






## REVIEW AND SYNTHESIS

Large Scale, Open Data, and a Big Tent: Leveraging Collaboration, Transparency, and Inclusion to Advance Macrosystems Biology

# Using a social-ecological macrosystems framework to understand how human activities alter ecological synchrony

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## Abstract

1. Different aspects of ecological systems, biotic or abiotic, often fluctuate in coordinated patterns over space and time. Such high concordance between ecological processes is often referred to as ecological synchrony.
2. Human activities, including and beyond climate change, have the potential to alter ecological synchrony by disrupting or enhancing existing synchrony. However, most studies have focused on single scales, limiting our understanding of how human activities alter ecological synchrony across spatial, temporal and organizational scales.
3. With a social-ecological macrosystems framework, we review how human activities, particularly beyond climate change, alter ecological synchrony from the ecosystem level to the population level. For each level, we present a case study that characterizes the roles of human agents in synchrony using data from large-scale observations.
4. We found that human activities alter ecological synchrony through interactions among drivers on multiple scales, often disrupting synchrony, but that adaptive management can maintain or restore synchrony. Human activities potentially modify cascades of synchrony through cross-scale interactions and cross-scale emergence.
5. Finally, we recommend a set of questions to facilitate the explicit consideration of ecological synchrony as a target in sustainable management.

## KEYWORDS

Anthropocene, asynchrony, climate change, global change, mismatch, phenology, social-ecological, synchronization

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## 1 | THE OVERLOOKED HUMAN DIMENSION OF ECOLOGICAL SYNCHRONY

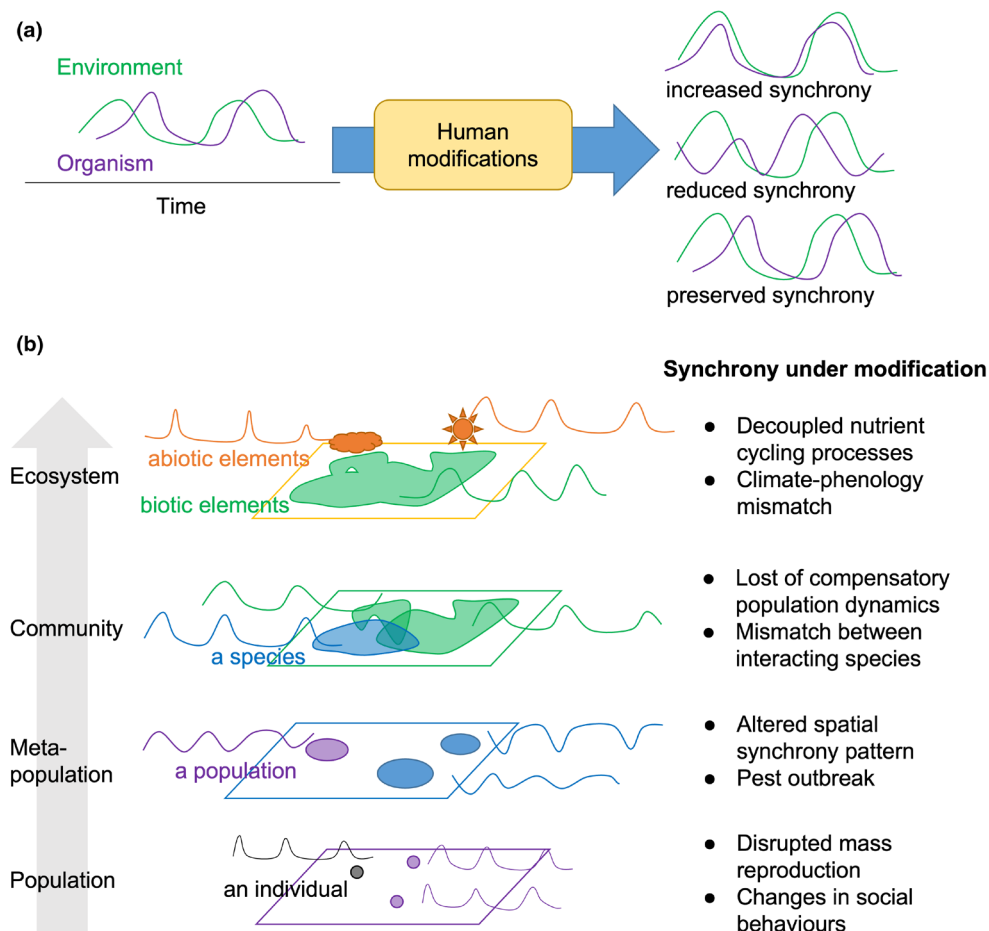
The study of ecological synchrony has become increasingly critical at various scales (Figure 1). For example, landscape ecologists have long recognized the role of metapopulation dynamics, in addition to population size, in determining the persistence of a species (A. Liebhold et al., 2004). Community ecologists have revealed the importance of complementarity over time in addition to species richness in maintaining community stability (Blüthgen et al., 2016; Valencia et al., 2020). Ecosystem ecologists are equipped to examine the coordination between ecosystem processes synthesizing time series in ecology, biogeochemistry, and hydrology (Seybold et al., 2022).

We follow and adapt a definition by Seybold et al. (2022) and define ecological synchrony (hereafter referred to as 'synchrony') as the condition when one or more ecological variables within an ecological system have high spatial and/or temporal coherence. Here, we adopt this general definition of synchrony that encompasses a diverse range of existing definitions of ecological synchrony (Box 1).

Conversely, asynchrony is the lack of coherence in fluctuations of ecological variables (Seybold et al., 2022). Note that phenology, that is, the timing of recurring biological events, is distinct from synchrony; however, the coordinated timing of multiple events is a form of synchrony (phenological synchrony).

The implications of changes in synchrony for the ecosystem and human well-being are far-reaching. The loss of phenological synchrony between species and favourable (abiotic or biotic) environmental conditions, such as resource availability, may negatively affect their persistence (Miller-Rushing et al., 2010; Visser & Gienapp, 2019), but spatially synchronized population dynamics can also increase the risk of extinction during extreme events (Heino et al., 1997; Post & Forchhammer, 2004), undermine demographic rescue among interacting subpopulations (Koenig & Liebhold, 2016), or promote more significant insect outbreaks (Sheppard et al., 2016). Such changes in synchrony can cascade to affect ecosystem (dis)services, including food production, pest outbreak and disease transmission.

Anthropogenic climate change has changed the pace of many aspects of ecological systems, such as temperature fluctuations, phenology and population cycles (Post, 2013) (Figure 1a). Furthermore,



**FIGURE 1** (a) Schematic representation of various possible changes in ecological synchrony with human modifications, including but not limited to climate change. (b) Human activities potentially alter ecological synchrony across levels of ecological organization. Examples are provided for each level. (Although a metapopulation is a spatial extension of the population level, we represent it here explicitly for the large body of literature and distinct characteristics of metapopulation-level synchrony.)

### BOX 1 Diverse definitions of ecological synchrony

We briefly review the development of definitions of ecological synchrony and asynchrony, using direct quotes whenever possible.

#### A Synchrony at a single location

- Ims (1990) defined reproductive synchrony as “the tendency of *individuals* to carry out some part of the reproductive cycle at the same time as other members of the *population*.”
- Loreau and de Mazancourt (2008) built on the temporal correlation of population-level variables *between two species* and defined an index for community-wide synchrony *among multiple species*.
- The terms “phenological synchrony” or “phenological asynchrony” have long been used in various ways. For example, “asynchrony” has been used to discuss phenological mismatches, which “occurs when the time in the annual cycle where resource demands of the *consumer* species are highest does not match with the period where this *resource* is most abundant” (Visser & Gienapp, 2019). Kharouba et al. (2018) considered “a change in phenological synchrony” to be “a directional change in the relative timing of *interacting species*.”
- Seybold et al. (2022) defined (ecosystem-level) synchrony as a “condition when one or more *ecosystem processes* within a designated system have high spatial and/or temporal coherence or consistent lagged behavior.”

#### B Synchrony across multiple locations

- The correlation in abundance (or changes in abundance) among populations was studied first with the term population synchrony. Bjørnstad et al. (1999) defined it as “spatial covariation in population density fluctuations.”
- The concept of population synchrony has then been discussed widely with the term of spatial synchrony. Liebhold et al. (2004) defined that “spatial synchrony refers to coincident changes in the abundance or other time-varying characteristics of *geographically disjunct populations*.” Koenig and Liebhold (2016) similarly defined it as “the coincident change in abundance or value *across the landscape*.” Note that the “coincident change(s)” in these two definitions include complex relationships such as time-lagged correlation.
- Extending spatial synchrony to the community level and building on the concept for community-wide synchrony (Loreau & de Mazancourt, 2008), Wang et al. defined community-level spatial synchrony as the “spatial synchrony of total community biomass *across patches*” (Wang et al., 2019; Wang & Loreau, 2014, 2016).
- Spatial synchrony has also been extended to the metapopulation level, with Larsen et al. (2024) defining regional synchrony as “the synchrony *among different metapopulation*.”
- Vagnon et al. (2024) defined ecosystem synchrony as “the similarity in the temporal fluctuations of a given ecosystem function *among multiple ecosystems*” (within a meta-ecosystem).

