Ecological Entomology

Ecological Entomology (2019), DOI: 10.1111/een.12830

Weather and regional crop composition variation drive spatial synchrony of lepidopteran agricultural pests

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Abstract. 1. Spatial synchrony, the tendency for temporal population fluctuations to be correlated across multiple locations at regional scales, is common and contributes to the severity of outbreaks and epidemics, but is little studied in agricultural pests.

2. This study analysed spatial synchrony from 1974 to 2008 in 16 lepidopteran agricultural pests in Maryland, U.S.A., and investigated whether pest synchrony is driven by interannual variability in seasonal weather and the areas planted in different crop types.

3. Lepidopteran pests exhibited high degrees of spatial synchrony, which was driven by environmental variation, a phenomenon known as the Moran effect. Region-wide variation in the areas planted in major crops drove spatially synchronous abundance fluctuations in more than half of studied species. The combination of weather and crop composition explained large fractions of synchrony in black cutworm, corn earworm, European corn borer, and spotted cutworm populations. Other pests, including forage looper and variegated cutworm, displayed a high degree of spatial synchrony, but without dependence on the tested drivers.

4. The study finding that synchronous variation in the area planted in different crop types contributed to synchronous pest abundance fluctuations suggests that strategies to reduce synchrony in changes in crop type across a region could reduce the severity of pest outbreaks and enhance the stability of agricultural systems.

Key words. corn earworm, European corn borer, insect outbreak, Moran effects, wavelet analysis.

Introduction

Many pest species exhibit abundance fluctuations that are correlated through time over large areas (Økland *et al.*, 2005; Liebhold *et al.*, 2012). This phenomenon, known as spatial synchrony (Liebhold *et al.*, 2004), is in part responsible for pests' deleterious impacts: synchronous local fluctuations reinforce each other, producing large variation in the aggregate (Schindler *et al.*, 2015). Thus, synchrony may make pest outbreaks more difficult to control, e.g. if the scale of the problem overwhelms management resources. Outbreaks of many Lepidopteran forest pests – including gypsy moth [*Lymantria dispar* (L.)], forest tent caterpillar [*Malacasoma disstria* (Hübner)], and spruce budworms [*Choristoneura* spp. (Lederer)] – exhibit spatial synchrony, and examining the drivers of synchrony has become a major lens for understanding the mechanisms of area-wide population fluctuations of these and many other species (Peltonen *et al.*, 2002; Haynes *et al.*, 2009; Cooke *et al.*, 2012; Sheppard *et al.*, 2016). However, spatial synchrony in populations of agricultural pests is less studied (but see, e.g., Bell *et al.*, 2012; de Valpine *et al.*, 2010; Jiang *et al.*, 2006), leaving

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open questions concerning the prevalence and drivers of spatial synchrony in these species. Efforts to determine long-term drivers of agricultural pest population dynamics, in general, have been hindered by a paucity of long-term studies (Ingram *et al.*, 2008; Gregory *et al.*, 2009).

Classically, the predominant general cause of spatial synchrony in population dynamics is environmental fluctuation – typically, in climate and weather – that is spatially synchronous (called 'Moran effects' after Moran 1953). Climate and weather, by which we distinguish between, respectively, long-term and short-term changes in atmospheric conditions, have long been recognised as important factors regulating insect populations (Andrewartha and Birch 1948), and in recent decades concerns have emerged that climate change may increase the frequency and severity of damaging insect outbreaks (Cannon 1998; Logan *et al.*, 2003; Gregory *et al.*, 2009; Björkman *et al.*, 2011). Documented responses of insect pest populations to climate change vary widely (Johnson *et al.*, 2010; Haynes *et al.*, 2014; Ouyang *et al.*, 2014), however, ostensibly due in part to differences in life history and physiology (Walter *et al.*, 2018). Identifying which environmental variables drive population fluctuations, and how, is a first step towards predicting pest outbreaks in a changing climate.

Agricultural pest populations are exposed to widespread temporal variation in the areas planted in different crop types (Lusk 2018), and though it is plausible such variations can drive spatial synchrony, whether they do so is unknown. We refer to the areas planted in different crop types in a region as 'crop composition'. Insect populations are greatly affected by the quantity and quality of forage (Wratten *et al.*, 2007). For instance, the developmental rates, survivorship, and fecundity of even highly polyphagous species can be affected by host plant type (Liebhold *et al.*, 1995). While host quality is in part related to weather (Kingsolver 1989), in agricultural systems, how much land area is planted, and in what crop, are affected by socio-economic factors including land-use change, environmental and agricultural policy (Kastens *et al.*, 2017; Garrett *et al.*, 2018), commodities prices, and choices related to changing agricultural technologies (Wu *et al.*, 2004). As many socio-economic factors operate at regional to global scales, the regional composition of crops, in terms of areas planted, may itself exhibit spatially synchronous fluctuations that induce synchrony in agricultural pest populations. Whether this occurs in practice has not been established.

Recent work has promoted timescale-specific approaches to synchrony to resolve challenges associated with the different timescales on which weather and other drivers of population dynamics operate (Sheppard *et al.*, 2016; Walter *et al.*, 2017; Anderson *et al.*, 2019). Weather variables, for example, exhibit interannual variation and periodic, multi-annual patterns driven by climate oscillations such as the El Niño Southern Oscillation and the North Atlantic Oscillation. Conventional approaches based on standard correlation are incapable of resolving oscillations at different timescales and may therefore fail to detect true relationships between weather and biological variables (Sheppard *et al.*, 2016; Defriez & Reuman 2017).

