populations were neither more nor less likely to exceed economic established thresholds, which is consistent with mean densities of these pests being neither far below, nor far above their respective thresholds (Figure 4; Appendix S1: Figure S3 and Table S5). In contrast, variable olive moth populations were less likely to exceed economic thresholds ($p = 0.040$; Appendix S1: Table S5 and Figure S3), which is consistent with the economic damage threshold being located below the mean population density for this pest. Importantly, exceeding economic thresholds for the olive fly and moth increased the likelihood of applying insecticides targeted to each pest, as was previously shown for the grapevine moth (Paredes et al., 2021; Appendix S1: Figure S4).

Increased PV, however, would always cause negative outcomes for farmers concerned about crop quality or catastrophic damage from olive flies and grapevine moths (damage data were not available for the olive moth). More variable olive fly populations were more likely to downgrade the quality of harvested olives ($p = 0.016$; Figure 4). Moreover, more variable olive fly and grapevine moth populations were more likely to cause major crop damage (Figure 4; Appendix S1: Figures S5 and S6, Table S6). For example, the likelihood of suffering >20% crop losses more than doubled when comparing the least versus the most variable olive fly populations.

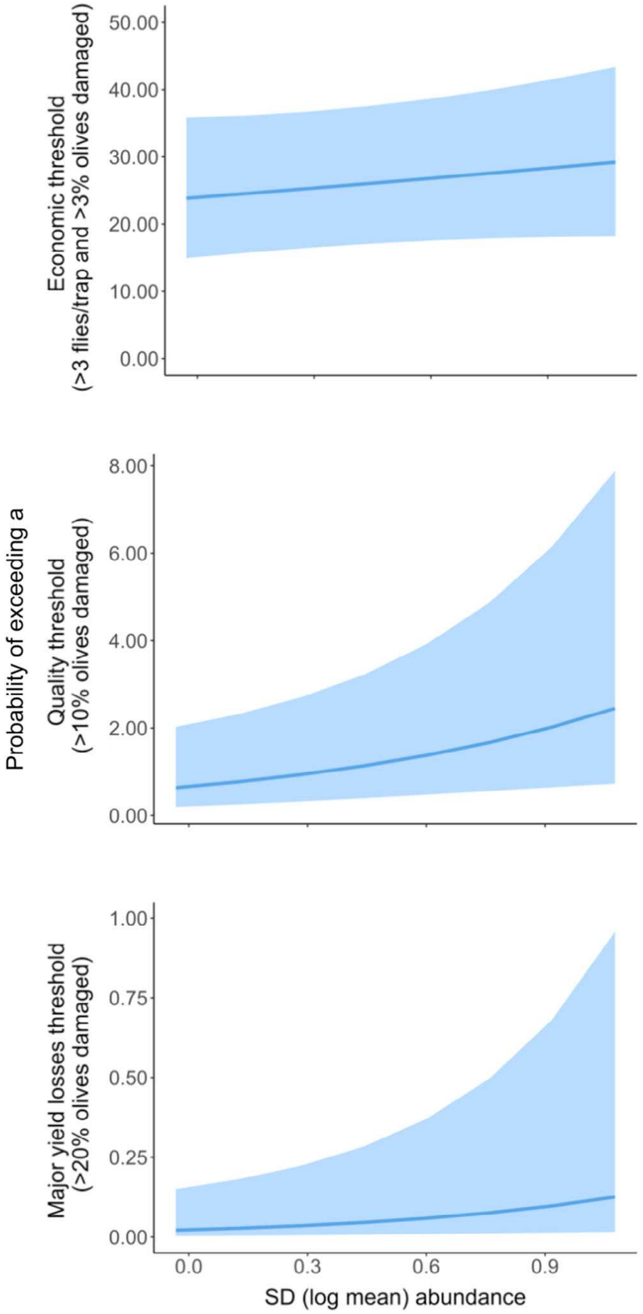

FIGURE 4 Effects of olive fly population variability on the probability of exceeding real-world economic, quality, and major losses thresholds. More variable populations are not more likely to exceed economic thresholds for spraying insecticides but are significantly more likely to cause severe crop quality declines and major yield losses. Blue lines and shaded regions correspond to predictions and 95% confidence regions from generalized linear mixed models ($N = 1270$ fields)