#### C Asynchrony

- Seybold et al. (2022) defined asynchrony as “the lack of coherence in fluctuations of ecological processes.”
- Asynchrony usually refers to the lack of a relationship, but not to the negative direction of a relationship. For example, the time series of predator and prey population sizes can be exactly out of phase but still in synchrony with each other.
- In practice, it is often hard to distinguish out-of-phase synchrony, the lack of synchrony, and undetectable synchrony with noisy data (Gouhier & Guichard, 2014).

climate change can alter synchrony through diverse mechanisms operating across various ecological, spatial and temporal scales. On the one hand, climate change has been found to disrupt ecological synchrony, as organisms differ in their sensitivity to climatic variables (Youngflesh, Socolar, et al., 2021). For example, disparate phenological changes between species in response to changing climate (Kharouba et al., 2018; Menzel et al., 2020) can change the outcome of their interactions, resulting in reduced fitness or ecosystem services (Cushing, 1969; Kharouba & Wolkovich, 2020). On the other hand, climate change can enhance the synchrony of a wide range of ecological dynamics in a single location (Youngflesh, Li, et al., 2021) or across multiple locations (Koenig & Liebhold, 2016), often acting through an underlying abiotic driver such as extreme weather (Rahmstorf & Coumou, 2011).

However, the role of human disturbance and management, in addition to anthropogenic climate change, is often lacking in discussions about ecological synchrony. Emerging evidence suggests that human activities, such as land use change or habitat management, might alter ecological synchrony in various ways (Figure 1a). For example, habitat fragmentation has been shown to disrupt spatial synchrony of population dynamics (Trenham et al., 2003; Zytynska, 2019). Human activities might also increase or enhance spatial synchrony through biotic homogenization (Olden & Rooney, 2006), seen in large-scale intensive farming in monocultural fields (Benton et al., 2003), and the replacement of native species by exotics during urbanization (McKinney & Lockwood, 1999). Such biotic homogenization can synchronize, for example, abundance

fluctuations in agricultural pests over space (Walter et al., 2020). There are also adaptive management practices with the goal of improving synchrony, such as changing sowing dates to alleviate phenology asynchrony between the life cycles of crops and temperature (Bai et al., 2019). Given the heterogeneous findings, we have a limited consensus or generalized understanding of how synchrony is shaped by management in human-dominated landscapes.

A key gap in the current literature is that human modification of ecological synchrony is often examined within subfields that focus on a single scale, but there is a need to study it across spatial, temporal, and organizational scales. This involves (1) synthesizing findings from local studies over larger scales (regional to continental), (2) comparing across levels of organization to reveal similarities and scale-dependent differences, and (3) characterizing how synchrony propagates and emerges across scales. Failing to consider large-scale patterns, scale dependency, and cross-scale processes limits our ability to anticipate cascading consequences and design effective management interventions.

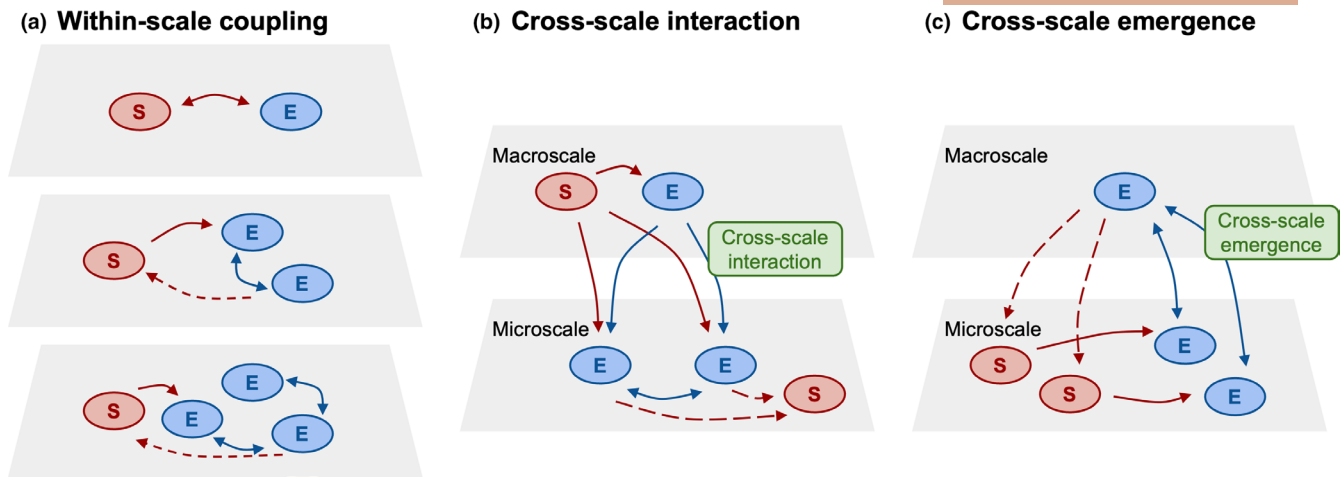
In this review, we address the understudied involvement of human activities in changing ecological synchrony under a social-ecological macrosystems framework. We review existing evidence and understandings on the impacts of anthropogenic activities, interacting with climate change, on ecological synchrony across levels of organization (Figure 1b). With ever-increasing data collection efforts, including observatory networks, remote sensing and citizen and community science projects, it has become increasingly feasible to systematically investigate the influence of human activities on synchrony. Here, we demonstrate with four case studies from a range of study systems (Table 1), quantifying the effects of (A) irrigation on ecosystem-level synchrony in croplands, (B) human footprint on community-level synchrony of bird species, (C) managed harvesting on metapopulation-level spatial synchrony in marine populations, and (D) temperature on population-level synchrony of mosquito emergence. With these case studies, we demonstrate ways to leverage the social-ecological macrosystems framework and big data on large spatial scales to enhance our understanding of human modification of ecological synchrony.

## 2 | A SOCIAL-ECOLOGICAL MACROSYSTEMS FRAMEWORK

Synchrony can be found across scales (Figure 1b), referring to individual behaviour, population fluctuations within (Saino et al., 2011; Visser et al., 2012) or between species (Rafferty et al., 2015; Renner & Zohner, 2018), and interactions between abiotic and biotic components (Beard et al., 2019; Seybold et al., 2022). Synchrony might be found between different systems at the same location, such as prey and predators (Vasseur & Fox, 2009), herbivores and plants (van Asch & Visser, 2007), organisms and abiotic environments (Özkan et al., 2016) and many more. Synchrony might also take place at disjunct locations across space (i.e. spatial synchrony) (A. Liebhold et al., 2004), including the masting behaviour of plants

TABLE 1 Summary of case studies across levels of organization.

Case study	A	B	C	D
Level of organization	Ecosystem	Community	Metapopulation	Population
Variables with possible synchrony	Temperature, latent heat flux, gross primary productivity	Abundance of birds of different species	Abundance of marine organisms among sites	Emergence of individual mosquitoes
Measure of synchrony	Correlation between start of season	Mean of pairwise correlation coefficients	Decay of correlation over distance	Spread of the timing of events
Human modification	Irrigation	Human footprint index	Managed harvesting	Possibly urbanization
Data sources	Long-Term Agroecosystem Research (LTAR) Network, AmeriFlux, Daymet	Breeding Bird Survey (BBS)	Northeast Fisheries Science Center (NEFSC) fall bottom trawl survey	National Ecological Observatory Network (NEON)
Related definition of ecological synchrony	Temporal coherence in ecosystem processes within a system	Correlated demographic fluctuations across species at a single location	Correlated changes in the abundance of geographically disjunct populations	The tendency of individuals to carry out some part of the reproductive cycle at the same time as other members of the population
Previous studies using this definition	Seybold et al. (2022), Song et al. (2023)	Lahoz-Monfort et al. (2013), Loreau and de Mazancourt (2008), Youngflesh, Li, et al. (2021)	Bjørnstad et al. (1999), Koenig and Liebhold (2016)	Ims (1990), Youngflesh et al. (2018)



**FIGURE 2** Social variables (S) interact with ecological variables (E) and modify ecological synchrony among Es through (a) within-scale coupling, (b) cross-scale interaction, and (c) cross-scale emergence. Solid double-headed arrows indicate synchronous relationships, single-headed arrows indicate directional influence, and dashed arrows represent feedbacks (not all feedbacks are shown to reduce visual clutter).

(Koenig et al., 2015; Lamontagne & Boutin, 2007), regional insect outbreaks (A. M. Liebhold et al., 2012) and wildlife disease outbreaks (Princé et al., 2018). Synchrony (and sometimes asynchrony) plays an important role across multiple scales of ecology, ranging from population persistence (K. C. Abbott, 2011) to species interactions (Kharouba et al., 2018), and to ecosystem functioning (Wang et al., 2021).

To better understand how human activities and ecological synchrony are coupled across scales, we propose a social-ecological macrosystems framework (Figure 2). This framework builds on the Coupled Human and Natural Systems (CHANS) framework (J. Liu et al., 2007) and the macrosystems ecology framework (Heffernan et al., 2014) to explicitly describe how social variables (S) modify the synchrony between ecological variables (E), and how such modified synchrony influences S in feedback.

### Within-scale coupling

Social variables can alter synchrony on the same scale through several pathways. S can be directly in synchrony with E (e.g. adaptive crop sowing dates) (Box 2). S can directly modify one or some of the Es that are involved in synchronous dynamics (e.g. changing population size of predators). S can also rewire the synchrony between multiple existing Es (e.g. irrigation that alters the synchrony at the water-energy-carbon nexus). Altered synchrony, in turn, affects ecosystem services (e.g. crop yield).