This study examines patterns and drivers of spatial synchrony in 16 lepidopteran agricultural pests over 36 years in Maryland, U.S.A. We first ask: how prevalent is spatial synchrony among lepidopteran pest populations across Maryland, at what timescale(s) does synchrony occur, and is synchrony episodic or consistent through time? We then ask: are synchronous, area-wide population fluctuations driven by temperature and precipitation variations in winter, spring, and summer, and by changes in the land area planted in major crop types? We examine how much synchrony is explained by these factors, whether drivers and their explanatory power differ by timescale, and how spatial synchrony and its drivers differ among species. This work contributes to a larger body of research on the effects of agricultural practices and climate on long-term population patterns of agricultural pest species, and is unique in its focus on non-target pest species and on spatial synchrony.

Materials and methods

Data

We determined abundances of 16 lepidopteran agricultural pests from a 1973–2008 black light network initially started by the Maryland Extension IPM programme and then later administered by the Maryland Department of Agriculture. Starting in 1973, black light traps were deployed throughout the growing season at different farms in eight regions across the state (Fig. 1), but some species were recorded beginning in 1984. Traps were deployed with spatiotemporally varying intensity from mid-April to mid-October for a total of 236 176 trapping nights over 36 years and eight regions. The number of trapping locations was generally highest from May through to September, typically peaking at six to 10 locations in a given region, but in some regions and years traps were deployed at as many as 15 locations. Because the number and locations of individual traps were not consistent through time, but each region was always represented by several distinct locations and many trapping nights throughout the growing season, we aggregated data to the regional level. Focal taxa were identified to species or, less commonly, genus. Focal taxa include: beet armyworm [*Spodoptera exigua* (Hübner)], black cutworm [*Agrotis ipsilon* (Hufnagel)], bilobed looper [*Megalographa biloba* (Stephens)], bristly cutworm [*Lacinipolia renigera* (Stephens)], celery looper [*Anagrapha falcifera* (Kirby)], corn earworm, cabbage looper [*Trichoplusia ni* (Hübner)], dingy cutworm [*Feltia jaculifera* (Guenée)], European corn borer, fall armyworm [*Spodoptera frugiperda* (J.E. Smith)], forage looper [*Caenurgina erechtea* (Cramer)], green cloverworm [*Hypena scabra* (Fabricus)], hornworms [*Manduca* spp. (Hübner)], spotted cutworm [*Xestia* spp. (Hübner)], true armyworm [*Mythimna unipunctata* (Haworth)], variegated cutworm [*Peridroma saucia* (Hübner)], and yellow striped armyworm [*Spodoptera ornithogalli* (Guenée)]. These species include notable pests of corn, a number of feeding generalists that may use corn or other host plants, and species that feed little or not at all on corn. Because sampling intensity varied by region and year, we took the total number of each species caught in each region and year and normalised it by the number of trapping nights to correct for trapping effort, producing for each species one abundance value for each trapping region and year.

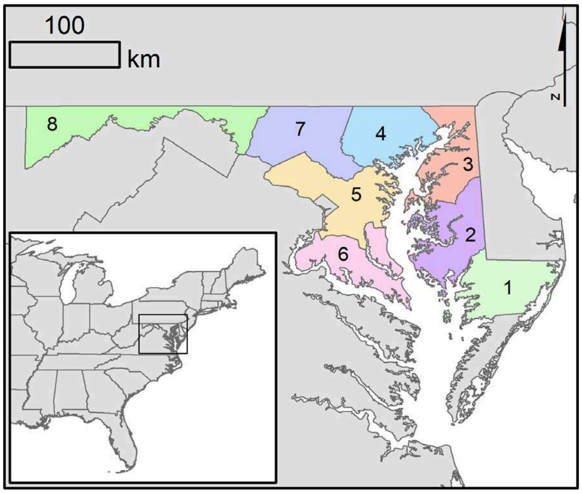

Fig. 1. Black light-trapping regions in Maryland, numbered 1–8. [Colour figure can be viewed at wileyonlinelibrary.com].

We used PRISM climate data (Prism Climate Group 2018) to develop time series of winter (January, February, March), spring (April, May, June), and summer (July, August, September) temperature and precipitation. Monthly data for 1973 to 2008 were obtained as 4-km × 4-km grid cells, which were aggregated to season by summation (precipitation) or averaging (temperature) and averaged by trapping region. Although weather over finer temporal intervals, e.g. monthly, is known to affect some species, we deemed aggregating to season a reasonable compromise between the ability to identify specific weather mechanisms and conducting a reasonable number of statistical tests.

To quantify variability in crop composition, we obtained data on the acreage planted in four major crops, by year and county or agricultural district (as available) from the United States Department of Agriculture National Agricultural Statistics Service. When data were available at the county level, they were aggregated by summation to the level of trapping regions (Fig. 1). Sometimes, agricultural districts were the finest spatial units at which crop area data were available, but these do not match perfectly the light-trapping regions. In these cases, crop areas were apportioned to counties in proportion to the area of the agricultural district comprised by that county, then aggregated by summation to trapping region, and $\log_{10}$-transformed to reduce dispersion of the data. We used principal components analysis to reduce the crop area data into two orthogonal variables, explaining 64% and 23% of the variance in crop areas. The first principal components axis (PC1) was moderately negatively correlated with the area planted in each of the four crop types, while PC2 was positively correlated with the areas planted in barley and corn, but negatively correlated with the areas of soy and wheat (Methods S1).