Determinants of mean pest abundances versus pest population variability

We found that environmental and landscape variables often influenced mean pest abundances and pest PV in fundamentally different ways. In some cases, entirely different variables shaped mean pest densities versus pest PV (Appendix S1: Table S7). For example, high levels of precipitation during the growing season tended to increase mean olive fly population densities but not PV, whereas elevated temperatures increased olive moth PV but not mean densities. In addition, olive moth densities were significantly affected by landscapes with more surrounding olive groves but the effect on variability was not significant. Unsurprisingly, interannual variability in landscape productivity, growing season temperatures, and growing season precipitation regularly increased interannual variability in pest populations but tended to have more muted effects on mean pest abundances (Appendix S1: Table S7 and Figures S7–S10).

In other cases, the same environmental variable affected both mean pest densities and density variability, but in fundamentally different ways. Perhaps the most important driver of mean pest abundances was elevation (olive fly: *p*-value <0.0001; olive moth: *p*-value = 0.0001; Figure 5; Appendix S1: Table S7). For the olive fly, increasing elevation had opposite effects on mean densities versus PV: mean densities increased strongly as elevation increased to ~800 m, where densities peaked, declining slightly at still higher elevations, whereas variability of population densities declined as elevation increased to ca. 800 m, and then increased at still higher elevations (Figure 5a,b). Mean densities of the olive moth increased steadily with increasing elevation, whereas the variability in population densities showed a U-shaped pattern (Figure 5d,e).

Finally, our analysis revealed a case in which landscape composition affected mean population densities and PV in parallel ways: both olive fly mean population densities and PV tended to increase in simplified landscapes (Figure 6).

DISCUSSION

Together, our results demonstrate that pest PV directly influences critical farm production outcomes related to insecticide applications, crop quality, and major yield losses. Specifically, we found that mitigating pest PV is