### Cross-scale interaction

In a top-down cross-scale interaction, macroscale S (e.g. environmental policies), could directly influence microscale Es in synchrony

### BOX 2 Social-ecological synchrony

The addition of the human modification axis revealed another direction in studying ecological synchrony that is worth further investigation: How humans synchronize our behaviour with the environment. During this period of rapid climate change, human activities are likely to be increasingly desynchronized with ecological events. For example, tourists' visits to wildflowers in a national park are increasingly mismatched with advancing flowering time (Breckheimer et al., 2020). Meanwhile, we actively organize ourselves in relation to ecological events through practices, rules, norms, and technologies. For example, plant breeding has been used to improve the synchrony of maturity in plant populations to enable more efficient harvests (Doebley et al., 2006; Pickersgill, 2007). Organic farmers who are less reliant on synthetic herbicides tend to plant crops later, so that there is greater asynchrony of crops and weeds, thus reducing weed-crop competition (Cavigelli et al., 2008). Expanding to a sociotechnical level, humans have designed physical (e.g. grain silos) and financial (e.g. futures markets) tools to reduce the asynchrony between the supply and demand of commodity crops. The unifying concept of ecological synchrony can be applied to social-ecological systems. Calls have been made for greater ecological intensification in agroecosystems to take advantage of ecological cycles, thereby reducing anthropogenic inputs and harm to intensively managed systems (Bommarco et al., 2013). Framing these issues through the lens of synchrony could be a useful approach to adapting and mitigating the effects of climate change.

(e.g. population of different species in a community) or indirectly influence them through a macroscale E (e.g. climate change). This pathway suggests the possibility of a social Moran effect, where shared or spatially correlated human activities induce synchrony among local-scale environmental variables. Altered microscale synchrony in turn affects ecosystem services on micro- or macro-scales.

### Cross-scale emergence

In a bottom-up cross-scale emergence, multiple microscale Ss (e.g. decisions of neighbouring local farmers) influence microscale Es, which then interact and accumulate across space to produce synchrony of E at the macroscale (e.g. spatial synchrony in metapopulations or metacommunities). This pathway suggests that large-scale synchrony could be managed through collective local actions of human agents. Altered macroscale synchrony in turn affects ecosystem services on micro- or macro-scales.

This framework is proposed to guide the integration of human dimensions into the study of ecological synchrony. First, by explicitly incorporating social variables, it shifts the treatment of human activities from being external covariates or confounders to being active drivers of (a)synchrony. This reframing opens the possibility of considering (a)synchrony as a management target for sustainability. Second, as a generalizable structure, it facilitates analogies and comparisons across systems, enabling the identification of appropriate analytical methods and the transfer of insights across contexts. Third, by linking across scales, the framework helps researchers and managers discover potential causal pathways, including interference from large-scale drivers and unintended large-scale consequences. We demonstrate the use of this framework in the following review and case studies. Our review is based on previously published literature, and our case studies are based on existing datasets, with no new data collection involving human or animal subjects.

## 3 | HUMAN AND ECOSYSTEM-LEVEL SYNCHRONY

Coordination of ecosystem-level processes, such as ecological, biogeochemical, and hydrological processes, has profound ecosystem consequences such as productivity and nutrient cycling (Beard et al., 2019; Seybold et al., 2022). A healthy ecosystem requires synchrony among coordinating processes to maintain stable functioning and services. For example, solute concentrations follow synchronous patterns among streams in a watershed, maintaining spatially stable water chemistry (B. W. Abbott et al., 2018). Ecosystem-level synchrony often follows complex patterns, such as synchrony with characteristic lags, spatial synchrony that decays with distance, or changing degree of synchrony (Seybold et al., 2022).

Synchrony between abiotic variables could be modified by anthropogenic land use, as detected by several local case studies. In aquatic biogeochemistry, a decrease in natural synchrony between

chemical concentrations could be driven by factors such as nutrient input to streams and groundwater, reduced hydrologic connectivity in altered channels, and regulated flow regimes with reservoirs (Van Meter et al., 2020). For example, nitrate concentration and stream discharge were generally in phase in forested and agricultural landscapes, but became more out of phase in urbanized landscapes (Van Meter et al., 2020). In another example, human-impacted watersheds had more asynchronous transport of  $\text{NO}_3^-$  and dissolved organic carbon across a river network, possibly leading to reduced denitrification reactions by microorganisms (Wymore et al., 2021). Climate change and human modifications interact to influence ecosystem-level synchrony, often altering broad-scale top-down and local-scale bottom-up drivers of synchrony, respectively (Figure 2a,b). For example, dual stressors of increased precipitation and urbanization make stream parameters more spatially synchronized in a watershed, potentially resulting in highly degraded water quality (Vogt et al., 2016). In a terrestrial case study, while climate oscillations naturally induce fire synchrony on a large scale, local land uses modify fire regimes and induce more asynchronous fires among sites (Yocom Kent et al., 2017).

Synchrony involving biotic processes, such as the relationship between the phenology and the environment, is also likely to be modified by human activities, but the effect is less understood. Vegetation phenology shifts rapidly in response to climate change but has not kept pace with temperature change in human-dominated landscapes, with a greater lag in more densely populated areas (Song et al., 2021). Climate change and urbanization interact to shift both plant reproductive phenology and frost dates, potentially changing plant frost risks (Park et al., 2023). Animals also shift in breeding phenology under warming temperatures, but are at risk of asynchrony with spring temperature changes (Saino et al., 2011), snowmelt (Lameris et al., 2018), or greenup (Mayor et al., 2017). Altered phenological synchrony has implications for agriculture, forestry, disease dynamics, and recreation. It has yet to be explored how the synchrony between animals and critical ecosystem processes is shaped by human activities. To mitigate the influence of climate change, humans can manage ecosystems to preserve ecological synchrony, such as redesigning sustainable agroecosystems that synchronize the supply of nutrients from soil biota with the fluctuating nutrient demand of plants (Crews & Peoples, 2005; Fontaine et al., 2024) (Figure 2a; Box 2).

### Case study A (ecosystem level)

The tight coupling between water, energy, and carbon cycles has been widely studied, but is usually not interpreted in the context of ecological synchrony. Here we present an example of human modifying ecosystem-level synchrony in highly managed agricultural systems such as croplands. Studies with remote sensing data reveal the possibility that not even the rapid shifts in plant productivity and phenology match the pace of recent warming (Huang et al., 2017; Song et al., 2021). This asynchrony between temperature and

productivity in agricultural systems leads to a novel yield gap under climate change (missed opportunity to enhance productivity despite the potential extension of the growing season), with ramifications for food security and agricultural sustainability (Browning et al., 2021; Mehrabi & Ramankutty, 2019; Spiegel et al., 2018). Nevertheless, adaptive agricultural practices of farmers, such as changing sowing dates and irrigation, could fundamentally alter the nature and degree of synchrony among ecosystem variables (Figure 2a). Here, we use flux data to demonstrate that an actively managed agricultural system introduces a pathway of synchrony at the water-energy-carbon nexus (Figure 3).

We compared managed agroecosystems from two cropland sites with contrasting water management regimes. The selected sites are within 1.6 km of each other at the LTAR Platte River–High Plains Aquifer network location near Mead, Nebraska, USA. Both sites are planted with maize-soybean rotations while one site (US-Ne3 RF) is rainfed and the other (US-Ne2 IR) is irrigated with a centre-pivot system. Irrigation management at US-Ne2 IR is based on the output from a hybrid-maize model, with field-based measurements of evapotranspiration as input (Bhatti et al., 2020). Both sites received similar natural temperature and precipitation, while the irrigated site has an additional  $187 \pm 110$  mm of water per growing season (May–September).

Daily mean temperature data at both sites were retrieved and processed from the 1 km Daymet reanalysis product (Thornton et al., 2016). Latent heat flux (LE, energy used for evapotranspiration) and gross primary production (GPP) at both sites from 2002 to 2015 were obtained from the AmeriFlux BASE data product (Chu et al., 2023) and summarized to daily resolution. After

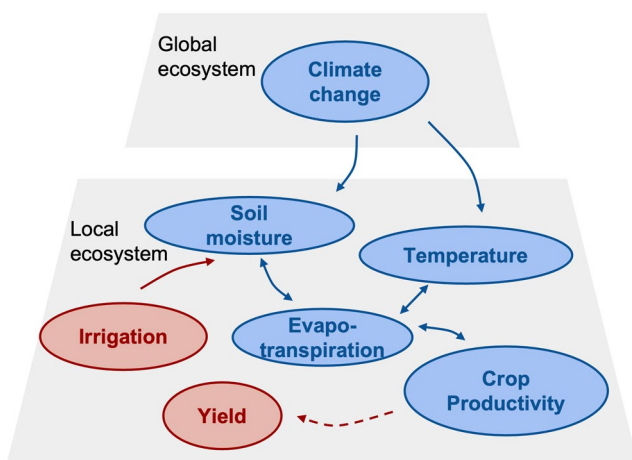
smoothing the three time series, we summarized three start of season (SOS) metrics for each site and year to capture the onset of ecosystem activities in the spring: the day of year when reaching 15°C temperature, 50% maximum LE, and 50% maximum GPP, respectively. We then examined the relationships among these metrics over years, with a higher correlation indicating a higher level of synchrony.

Both sites show clear seasonal patterns in temperature, LE, and GPP, with the irrigated site exhibiting a distinct early and rapid onset of both LE and GPP compared to the rainfed site (Figure 4a). Across years, the SOS of temperature was significantly positively correlated with the SOS of LE only in the irrigated site ( $p < 0.05$ ), but showed no significant correlation at the rainfed site (Figure 4b). While the increase in evapotranspiration in spring is limited by the increase in not only temperature but also natural precipitation, additional water input through irrigation alleviates the constraint of precipitation and allows for a more synchronized onset of evapotranspiration with temperature. The SOS of LE was positively correlated with the SOS of GPP at both sites, but was only significant at the irrigated site ( $p < 0.05$ ) (Figure 4c). Such correlations reflect how the increase of productivity is inherently coupled with the increase in evapotranspiration through stomatal opening.