Analyses

We first prepared the data to meet assumptions of our statistical procedures. We removed temporal trends in pest abundance using generalised additive mixed effects models (GAMMs). These models extend linear mixed-effects models by replacing linear regression coefficients with penalised regression splines (Wood 2006). This allowed us to detect non-linear temporal trends in pest abundance, while the mixed-effects component allowed the y-intercept to vary by trapping region to account for regional differences in average abundance. Specifically, natural-log-transformed pest abundance was modelled as a function of one fixed effect, year, and one random effect of trapping region on the intercept. We expected non-linear abundance trends in at least some of our focal species given prior work demonstrating population declines following the introduction of transgenic, insect-resistant ‘*Bacillus thuringiensis*’ crops in 1996 (Dively *et al.*, 2018). We restricted the maximum number of degrees of freedom of the spline to $k = 3$ so that the GAMM captured only general long-term trends, not oscillatory patterns that were the focus of our synchrony analyses. Before performing the synchrony analyses, all variables had trends removed, were Box-Cox transformed to improve normality, and scaled to have mean = 0 and SD = 1.

Spatial synchrony in agricultural pest abundances was assessed using wavelet phasor mean fields (WPMFs; Sheppard *et al.*, 2016). The WPMFs produce a time- and timescale-specific depiction of synchrony by aggregating information from multiple wavelet transforms (Torrence and Compo 1998). The WPMF is large when, across regions, abundance oscillations at a given time and timescale are synchronised, or in phase (see Fig. 2a,b for a pedagogical illustration of the WPMF). Values of the WPMF range from 0 (independent oscillations) to 1 (oscillations perfectly synchronised) (Sheppard *et al.*, 2016). We considered spatial synchrony statistically significant if it exceeded the 95th percentile of a distribution of phase synchronies generated under a null hypothesis of complete phase independence (Sheppard *et al.*, 2013). The surrogate distribution was generated by computing 100 000 sums of N independent random unit complex numbers (called ‘phasors’), where N is the number of regions ($N = 8$). We used the continuous complex Morlet wavelet transform (Torrence and Compo 1998).

We used spatial wavelet coherences (Sheppard *et al.*, 2016, 2017) and wavelet linear models (Sheppard *et al.*, 2019) to assess how weather and crop composition drive synchronous, area-wide pest abundance fluctuations. We tested for spatial wavelet coherence to identify major drivers of pest population dynamics, and used wavelet linear models, in conjunction with the wavelet Moran theorem (Sheppard *et al.*, 2016), to determine the percentage of spatial synchrony in pest abundances that was explained by that combination of environmental drivers. The environmental drivers we considered were seasonal (winter, spring, and summer as defined earlier) total precipitation and average temperature and crop composition, represented by the first two principal components axes.

Spatial wavelet coherences detect drivers of synchrony by determining whether timescale-specific oscillations in two spatiotemporal variables have consistent phase differences and similar variation in magnitude through time, and whether these relationships are consistent over space (Sheppard *et al.*, 2016). Coherence between a biological and an environmental variable, such as weather or crop composition, provides strong evidence