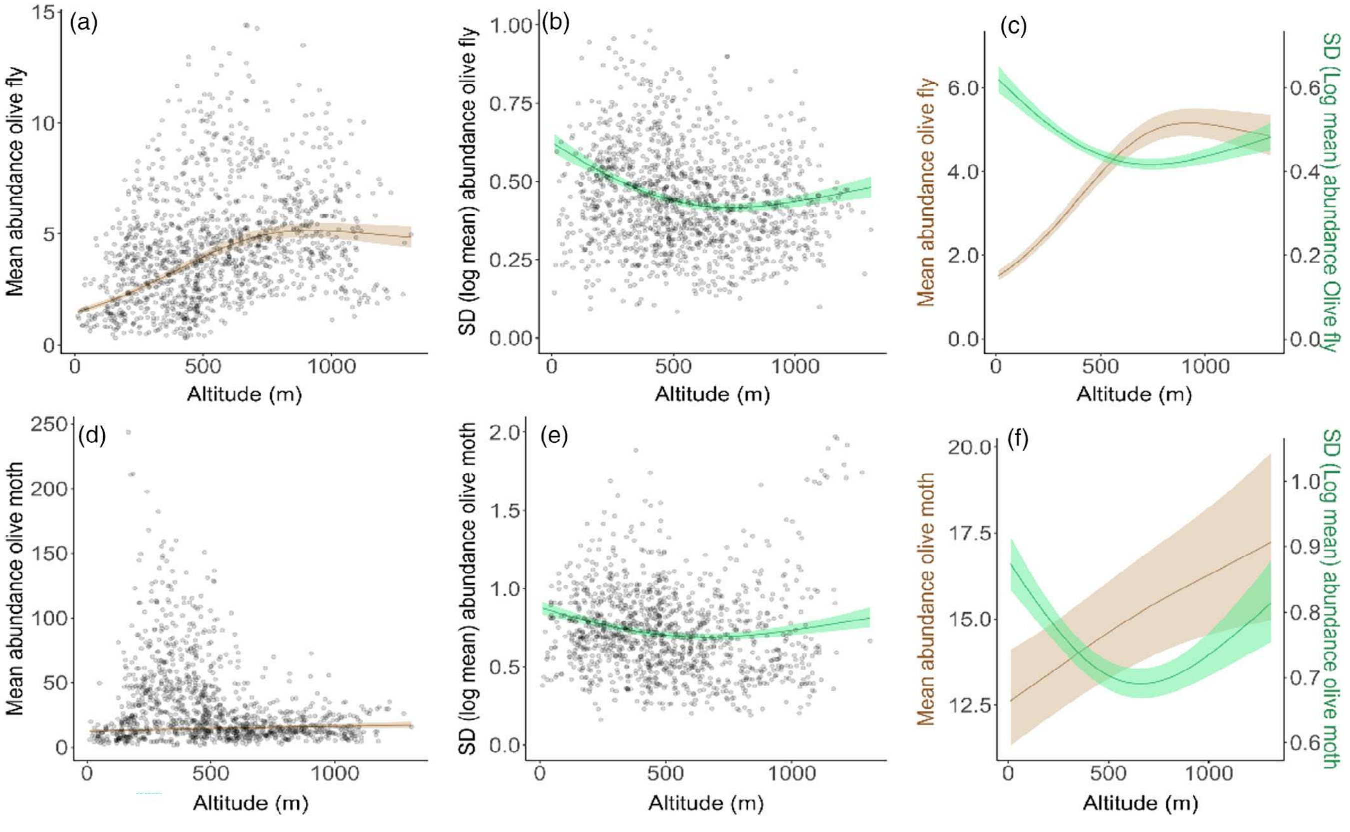

FIGURE 5 Effects of altitude on olive fly and olive moth population mean abundance and variability. At intermediate elevations, olive fly populations are most abundant (a) but also most stable (b). Similarly, at intermediate elevations, olive moth populations are most stable (e) but abundance tends to increase continuously with altitude (d). Brown lines and shaded regions represent predictions and 95% confidence intervals for mean abundance from generalized additive mixed models; green lines and shaded regions correspond to variability. Panels (c) and (f) are zoomed in to better view effects ($N_{\text{olivefly}} = 1315$ fields; $N_{\text{olivemoth}} = 1184$ fields)