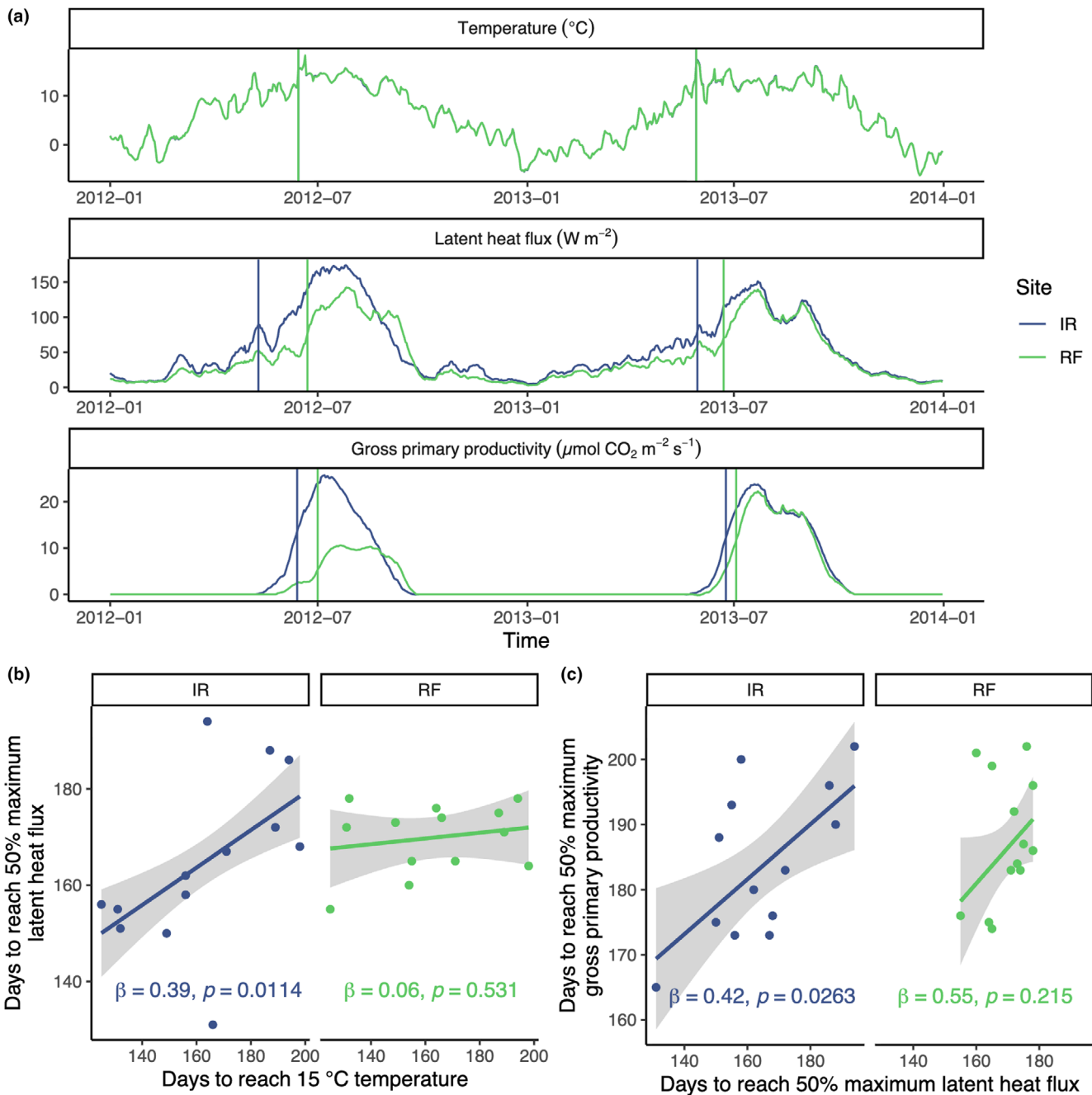
Our results suggest that irrigation introduces a synchrony between temperature and evapotranspiration, which is weaker in rainfed croplands. Combined with the coupling between evapotranspiration and productivity, irrigation strengthens the causal pathway that synchronizes productivity with temperature (Figure 3). From a synchrony perspective, we show how adaptive agricultural practices extend crop growing seasons and increase yields under a warming climate (Troy et al., 2015). Nevertheless, irrigation practices that are synchronized with temperature change but decoupled from precipitation regimes have the risks of exacerbating water scarcity (Fischer et al., 2007; Fujihara et al., 2008) and increasing runoff (Holden & Brereton, 2006). What type of ecological synchrony in human-dominated landscapes should we expect and use as a target for management remains an open question.

## 4 | HUMAN AND COMMUNITY-LEVEL SYNCHRONY

The abundance of species and species interactions within ecological communities drives the structural and functional stability of ecosystems and are therefore main goals for biodiversity conservation and sustainable management (Blüthgen et al., 2016; Hansen et al., 2013; Raimondo et al., 2004). Community-level synchrony has been discussed both on the inter- and intra-annual timescales, in the contexts of community stability and phenological mismatch, respectively. On an interannual timescale, researchers examine how fluctuations in the population of species are coordinated to inform community stability. On an intra-annual timescale, researchers examine how the life cycles of species are coordinated to inform phenological mismatch.



**FIGURE 3** Irrigation alters the synchrony at the water-energy-carbon nexus by reshaping within-scale coupling and interacting with global climate change. Irrigation alleviates water limitation on evapotranspiration and strengthens the synchrony between evapotranspiration and temperature. Along with the synchrony between evapotranspiration and crop productivity, irrigation introduces a pathway to enhance the synchrony between a warming climate and crop yield. The red and blue circles represent social (S) and ecological (E) variables, respectively, following Figure 2.



**FIGURE 4** (a) Example time series of temperature ( $^{\circ}\text{C}$ ), latent heat flux (LE,  $\text{W m}^{-2}$ ) and gross primary productivity (GPP,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) at an irrigated cropland (IR) and a rainfed cropland (RF). Time series have been smoothed with rolling means. Vertical lines indicate dates when reaching 15°C temperature, 50% maximum LE or 50% maximum GPP. (b) Correlation between days to reach 15°C temperature and days to reach 50% maximum LE among years in IR and RF sites, respectively. (c) Correlation between days to reach 50% maximum LE and 50% maximum GPP among years at the IR and RF sites, respectively. Lines and ribbons show predictions with standard errors from robust linear regression. Slopes ( $\beta$ ) and  $p$ -values (robust  $F$ -test) from robust regression are reported.

Although the abundance of single species tends to fluctuate, the total abundance in a community is stabilized, not only by the number of species, but also by their asynchrony, known as the portfolio effect, insurance hypothesis (Blüthgen et al., 2016), or compensatory dynamics (Valdivia et al., 2012; Viviani et al., 2019). Asynchronous fluctuations are often a sign of a stable community, and synchronous community-wide fluctuations possibly represent

a risk to stability (Gouhier et al., 2010). Note that asynchrony here refers to the lack of synchrony (independent fluctuations), rather than out-of-phase synchrony (negatively correlated fluctuations) (Gouhier & Guichard, 2014; Houlahan et al., 2007). Asynchrony might play an even more central role than biodiversity in promoting community stability (Valencia et al., 2020). A series of metrics have been developed to quantify community-level synchrony, often by

comparing the variance of aggregated abundances of taxa to the summed variances of individual taxa (Gouhier & Guichard, 2014; Gross et al., 2014; Hallett et al., 2016; Lepš et al., 2018; Loreau & de Mazancourt, 2008). In addition, community-level between-species synchrony interacts with between-community spatial synchrony to influence the stability of metacommunities (Wang et al., 2019). Reduced species turnover across space, also referred to as ‘loss of  $\beta$ -diversity’ or ‘biotic homogenization’ (Smart et al., 2006), has been shown to synchronize the productivity of grassland communities, destabilizing ecosystem functioning (Wang et al., 2021).

Intense and homogeneous human modifications have frequently been found to increase synchrony among species and thus threaten community stability (Figure 2b). Anthropogenic climate change has been suggested to expose species to warmer temperatures in a synchronized way, changing ecological assemblages, although the extent remains debatable (Colwell, 2021; Trisos et al., 2020). Increasing management intensity increased synchrony in plant and animal communities in grasslands and forests (Blüthgen et al., 2016). Human land use and local water pollutants increased synchrony in aquatic communities in a river basin (Li et al., 2023). Anthropogenic activities measured by nutrient concentrations increased synchrony in riverine bacterial communities (L. Liu et al., 2021). Human management has the potential to promote asynchrony and community stability, such as through herbivore exclusion and reducing grazing intensity, according to a long-term global analysis (Valencia et al., 2020). However, the effects of many management practices are unclear: fertilization and grazing intensification have both been found to have varying effects on synchrony between studies (Blüthgen et al., 2016; Valencia et al., 2020; Zhang et al., 2016).

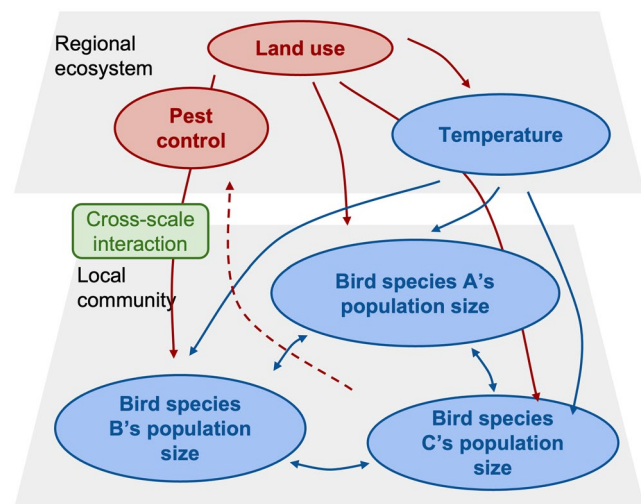
Phenological mismatch, uncoordinated shifts in the timing of interacting key biological events, is a longstanding field that is increasingly studied under the synchrony framework (Bartomeus et al., 2013; Kharouba et al., 2018; Song et al., 2023). Establishing a baseline for synchrony between phenological events (i.e. no phenological mismatch) is challenging (Lindén, 2018). Some phenological events, such as flowering and pollinator emergence, are expected to be highly synchronous (Lindén, 2018; Renner & Zohner, 2018); some, such as the life history of parasites and hosts, have evolved superficially maladaptive asynchronous strategies (Lindén, 2018; Singer & Parmesan, 2010).