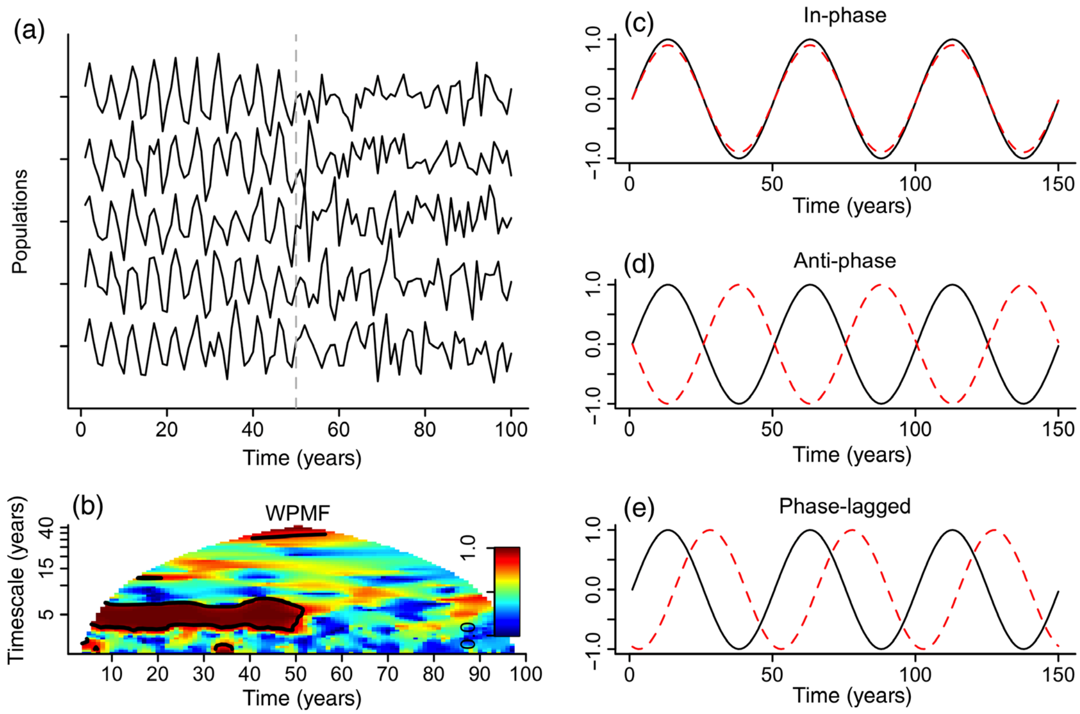

Fig. 2. Pedagogical figure for the wavelet phasor mean field and phase relationships. (a) Time series of five populations exhibiting synchronous cycles with 5-year periods for the first 50 time steps, and independent random fluctuations thereafter. (b) Matching the construction of the time series in (a), the wavelet phasor mean field (WPMF) shows high and statistically significant phase synchrony at 5-year timescales during the first half of the time series, but no consistent synchrony thereafter. The black line denotes statistical significance at the $\alpha = 0.01$ level. (c–e) Examples of in-phase ($\phi = 0$), anti-phase ($\phi = \pm 1$), and phase-lagged ($\phi = 0.5$) relationships; phase relationships, denoted ϕ, are given in fractions of π. Relationships depicted in (c–e) would all be considered coherent, but the relationships in (d, e) would not produce high values of the WPMF because they are not in-phase. [Colour figure can be viewed at wileyonlinelibrary.com].

that the environmental variable, or some third factor having a close relationship to the environmental variable, drives the biological variable (Sheppard *et al.*, 2016). Given input data consisting of insect abundance time series and environmental time series corresponding to the same locations, spatial wavelet coherence produces a test of association between the time series as well as a phase difference describing potential temporally lagged effects. Considered in fractions of π, the phase difference $\phi \approx 0$ corresponds to an in-phase relationship (positive cross-correlation), and $\phi \approx \pm 1$ corresponds to an anti-phase relationship (negative cross-correlation), or equivalently a phase-shift of half the period of a sine wave. Intermediate values of ϕ represent relationships lagged by a fraction of cycle length. Illustrations of coherent time series with such phase relationships are given in Fig. 2(c)–(e). The statistical significance of spatial wavelet coherence was assessed by comparing empirical coherences against a null hypothesis of no coherence. Tests were performed separately for short and long timescales; short timescales were defined as those having 2- to 4-year period lengths, and long timescales were those having period lengths > 4 years. Additional details on significance testing are given in Methods S2.

To determine the percentage of synchrony explained by weather and crop composition for each pest species, we selected environmental drivers that were coherent with pest abundances at $P < 0.1$, built a wavelet linear model with selected environmental variables, and applied the wavelet Moran theorem (Sheppard *et al.*, 2016). We used a threshold of $P < 0.1$ due to the conservatism of our test (Methods S2). Again, short and long timescales were considered separately. Wavelet linear models extend coherence testing from examining the relationship between a pair of variables to examining effects of multiple predictors on a response variable by finding timescale-specific, complex-valued coefficients that maximise the coherence between a response variable and one or more predictors (Sheppard *et al.*, 2019). The difference between wavelet spatial coherence and wavelet linear models is analogous to the difference between correlation and multiple linear regression. The wavelet Moran theorem (Sheppard *et al.*, 2016) was then applied to determine the percentage of synchrony in the response variable explained by the model, for both short and long timescales. As part of this procedure, we also calculated ‘cross-terms’ that provide a test of whether assumptions of the wavelet Moran theorem are sufficiently met to have confidence in the result. The precise mathematical meaning of cross-terms is explained in Sheppard *et al.* (2016). If the cross-terms were ≥ 15% of synchrony explained, we considered these assumptions unmet and consequently do not report the percentage of synchrony explained in these cases.