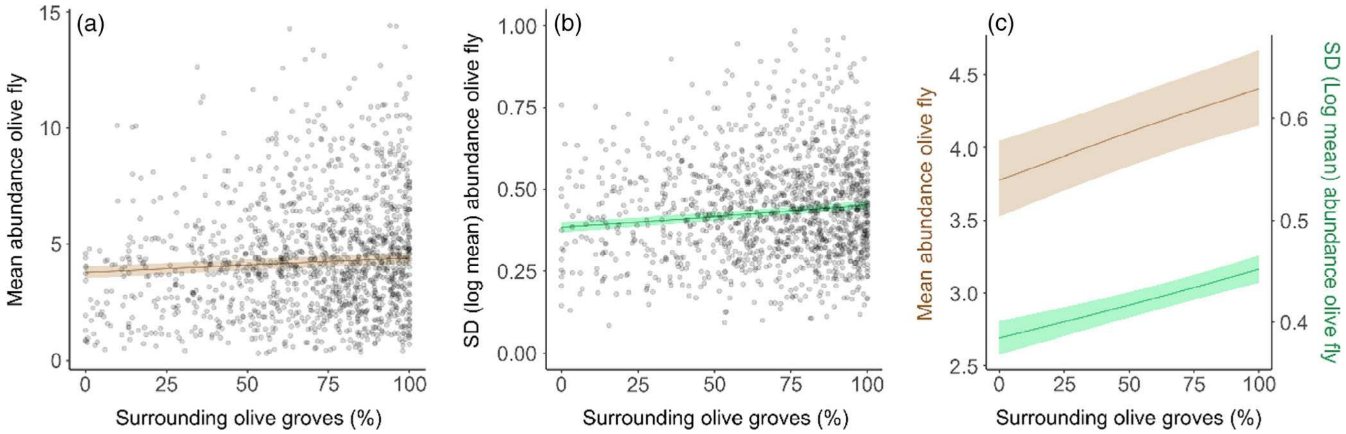

FIGURE 6 Effects of landscape composition on olive fly population mean abundance and variability. More simplified landscapes with higher fractions of surrounding olive groves are most likely to host both abundant (a) and variable (b) fly populations, conditions that elevate the chances of major crop losses. Brown lines and shaded regions represent predictions and 95% confidence intervals for mean abundance from generalized additive mixed models; green lines and shaded regions correspond to variability. Panel (c) is zoomed in to better view effects ($N = 1315$ fields)

crucial if farmers are either growing crops that can tolerate some damage from pests that are usually rare but occasionally problematic or are concerned about catastrophic outbreaks. Pest PV strongly increased the likelihood of farmers experiencing major yield losses from both the olive fly and grapevine moth. Critically, however, our analyses also suggested that high pest PV can sometimes result in positive outcomes for farmers; this occurs when their tolerance for damage is extremely low and therefore the usual pest densities are above the threshold at which control measures are applied. This is because more variable pest populations are more likely to occasionally dip below the control threshold level.

When olive flies damage >10% of the olives, crop quality is automatically downgraded, and farmers receive a lower price for their crop (Mraicha et al., 2010). This creates a non-linearity in the relationship between olive fly densities and economic damage, in which losses jump up when olive fly densities pass a critical threshold. Under such a non-linear density–damage relationship, variability of pest densities will create more economic damage than would be expected if the olive fly populations were stable at their long-term means (as expected under Jensen's inequality; Jensen, 1906). Correspondingly, the most variable olive fly populations were twice as likely to experience quality downgrading compared with the least variable populations. Therefore, any time economic damage accelerates as pest densities rise (i.e., greater than linear increases in damage), farmers will benefit from managing pest populations to reduce their variability.

Ecologists have long been interested in the determinants of PV and how patterns of population fluctuations are shaped by processes that regulate population densities (e.g., Hassell et al., 1976; Murdoch et al., 1995; Walter et al., 2018; Lamb et al., 2019). Yet most of these studies treat population variation as a species-specific characteristic, often analyzing a single time series per species. Given the data requirements required to produce a long time series, this is not surprising. By capitalizing on highly decentralized, massive data gathering efforts that occur in production agriculture, we were able to produce well replicated time-series data for three insect herbivores and examine, for the first time, a broad suite of correlates of across-population differences in population variation.

Our analyses suggest that variability may need to be managed independently from mean pest population densities, as the factors that influenced population means versus variability often differed. For example, precipitation metrics tended to more strongly affect mean pest densities, whereas growing season temperatures tended to affect pest PV. We also found that the same variable can affect pest population means and variability in distinct ways, with significant implications for field management. For example, we found that mean olive fly abundance showed a hump-shaped response to elevation (as in Castrignanò et al., 2012; Kounatidis et al., 2008), whereas variability instead showed a U-shaped response.

The strong effects of elevation on olive fly mean abundance and variability may reflect the thermal ecology of this pest. *B. oleae* is very sensitive to high temperatures, which can cause heavy mortality (Abd El-Salam et al., 2019; Gutierrez et al., 2009; Wang et al., 2009). In the Andalusia region of southern Spain, low-elevation olive groves experience periods of extremely high temperatures during the summer and early fall, when fly populations are active. Fly populations found in cooler, higher elevation locations escape these severe heat waves, allowing them to reach higher densities and avoid major episodes of mortality that can cause population collapses. This results in both higher and less variable populations. Further warming, as expected under global climate change, could lead to further increases in olive fly population volatility, creating novel management challenges. Careful monitoring of olive fly population densities may be especially important, given the links we found between increased PV and major crop damage.