Despite extensive discussion on phenological mismatch driven by climate change (Kharouba & Wolkovich, 2020; Miller-Rushing et al., 2010; Renner & Zohner, 2018; Visser & Gienapp, 2019), the influence of human modification has yet to be systematically examined. Urban phenology has been shown to be modified by multiple factors, including urban heat island effects (Meng et al., 2020), modified water regimes (Buyantuyev & Wu, 2012), artificial light at night (Zheng et al., 2021), and the introduction of non-native species (Alexander & Levine, 2019). For example, an increase in urbanization intensity has been found to drive an early spring for plants but not for pollinators along the same urbanization gradient, potentially leading to changes in the structure of plant–pollinator networks (Fisogni

et al., 2020) (Figure 2c). In another example, non-native urban trees were shown to have a delayed spring phenology compared to native species, but the phenology of caterpillars better matches their native hosts; this phenological mismatch explains the significantly lower caterpillar abundance on non-native trees, suggesting risks for invertebrate declines in urban areas (Jensen et al., 2022).

## Case study B (community level)

Rich and stable bird diversity is critical to regulating ecosystem services such as pest control, especially in agricultural landscapes (Barbaro et al., 2017; Boesing et al., 2017; Díaz-Siefer et al., 2022; Martínez-Salinas et al., 2016), with other services such as pollination, seed dispersal, and recreation (Booth et al., 2011; Sekercioglu, 2012). Birds offer an excellent system for studying ecological synchrony, with bird reproductive dynamics often strongly regulated by weather conditions (Shipley et al., 2020), food availability (McKinnon et al., 2012), and interactions with sympatric species (Sanz-Aguilar et al., 2015). These factors have been shown to drive strong within-species population synchrony across space (A. Liebhold et al., 2004). Studies of population synchrony among species, however, are much less common. Quantifying synchrony at the community level (among species at a given location) has the potential to assist in determining the factors that drive large-scale change and to detect the effects of human influence (Figure 5).



**FIGURE 5** Anthropogenic land use (e.g., agriculture) might synchronize the demographic changes of bird species in a community with cross-scale interactions, either directly through the available habitat for species, or indirectly through elevated fluctuations in temperature. The increased synchrony among bird species might threaten the stability of the community and the pest control ecosystem service it provides. Only three species are drawn as examples. Species-specific habitat availability as local-scale ecological variables are not drawn to avoid visual cluttering. Red and blue circles represent social (S) and ecological (E) variables, respectively, following Figure 2.

Using standardized count data on North American birds from 1966 to 2019 obtained as part of the Breeding Bird Survey (BBS) (Robbins et al., 1986), we quantified the degree to which the recorded abundance of passerine bird species fluctuated similarly over time (Figure 6a). At each survey location (Figure 6b), we considered only species that were observed in all years. We retained only locations with ten or more species observed in all years and at least 10 years of abundance data. In total, data from 3190 locations were used, with a mean of approximately 19 species at each site (range 10–46) and a mean of approximately 29 years (range 10–54). We detrended the time series of logged abundance to remove any potential effect of similar long-term trends on estimates of synchrony. At each location, we then calculated Pearson correlation coefficients of the log-transformed abundance for each pair of species. We computed the community-level population synchrony for each location as the mean of these pairwise correlation coefficients (Gouhier & Guichard, 2014; Youngflesh, Li, et al., 2021).

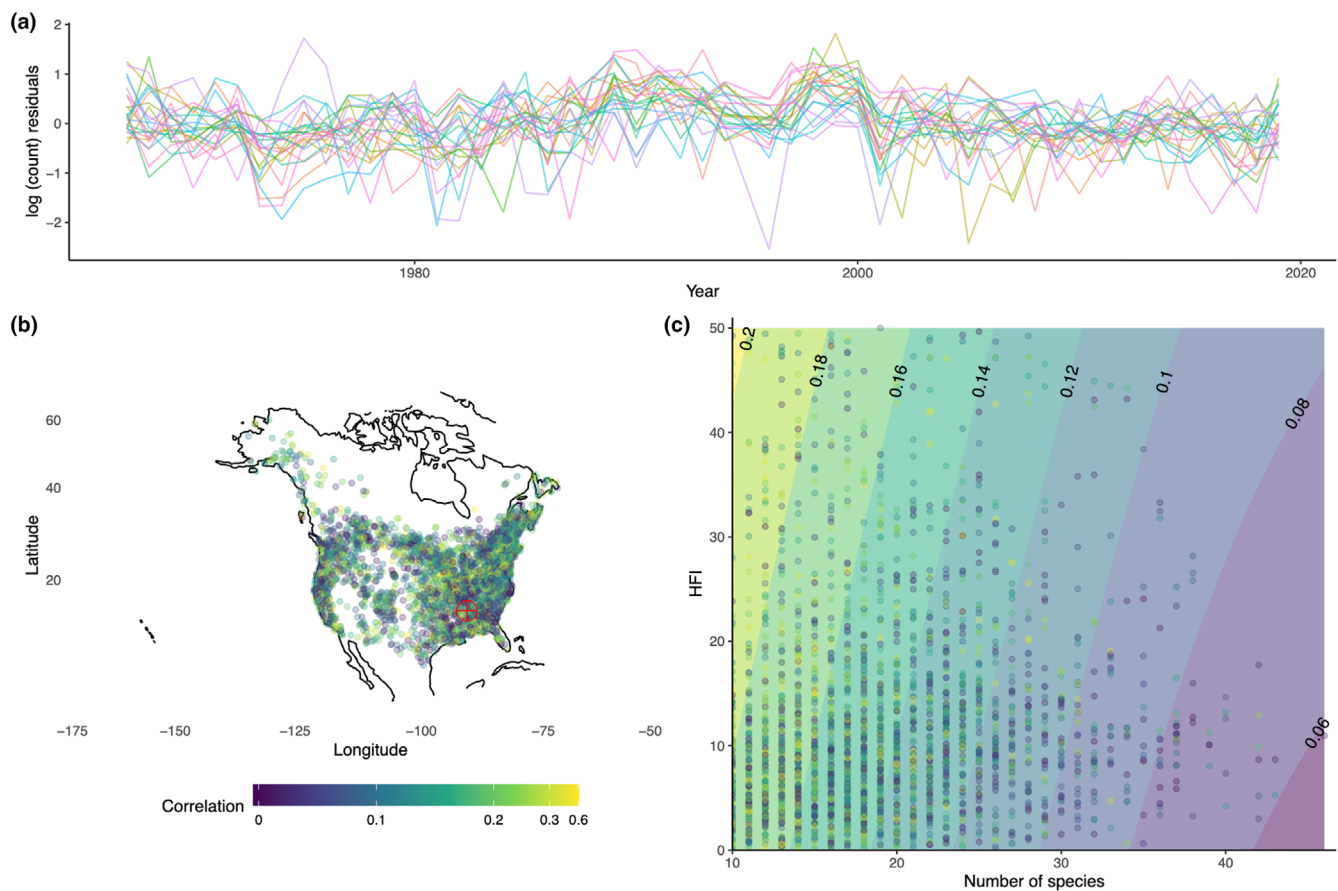
We extracted data on the intensity of human impact on these bird communities from the Human Footprint Index (HFI), which provides a continuous quantitative estimate (from 0 to 50) of cumulative pressure

on the environment in 1993, a midpoint of the study period (Venter et al., 2018a). Although the pressure on this environment is likely to have changed over time, we assess synchrony over the entire time period at each location. At each BBS location, we took the average HFI value within a 40km radius, as the BBS surveys are conducted along a ~40km transect. We modelled community demographic synchrony as a function of HFI and the number of species ( $N$ ) in a given community (as more species within a community will make it more likely that community synchrony is near zero; Loreau & de Mazancourt, 2008), using a generalized additive model (GAM) (Equation 1),

$$y_i = \alpha + \beta \times \text{HFI}_i + f(N_i) + \varepsilon_i,$$

$$\varepsilon_i \sim N(0, \sigma^2), \quad (1)$$

where  $\alpha$  is the intercept,  $\beta$  is the effect of HFI on synchrony.  $f(N)$  is a smooth empirical function to characterize the impact of the number of species on synchrony, as we had no prior expectation for the functional form of this relationship. Models were fitted in a Bayesian framework using the R package 'rstanarm' (Goodrich et al., 2022).



**FIGURE 6** (a) Time series of detrended (using a linear regression) of log-transformed abundance for a community of birds at a random site (St. Florian). Coloured lines each represent a separate species at the site. (b) Spatial pattern of community-level demographic synchrony measured in mean pairwise correlation coefficients. The site shown in (a) is highlighted in red. (c) Community-level demographic synchrony increases with the Human Footprint Index (HFI) (a measure of the intensity of human pressure on the landscape) and decreases with the number of species in each community. The points are empirical demographic synchrony from (b). The points are overlaid on contours of model-predicted demographic synchrony, with contour lines annotated with predicted values.

Most locations had positive estimates of community-level population synchrony ( $0.14 \pm 0.10$ ), though estimates varied across space (Figure 6b). This is in agreement with previous work that has suggested that compensatory dynamics among species are relatively uncommon in ecological communities (Houlahan et al., 2007). The relatively low estimates of community-level synchrony (which could vary from  $-1$  to  $1$ ) are also in line with previous work that has suggested that among-species population synchrony may be quite limited (Michel et al., 2016; Youngflesh, Li, et al., 2021), possibly due to niche separation (Sherry, 1979; Youngflesh, Li, et al., 2021) or differential responses to environmental conditions such as climate and land use change (Michel et al., 2016).