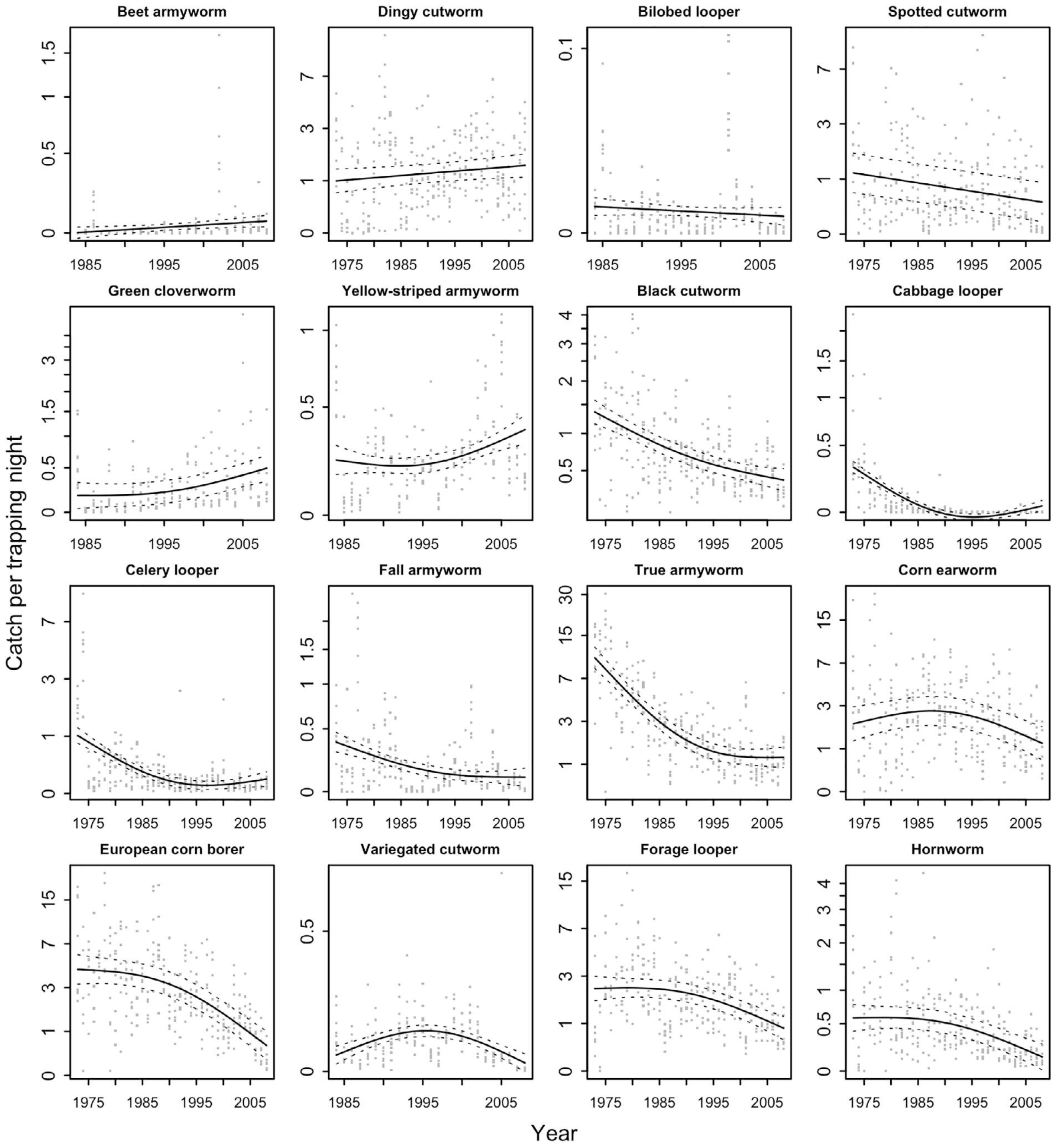

Fig. 3. Temporal trends in pest abundances from generalised additive mixed models. Panels are ordered to group species with similar dynamics. Dashed lines indicate 2 SE.

Analyses were performed in R v.3.5.1 (R Core Team 2018) using the MGCV (Wood 2006) and WSYN (Reuman *et al.*, 2019) packages.

Results

Modelling possibly nonlinear temporal trends in pest abundances, while mainly for the purpose of removing these trends, revealed some noteworthy patterns. Abundance of many lepidopteran agricultural pests in Maryland declined over 1973–2008 (Fig. 3). About half of the patterns were notably non-linear, including some exhibiting changes in the direction or rate of change in the mid-1990s.

All species exhibited statistically significant spatial synchrony, but varied considerably in their patterns of synchrony (Fig. 4). European corn borer, variegated cutworm, and yellow-striped armyworm showed synchrony very consistently at certain timescales, while showing asynchrony at other timescales; this