Importantly, our models also provide key insights into how landscapes could be managed to simultaneously achieve reductions in both mean population density and PV. We found that landscape simplification (i.e., cultivating expansive monocultures) increased both mean olive fly densities and pest PV. This suggests that conserving or restoring patches of natural habitat, or planting multiple crop types, may reduce the potential for major crop damage in olive groves. To our knowledge, our study is the first to directly explore landscape impacts on pest variability in agroecosystems. Nonetheless, our findings align with recent work documenting elevated pesticide application variability in simplified agricultural landscapes (Larsen & Noack, 2020).

In contrast, more work has focused on linking landscape patterns to mean pest abundances, often with conflicting and context-dependent results (Karp et al., 2018; Tscharntke et al., 2016). So why does landscape complexity seem to improve olive fly control? One explanation is that the olive fly is a specialist, and landscape diversification has been shown to better control specialist than generalist pests (Tamburini et al., 2020). Indeed, simplified landscapes may concentrate resources for specialist pests, removing dispersal barriers such that pests can rapidly move into areas of relatively low abundance and increase in population size (O'Rourke & Petersen, 2017; Perovic et al., 2010; Root, 1973; Villa et al., 2021). Complex landscapes may also provide key resources for natural enemies, contributing to top-down control (Chaplin-Kramer et al., 2011; Landis et al., 2000). Regardless of mechanism, our results contribute to a small but growing body of literature that suggests simplified landscapes may lack key density control mechanisms that temper rapid population growth of specialist pests (Dainese et al., 2019; Paredes et al., 2021).

CONCLUSIONS

Despite its importance, PV is rarely studied in agricultural landscapes, let alone managed directly. One barrier is the high level of spatiotemporal replication needed to quantify interannual variability in pest populations and then relate it to field, landscape, or regional factors. A prior analysis of the grapevine moth data set demonstrated that pest population stochasticity can easily mask strong drivers of pest population densities if sample sizes are similar to those reported in most landscape pest control studies (e.g., ∼25 fields surveyed for 2 years; Paredes et al., 2021). Understanding drivers of pest variability is an even more data-demanding endeavor. Here, we show that the 447 field-years of grapevine moth observations (60 vineyards surveyed for an average of 7.91 years) was still insufficient to resolve any factors that significantly influenced grapevine moth variability (Appendix S1: Table S1). Only through analyses of substantially larger data sets could we understand drivers of pest PV (i.e., $N = 9343$ field-years for the olive fly and $N = 8939$ field-years for the olive moth).

One promising path forward is for researchers to partner with governments, private industry, or distributed working groups to acquire and analyze large pest monitoring data sets, using ecoinformatic approaches (Rosenheim & Gratton, 2017). Indeed, the causes and consequences of pest PV are likely to differ among regions and cropping systems. Still, based on the few studies that have been conducted to date (Dalin et al., 2009; Larsen & Noack, 2020), it appears that farms and landscapes can be managed to mitigate pest PV. In particular, policies that incentivize the diversification of farms and farming landscapes may not only result in positive conservation outcomes (Batáry et al., 2015), but also dampen the volatile pest populations that provoke excessive insecticide applications (Larsen & Noack, 2020) and threaten farmers' livelihoods.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

All authors reviewed and edited the manuscript. Daniel Paredes, Jay A. Rosenheim, and Daniel S. Karp conceived the study and designed the methodology. Daniel Paredes performed the analyses and wrote the original draft supervised by Jay A. Rosenheim and Daniel S. Karp.

DATA AVAILABILITY STATEMENT

Data (Paredes et al., 2022) are available from Dryad: https://doi.org/10.25338/B86S6J.

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SUPPORTING INFORMATION

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