We found a positive association between the intensity of human impact on the landscape and synchrony (posterior mean = 0.0006, 95% CI = [0.0002, 0.0010]) (Figure 6c). This suggests that either ecological communities in human-dominated landscapes respond more similarly to fluctuations in environmental conditions or, alternatively, experience larger interannual fluctuations in environmental conditions relevant for population processes. Humans might be altering ecological synchrony by altering community composition or inducing converging responses among species in the former case or increasing the magnitude of relevant environmental fluctuations in the latter case (Figure 5). While the precise causal factors of greater synchrony among species in more human-dominated landscapes warrant further exploration, this finding suggests that the persistence and stability of these communities may shift over time (Valencia et al., 2020). Such heightened synchrony among species might also amplify pest outbreaks.

## 5 | HUMAN AND METAPOPULATION LEVEL SYNCHRONY

The population dynamics in a metapopulation of a species is often spatially synchronous, widely studied for marine organisms (Bjørnstad et al., 1999; Koenig, 1999; A. Liebhold et al., 2004). Such spatial synchrony is driven by multiple mechanisms, including coupling through larval dispersal (Molofsky, 1994; Ranta et al., 1998), the Moran effect (Hansen et al., 2020; Moran, 1953; Ranta et al., 1997), and interactions with synchronized species (Blasius et al., 1999; Cazelles & Boudjema, 2001; Ims, 1990). Meanwhile, factors such as heterogeneity in environmental conditions (Lande et al., 1999; Pecora & Carroll, 2015), variable or nonlinear population dynamics (S. B. Hagen et al., 2008; Saether et al., 2008; Stenseth et al., 1999; Swanson & Johnson, 1999), and chaos (Allen et al., 1993; Becks & Arndt, 2013) might reduce or eliminate synchrony (Rogers & Munch, 2020).

Species persistence in a metapopulation is often sustained by a combination of complex patterns of phase synchrony (phase-locked rhythms) via local dispersal (Blasius et al., 1999; Vasseur & Fox, 2009) and asynchrony due to local noise and chaos (Blasius et al., 1999; Heino et al., 1997). On the contrary, perfectly synchronous oscillations, via strong dispersal or large-scale environmental

drivers, increase landscape-level extinction risk and threaten species persistence (K. C. Abbott, 2011; Duncan et al., 2015; Koenig & Liebhold, 2016; Luo et al., 2021; Plitzko & Drossel, 2015). As metapopulation level synchrony cannot simply be quantified by a single metric and evaluated by a single threshold, perturbations to the established spatial synchrony can take place in several dimensions, such as correlation strengths, phase differences, and spatial scales.

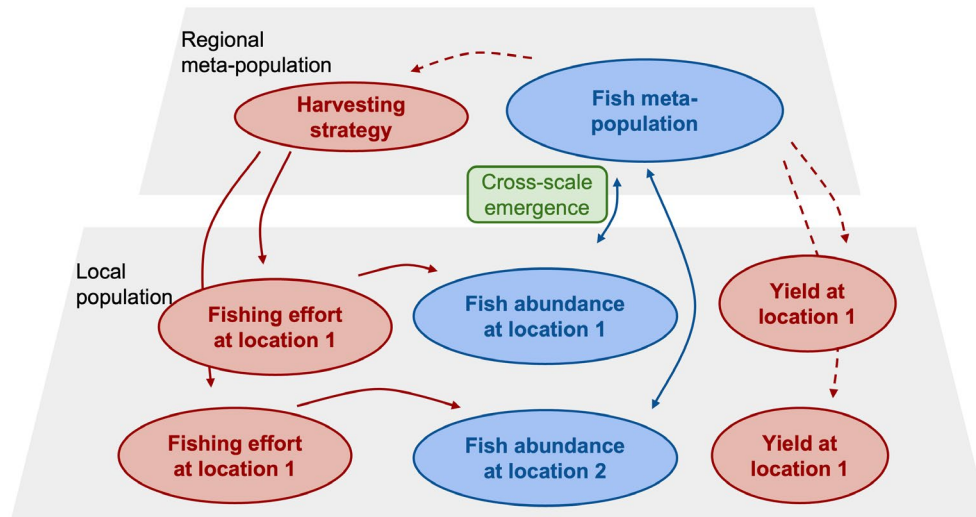
Human modifications often interact with climatic factors to alter spatial synchrony (Figure 2b,c). Historical overexploitation, compounded by the loss of sea ice corridors under climate change, reduced the spatial synchrony of an Arctic Svalbard reindeer metapopulation, threatening the remaining few critically small populations (Herfindal et al., 2022; Peeters et al., 2020). Roe deer populations in North Germany underwent synchronized fluctuations attributed to an expansion in rapeseed cultivation and the North Atlantic Oscillation (NAO) (R. Hagen et al., 2014). Changes in spatial synchrony can impact human well-being by destabilizing human food resources and disrupting the ecological regulation of prey populations.

A unique topic in metapopulation-level (or population-level) synchrony is pest outbreak, with a focus on risks on the persistence of host tree populations. Human modifications have been found to increase spatial synchrony and induce widespread synchronous pest outbreaks through elevated temperature and drought during climate change (Raffa et al., 2008), management practices that favour homogeneous stands of susceptible hosts (Flower, 2016; Raffa et al., 2008), introduction of invasive pests (Potter & Urquhart, 2017), and even pest management practices in conservation lands (Aukema et al., 2006). Taken together, changes in metapopulation-level synchrony driven by human modifications often represent challenges to the persistence of populations and species, including interacting species, although the specific consequences are context dependent.

### Case study C (metapopulation level)

Humans actively manage the populations of marine organisms by changing harvesting efforts based on estimates of current population size and sustainable yields (Methot & Wetzel, 2013), but the effect of such management on spatial synchrony is often overlooked. While traditional optimal harvesting strategies focus on modelling the dynamics of a single population, recent modelling studies have shown the potential of harvesting to reduce or increase the scale of spatial synchrony, depending on the spatial characteristics of the harvesting strategy (Engen et al., 2018) (Figure 7). It is important to avoid the increase of magnitude and scale of spatial synchrony, as highly synchronous metapopulations are more likely to undergo unexpected quasi-extinctions (Engen, 2007). Here we quantify the impact of managed harvesting on the scale of spatial synchrony with long-term empirical data.

We used data from the NEFSC Fall Bottom Trawl Survey (Azarovitz, 1981) from 1973 to 2016 to examine the spatial synchrony of species with managed and unmanaged harvesting (Figure 8a). The



**FIGURE 7** Local fishing effort under a regional strategy of managed harvesting influences fish abundance as geographically disjunct locations, thereby altering the spatial synchrony in the fish metapopulation through cross-scale emergence. Total abundance in the metapopulation, in turn, influences local yield and harvesting strategy. Only two locations are drawn as examples. Red and blue circles represent social (S) and ecological (E) variables, respectively, following Figure 2.

standardized NEFSC Fall Bottom Trawl Survey covers a large area from Cape Hatteras, NC, to the Gulf of Maine (Figure 8b), with the intention of determining the distribution, relative abundance, and biodiversity of fish and invertebrate species found on the continental shelf in autumn (September to November) in the northeastern United States. As the Survey was conducted through stratified random sampling, we considered the centre of each stratum as a site. We selected 16 species (Table S1) that are abundant in the region and estimated their fall abundance with log-transformed catch per unit effort (CPUE). For each species, we removed sampling sites with zero CPUE in half of the time or more in order to focus on sites with reasonable population sizes.

Similarly to case study B, we estimated pairwise temporal correlation in detrended log-transformed abundance with Pearson correlation coefficients between sites (Figure 8b,c). As correlation typically decays with increasing distance, we fitted exponential models to characterize the magnitude and scale (i.e. distance where correlation decays to half) of spatial synchrony (Figure 8c). Finally, we compared the magnitude and scale of synchrony between species with and without active management (Figure 8d). In addition, we also compared the rate of change in abundance by performing a linear regression of total abundance against year (Figure 8d).