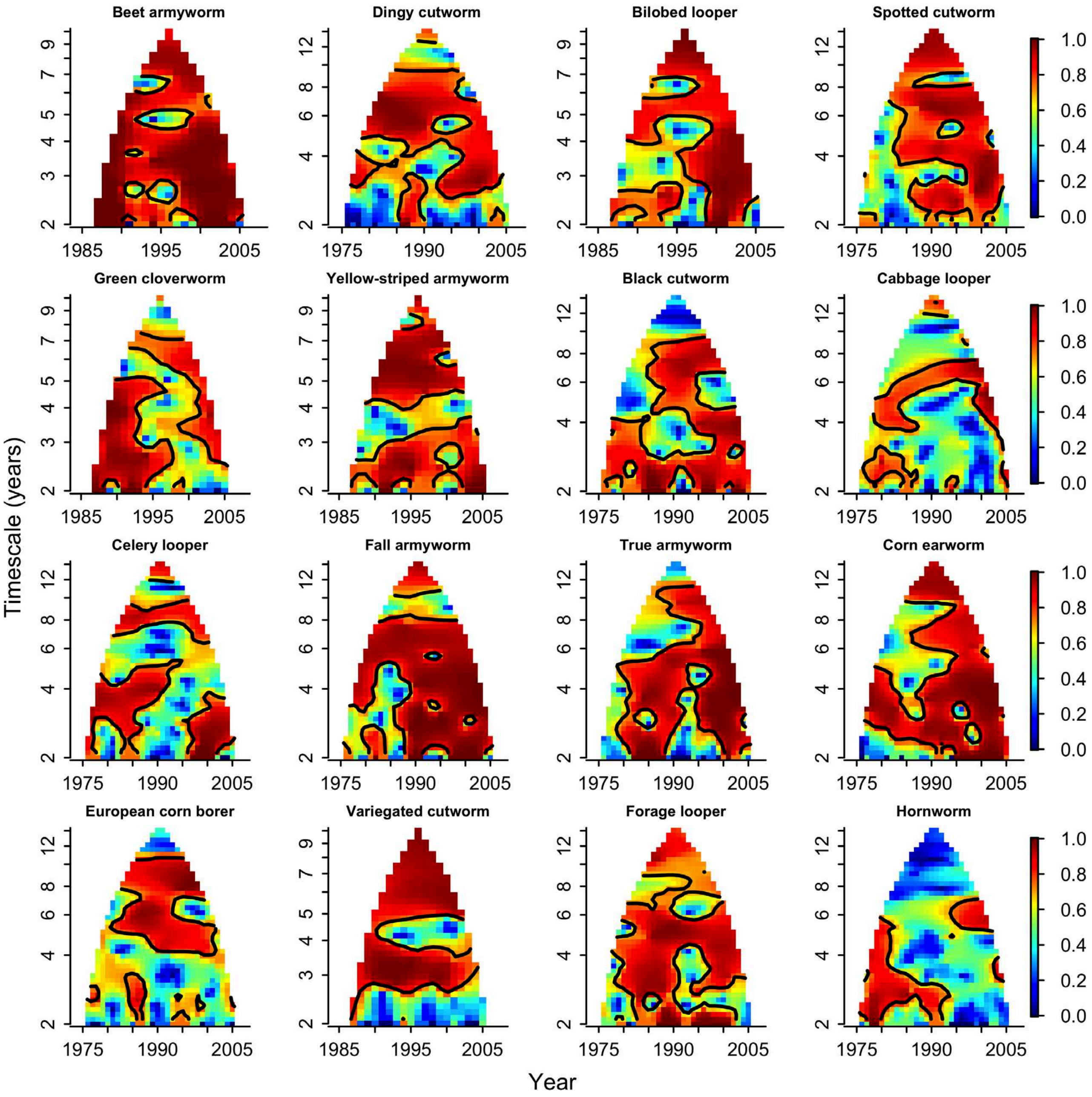

Fig. 4. Wavelet phasor mean fields depicting time and timescale-specific spatial synchrony in pest populations. The order of panels mirrors that in Fig. 3. The black line delineates times and timescales with statistically significant phase synchrony ($P < 0.01$). Plots are 'scalloped' to omit wavelet components that are poorly supported because they overlap the edges of the time series. [Colour figure can be viewed at wileyonlinelibrary.com].

pattern is indicative of population cycles. For example, European corn borer displayed strong synchrony at 5- and 10-year timescales, as evidenced by very high and statistically significant values of the WPMF at these timescales, which were consistent over time. Beet armyworm and fall armyworm showed strong synchrony at nearly all times and timescales, whereas for hornworm the predominant pattern was asynchrony, with synchrony occurring only episodically at certain timescales. Such a pattern may be consistent with the occurrence of occasional synchronising events on a background of asynchrony (Klapwijk *et al.*, 2018). Some species showed synchrony that appeared to change its dominant period over time, such as cabbage looper, for which synchrony shifted from *c.* 5- to *c.* 7-year timescales.

Nearly all species were coherent with one or more environmental variables over at least one timescale band, and weather and crop composition in one case explained 96% of spatial synchrony in pest abundances (Fig. 5). Taking corn earworm

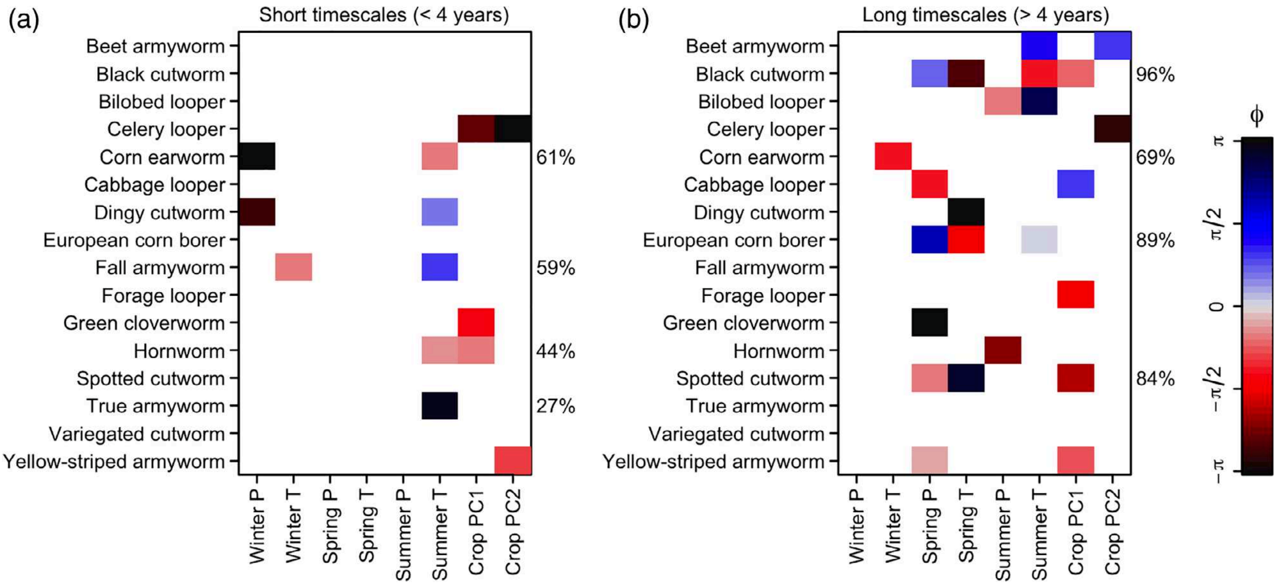

Fig. 5. Spatial coherences between pest abundances and weather variables (P, precipitation; T, average temperature). For coherence relationships with $P < 0.1$, colours denote the phase relationship (ϕ) in fractions of π. Values of ϕ in the range $-0.25 < \phi < 0.25$ are considered approximately in-phase, and $\phi < -0.75$ or $\phi > 0.75$ are considered approximately anti-phase. Intermediate values indicate that one variable leads/lags the other by a fraction of a cycle length. Negative values indicate time-lagged positive effects of the environmental variable on pest population fluctuations, and positive values correspond to time-lagged negative relationships. Values in the right margin give the percentage of synchrony explained by a model containing all variables that individually had $P < 0.1$; no value is given if large cross-terms indicated that assumptions of our partitioning method were unmet. [Colour figure can be viewed at wileyonlinelibrary.com].

as an example, at short timescales its abundance fluctuations exhibited an anti-phase relationship with winter precipitation and a phase-lagged relationship with summer temperatures. In other words, when considering short-timescale fluctuations, increases in winter precipitation tended to reduce corn earworm abundances later that same year; increases in summer temperature tended to increase corn earworm abundances, but in the following year. For an example of a different type of relationship, at short timescales fall armyworm had a phase-lagged relationship with summer temperature, but the positive sign on ϕ indicates a phase-lagged negative relationship; fall armyworm abundances tended to peak approximately a year after years with relatively low summer temperatures. Only variegated cutworm was not substantially coherent with any tested variables. Environmental drivers were more commonly coherent with pest abundance at long (> 4 years; 24 coherent relationships) than at short timescales (< 4 years 13 coherent relationships), and drivers tended to differ between short and long timescales, both in terms of which variables tended to be more frequently coherent across species, and in terms of individual species where the same environmental variable was rarely substantially coherent at both short and long timescales. At short timescales, summer temperature was most frequently coherent with pest abundances (Fig. 5a), while at long timescales spring precipitation and crop PC1 were most frequently coherent with pest abundances (Fig. 5b). While our models explained a larger fraction of synchrony at long than at short timescales, this can be attributed in part to the smaller number of long-timescale oscillations in finite-length time series.

Although we performed 256 tests and most relationships did not receive statistical support, the number of detected relationships exceeds the number expected under type 1 error rates, if that expectation is based on independent tests. For instance, 37 tests were significant at the $P < 0.1$ level (i.e. coherence > 90% of surrogates), whereas the expected number for 256 independent tests was 25.6; similarly, 16 tests were significant at the $P < 0.05$ level, whereas the expected number was 12.8. The probabilities of getting at least this many significant tests by chance alone, taken from a binomial distribution and again assuming independent tests, were 0.009 and 0.14, respectively. Many detected relationships (25 of 37) were phase-lagged, as opposed to in-phase or anti-phase, highlighting the value of coherence methods. Only if expected time lags were hypothesised *a priori* or models with many different time lags were considered could standard linear regression produce equivalent results.

Discussion

The population dynamics of 16 lepidopteran agricultural pests were spatially synchronous over the state of Maryland, U.S.A., and synchrony in these species was largely explained by Moran effects arising from variation in weather and in the areas planted in different major crop types. Despite all focal species exhibiting spatial synchrony, patterns of synchrony differed substantially among species. The dynamics of beet armyworm were spatially synchronous over nearly all timescales and consistently throughout the study period, whereas synchrony occurred more episodically for hornworms, and, for species like European corn borer and variegated cutworm, synchrony was consistent throughout the time series but occurred predominantly at particular timescales. Weather and crop composition shaped patterns of synchrony in these species, with summer temperatures most commonly driving short-timescale pest abundance fluctuations, and long-timescale abundance fluctuations most commonly related to spring precipitation and crop composition. Weather and crop composition explained a larger proportion of synchrony at long timescales. Our finding that regionally synchronous fluctuations in crop composition can drive spatially synchronous crop pest abundance fluctuations appears novel and suggests that the severity of crop pest outbreaks could be moderated by managing the spatiotemporal distribution of crop types to promote asynchrony. Similarly, recent work shows that higher levels of crop heterogeneity enhanced biodiversity, and possibly associated ecosystem services, like biocontrol, in an agricultural region (Sirami *et al.*, 2019).