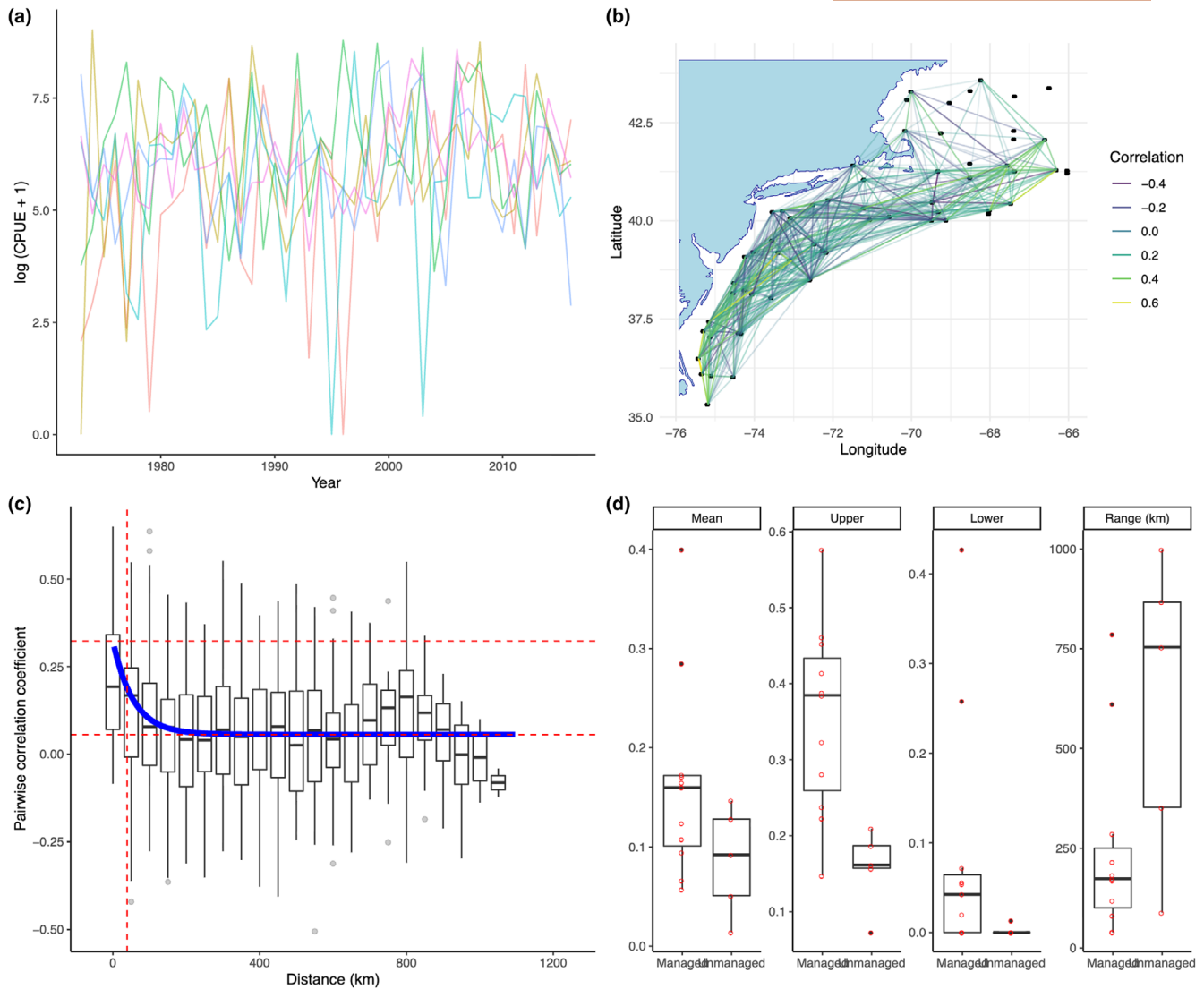
The mean correlations in managed and unmanaged species were  $0.16 \pm 0.10$  and  $0.09 \pm 0.05$ , respectively. The mean correlation (overall synchrony) and the correlation at zero distance (neighbourhood synchrony) were significantly higher in managed species ( $p < 0.05$ , Figure S1), although the former difference cannot be easily interpreted due to the different geographical distribution of species. The distance at which the correlation decayed by half was higher in unmanaged species,  $612 \pm 380$  km, compared to managed species,  $246 \pm 239$  km ( $p < 0.05$ ) (Figure 8d). This pattern can be compared with that in the rate of change in abundance, where managed species generally have faster increases in abundance ( $p < 0.05$ ) (Figure 8d).

The results suggest that active management of marine population size might not only promote increases in total abundance but also reduce the spatial scale of synchrony.

Elevated local and overall synchrony correlated with managed harvesting implies a higher risk of quasi-extinction and more variable or unpredictable harvests at local scales, but the smaller spatial scale of synchrony likely implies limited risks at the regional scale. Even though the maintenance of spatial asynchrony has not been a management objective, the result is understandable, as harvesting quota is often managed within states or in even smaller units (Figure 7). Given the important implications on the persistence of metapopulations (Earn et al., 1998; Harrison et al., 2020; Schindler et al., 2010), spatial synchrony might be explicitly incorporated into future management considerations.

## 6 | HUMAN AND POPULATION-LEVEL SYNCHRONY

While previous case studies focus on ecological synchrony on large spatiotemporal scales and higher levels of organization (ecosystem, community, metapopulation), synchrony between organisms within a population is also common but less studied (Heard et al., 2012; Lamontagne & Boutin, 2007). In the field of phenology, researchers have observed the prevalence and importance of population-level synchrony. Key life cycle events, such as reproduction, often synchronize within a population because of environmental conditions, interactions between individuals, and selection from predators (Fletcher et al., 2010; Koenig et al., 2015; Loe et al., 2005). While most phenological studies focus on point estimates (e.g., first or mean phenological date), assessment of population-level synchrony involves the distribution of phenological dates (e.g.



**FIGURE 8** (a) Time series of log-transformed abundance at different sites for a marine species under managed harvesting, *Loligo pealeii* (longfin squid), as an example of all 16 species. Each colour shows data from a site. Four sites with the highest total abundance are visualized. (b) Map of sampling sites (strata) in the NEFSC bottom trawl survey. Colours show pairwise Pearson correlation coefficients in the population dynamics of *L. pealeii* between some neighbouring sites. (c) Decay of correlation with distance for *L. pealeii*. Blue line shows the fitted exponential decay curve. Red dashed lines show the maximum correlation at a short distance, the minimum correlation at a long distance, and the distance where correlation decays to half. (d) Boxplots comparing managed and unmanaged species by distance where correlation decays to half (km) and rate of change in total abundance (CPUE per year).

standard deviation, quantiles) (Bolmgren, 1998; Carter et al., 2018; Carter & Rudolf, 2019). Phenological synchrony is crucial for fitness of offsprings (Loe et al., 2005), high fertilization success (Koenig et al., 2015), and escape from predators (Fletcher et al., 2010). Furthermore, phenological synchrony strongly influences intraspecific competition by changing the population density and relative competitive advantages of early versus late-arriving individuals (Carter & Rudolf, 2019). As a result, phenological synchrony within populations can affect human food resources and the risk of pest outbreaks.

Established phenological synchrony has been suggested to be disrupted by climate change (Koenig et al., 2015; Loe et al., 2005), further complicated by human modifications. A pronounced example

is the gradual breakdown of coral spawning phenology in the Gulf of Eilat, reducing the probability of successful fertilization and threatening the persistence of the population (Shlesinger & Loya, 2019). The loss of coral phenological synchrony was postulated to be driven by changing sea temperature regimes and hormonal (endocrine-disrupting) pollutants. In another case, the emergence of salmonfly, an aquatic insect species, was more synchronized at sites in a human-impacted river and less synchronized at sites in a natural river (Anderson et al., 2019), possibly due to changing water temperature regimes that altered river channels. Such a change in synchrony led to a shortened duration of subsidy to consumers of salmonfly. Interestingly, along the entire rivers, salmonfly emergence was more synchronized in a natural river compared to a human-impacted river,

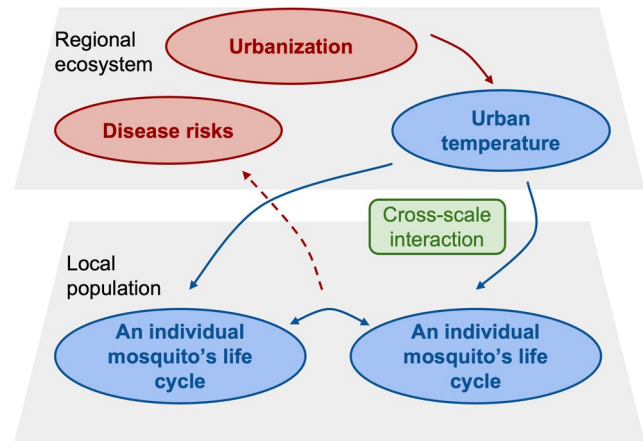
highlighting that the impact of human modification might be scale-dependent (Figure 2a,b).

Apart from synchrony in phenology, individuals in a population might also have distinct synchrony patterns in behaviours, especially in social animals. Synchrony might appear as collective behaviours, a sign of social cohesion, which can be induced or disrupted by human modification. In areas with more pervasive illegal hunting, impala increased behavioural synchrony in response to higher predation risk (Setsaas et al., 2018). The breathing synchrony of pairs of swimming Guiana dolphins has been noted to be disrupted by aluminium research boats, possibly due to interference with acoustic communication (Actis et al., 2018). Synchrony might also appear as alternating behaviours, a form of coordination and cooperation, which again can be altered by human modification in either direction. Parents of house wrens have the behaviour of synchronized nest visits, alternating between parents, more in a rural site compared to a suburban one, likely due to the more fragmented habitat and reduced food availability in suburban areas (Baldan & Ouyang, 2020). Human disturbance measured by tourist accessibility changed the form of synchrony from collective to alternating in the antipredator vigilance of black-necked cranes (Kong et al., 2021). Population-level studies together suggest that human modifications have the potential to alter phenological and behavioural synchrony at fine organization scales, but much is unknown about the prevalence, direction, and magnitude of impacts.

### Case study D (population level)

Mosquitoes (Diptera: Culicidae) are a diverse family of insects that are aquatic in larval and pupal stages and flying adults. They are both an important food source for other organisms and a common vector of pathogens and parasites. The duration of the mosquito season is directly relevant to disease risks, representing an ecosystem disservice. As mosquito emergence is strongly linked to temperature through physiological development rates, climate change and urban heat island effects are likely to shift mosquito season, with feedback to public health (Figure 9). Despite studies on the seasonality of mosquito emergence (Packer & Corbet, 1989), synchronized behaviour on the population level is rarely explored, and even less so for the impacts of anthropogenic global changes.

Here, we study a case of mosquito emergence synchrony across a climatic gradient, showing a viable method that can be used to investigate human influence, such as through urban heat islands. We use the continental-scale high-temporal resolution adult mosquito sampling data from National Ecological Observatory Network (NEON) to examine the ecological synchrony of adult activity within species. Consistent mosquito sampling effort offers an opportunity to study intra-annual synchrony in mobile species populations. While NEON sites are generally located in protected areas with minimal human modification, here we explore environmental conditions that influence synchrony, with application to future research on the role of human activities in mosquito synchrony.