The high degree of spatial synchrony exhibited by pest populations across Maryland indicates that pest populations tended to fluctuate in unison, at least over certain timescales that differ by species. Because synchronous local patterns are amplified in the area-wide total (Schindler *et al.*, 2015), these synchronous fluctuations can manifest as intermittent or periodic outbreaks, particularly for relatively abundant species like corn earworm, true armyworm, and forage looper. State-wide population fluctuations of beet armyworm, celery looper, corn earworm, dingy cutworm, and forage looper were characterised as cyclic in a separate analysis (Walter *et al.*, 2018), and spatial synchrony probably magnifies the negative impacts of cyclic outbreaks. Although its overall abundance declined, due in part to the introduction of *Bt* corn (Bohnenblust *et al.*, 2013), corn earworm remained relatively abundant throughout the study period, and its populations have become increasingly synchronous since the 1990s. There are possible analogues with whooping cough in the U.K., outbreaks of which became increasingly cyclical and spatially synchronous following introduction of a vaccine that limited the overall incidence of the disease (Rohani *et al.*, 1999).

Synchronous, area-wide pest abundance fluctuations were driven in part by spring and summer weather. Winter weather conditions played less of a role, possibly because the abundances of many pests in Maryland reflect, at least in part, long-distance dispersal from milder locales to the south (Walter *et al.*, 2018). In-phase (positive) responses to temperature could be explained by warm temperatures promoting additional generations, while anti-phase (negative) responses could reflect supra-optimal temperatures hindering development (Thompson *et al.*, 2017). Most often, however, relationships between pests and weather were phase-lagged, suggesting that the biological mechanisms involve effects on generations maturing in future years, e.g. fecundity. Significant coherence between pest abundance and climate occurred more often at long timescales (i.e. period lengths >4 years), suggesting that long-timescale synchrony may be easier to explain in terms of climate drivers than short-timescale synchrony, but the same pattern has not necessarily been observed in other systems (Anderson *et al.*, 2019; Sheppard *et al.*, 2019). Although spring and summer weather influenced dynamics of many pests, the variety of phase differences and timescale-specific relationships exemplify how species-specific ecology and physiology can underpin particular responses to climate variability and change (Haynes *et al.*, 2014; Walter *et al.*, 2018).

Although spatial synchrony was the primary focus of this study, we observed a number of multi-decadal temporal trends that are notable given changes in agricultural practices and technology over the study period, and the status of several studied species as economically significant pests. Species including corn earworm, European corn borer, forage looper, green cloverworm, hornworm, variegated cutworm, and yellow-striped armyworm exhibited qualitative changes in the direction or rate of change in long-term abundance trends during the middle portion of our time series. Major changes in agricultural technology occurred concurrently, including the introduction of *Bt* corn and glyphosate-resistant soybeans in the mid-1990s (Padgette *et al.*, 1995; Fernandez-Cornejo and Wechsler 2012). Consistent with previous reports for the region, corn earworm and European corn borer showed population declines attributable to *Bt* corn (Dively *et al.*, 2018). Not previously reported, populations of forage looper also declined. Forage looper is not a major pest of corn, but has been observed in substantial abundance on fresh corn silks (G.P. Dively, unpublished). Alternatively, enhanced weed control associated with glyphosate-resistant crops may have reduced forage for this and other species.

We also found declines in true armyworm and black cutworm, notable because these are significant pests of corn and other commodities. These declines began well before the introduction of *Bt* corn hybrids, but *Bt* toxins can limit populations of both species (Schaafsma *et al.*, 2007; Kullik *et al.*, 2011; United States Environmental Protection Agency 2013). Declines in these species are more likely driven by significant improvements in controlling weeds that attract ovipositing moths, a trend towards earlier destruction of winter cover crops, and the widespread and increasing use of neonicotinoid-treated corn seed (Douglas and Tooker 2015).

Understanding the responses of pest populations to environmental variation is fundamental to the prediction and management of pest outbreaks. In particular, documenting relationships between weather and pest abundances is an important step towards projecting changes in pest impacts accompanying climate change. We also found that region-wide variation in the areas planted in major crops drove spatially synchronous abundance fluctuations in more than half of studied species. The finding that spatially synchronous crop composition variation can lead to synchrony in agricultural pest population dynamics appears to be novel, and suggests that increasing the asynchrony of changes in crop composition could reduce the regional severity of pest outbreaks. Although locally high populations may still cause yield loss, it might be less likely that pests reach epidemic population densities across the whole region. If our supposition holds, increasing asynchrony would reduce region-wide yield losses during pest outbreaks and increase the stability of regional yields. While the weather is not, to a meaningful degree, under the control of farmers or government agencies whose activities influence agricultural practices, there is some potential to control which crops are planted where and in what quantity. While there are many considerations regarding whether to pursue such a strategy, future research can address how to optimise the scale and spatial configuration of different crop types, and quantify the expected benefits of reducing spatial synchrony of agricultural pest populations.

Acknowledgements

This work was supported in part by USDA-NIFA grant 2017-67012-24694 to JAW. JAW was also supported by a NatureNet Science Fellowship from The Nature Conservancy and the University of Virginia. DCR was partly supported by the James S. McDonnell Foundation and by NSF grants 1442595 and 1714195. We acknowledge the Maryland Extension IPM programme and the Maryland Department of Agriculture for collecting and providing crop pest data. The authors declare there are no conflicts of interest.

Author contributions

JAW conceived the study, led analyses, and drafted the manuscript. GPD and JFT provided the data. LWS and DCR developed statistical methods. LWS, DCR, PDV, and DMJ contributed statistical advice. All authors contributed to manuscript preparation and editing.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Methods S1. Principal components analysis of crop area trends.

Methods S2. Supplementary wavelet analysis methods.

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Accepted 25 November 2019

Associate Editor: Simon Leather