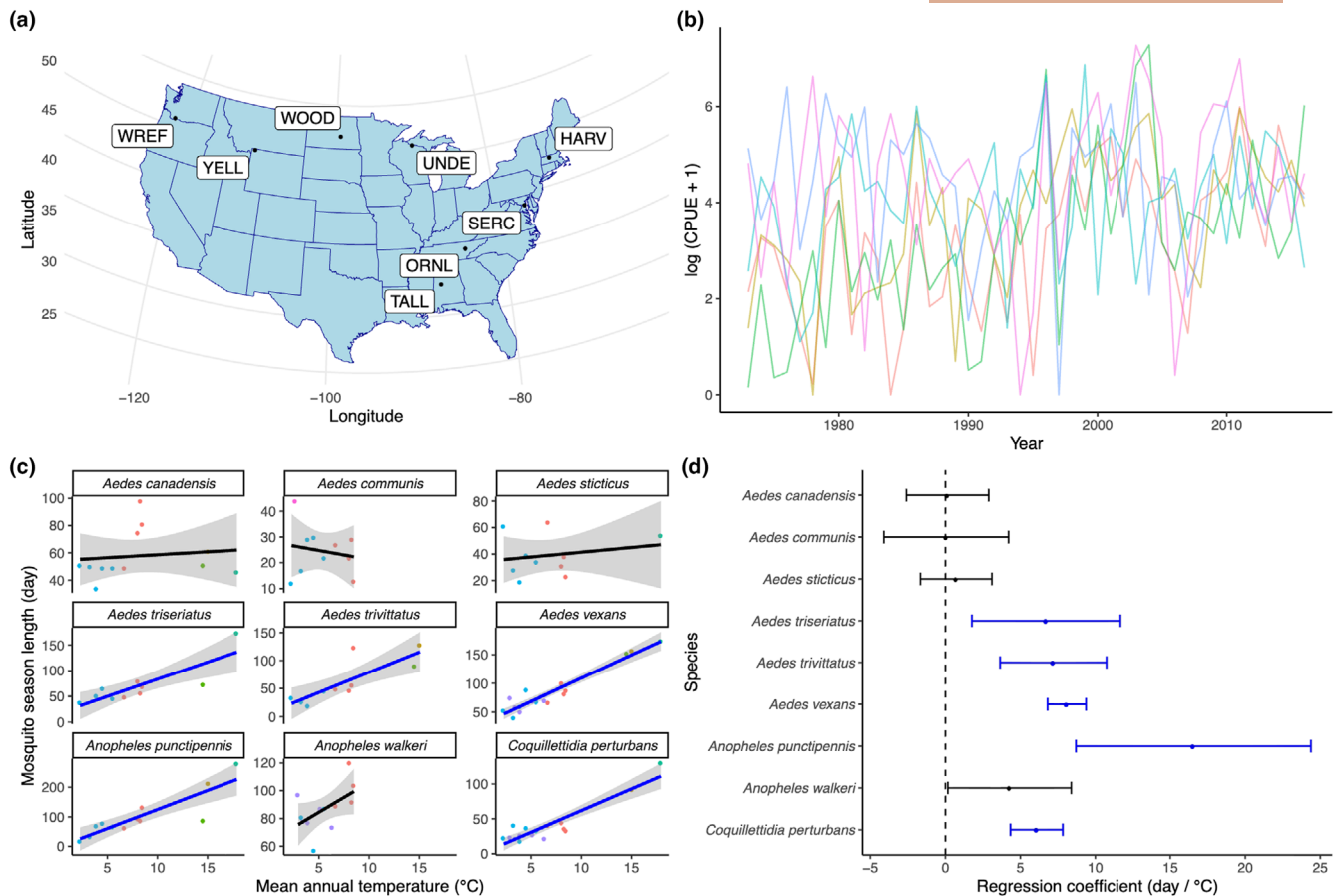


**FIGURE 9** We hypothesize that urban heat islands alter the synchrony of mosquito life cycles within local populations (cross-scale interaction), which in turn influences the timing and magnitude of disease risk in urban areas. Only two individuals are drawn as examples. Red and blue circles represent social (S) and ecological (E) variables, respectively, following Figure 2.

We selected eight NEON sites in the contiguous United States with consistent mosquito sampling efforts (Figure 10a). All sites have low human impacts based on the most recent (2009) Human Footprint Indices (Venter et al., 2018b). NEON mosquito data (DP1.10043.001) (NEON, 2021) for selected sites during 2016–2020 (Hoekman et al., 2016) were trapping data aggregated to weekly values. We estimated daily abundance as the average abundance per trap hour and processing effort for each sampling event to account for differences in the numbers of hours of mosquito trapping and the proportion of the collected sample processed. Given the gaps and observational noise in the data, we modelled seasonal population dynamics for each species by location by year using Bayesian GAMs with the R package ‘rstanarm’ (Goodrich et al., 2022) (Text S1).

After extracting the fitted seasonal population trends, we quantified the population-level synchrony of adult emergence as the length of mosquito season, that is, the number of days between the population reaching 10% and 90% cumulated species-specific abundance in the particular site and year. This metric quantifies how synchronized the emergence events are in time: a lower season length indicates more synchronized emergence events, whereas a higher season length indicates more varied emergence timing among individuals, resulting in a longer duration of species emergence. This metric is commonly used to characterize reproductive synchrony (Thel et al., 2022). For each species, we assessed how season length correlates with mean annual temperature retrieved from Daymet (Thornton et al., 2016) by conducting random intercept-only linear mixed effect models with the site as random effects using the R package ‘nlme’ (Pinheiro et al., 2017). We focused on species with sample sizes (site × year) greater than 10.

We found that intra-annual synchrony measured by mosquito season length varied among species, year, and site (Figure 10b). For five of nine species, there were significant positive correlations



**FIGURE 10** (a) Map of National Ecological Observatory Network sites with adult mosquito sampling data. (b) Smoothed time series of the cumulated abundance of *Aedes trivittatus* at the Harvard Forest (HARV) site as an example. Shaded areas show the mosquito season marked by the population reaching 10% and 90% of the cumulative abundance at that site and year. (c) Correlation between mosquito season length (day) and mean annual temperature (°C). Regression lines with standard errors are shown for each species. Each data point is a site-year, with colours showing different sites. (d) Regression coefficients of linear mixed effect models describing the climate-synchrony relationship for each species. Error bars show 95% confidence intervals. Significant effects are shown in blue.

( $p < 0.05$ ) between mean annual temperature (MAT) and mosquito season length, while accounting for the random effect of sites (Figure 10c,d). The positive correlations are not only the result of climatic differences among sites but also from interannual variations between warmer and colder years (Figure 10c). The result suggests that mosquito species may be less synchronized in warmer years and at warmer sites, leading to more prolonged mosquito seasons. Such relationships between synchrony and temperature, although inferred from data from protected areas, may have implications on the influence of human modifications such as deforestation and urban heat islands (Figure 9).

Exploring the role of human modifications in the population-level synchrony of mosquitoes has important public health implications, as the degree of synchrony in mosquito emergence may influence the strength and duration of vector disease outbreaks (Yang et al., 2009). Human activities potentially alter the timing of mosquito emergence by urban heat island effects (LaDeau et al., 2015), vector control (Bisanzio et al., 2011), and chemical use (Rochlin et al., 2016). However, gaps in data availability prevent us from analysing such effects. NEON mosquito sampling is done in

relatively less disturbed sites, without an urbanization gradient, while data from disease vector control agencies, such as timing, species, and efforts, are not well documented. Although we are not able to test the human modifications to mosquito synchrony, we propose that future mosquito sampling done along urbanization gradients, with both vectors and non-vectors, interpreted in the context of disease vector control, may help us understand this question.

## 7 | SYNTHESIS AND RECOMMENDATIONS

In a changing world, future studies on ecological synchrony should explicitly address the role of not only climate change but also other aspects of human activities. On the one hand, changes in synchrony during climate change may be exacerbated by anthropogenic disturbance; on the other hand, humans may actively manage synchrony to mitigate the negative consequences of climate change. Reviewing the literature on ecological synchrony, we identified multiple streams of evidence on the impacts of human modification, leading

to different responses in synchrony in human-dominated landscapes compared to natural landscapes. With four case studies from distinct systems, we demonstrated methods to characterize the roles of human agents in modifying ecological synchrony with big data on large scales across levels of ecological organization.

Despite diverse findings, we summarize general relationships between humans and synchrony on each level of organization.

1. Ecosystem level: Urbanization disrupts ecosystem synchrony and thus destabilizes regulating ecosystem services. Climate change and urbanization interact to induce phenological asynchrony between organisms and environmental conditions, but adaptive management in agroecosystems could alleviate such phenological asynchrony.
2. Community level: Intense and spatially homogenous management of the landscape increases community-wide synchrony among species with complementary ecological functions, threatening community stability. Urbanization exacerbates phenological asynchrony among interacting species.
3. Metapopulation level: Large-scale homogeneous management is likely to increase the magnitude and scale of spatial synchrony in metapopulations, thus risks for the collapse of resources or pest outbreaks.
4. Population level: Diverse human activities, such as pollution and noise, disrupt the synchrony of the reproduction or social behaviours of individual organisms.

The social-ecological macrosystems framework allows us to integrate across scales and uncover insights that are not apparent when focusing on a single scale.

1. The standard for healthy ecological synchrony is often context dependent, but in general, synchrony among functionally distinct but coordinating processes maintains stable ecosystem services, while asynchrony among functionally similar or redundant processes provides temporal and spatial buffering that enhances resilience.
2. Deviation from the historical baseline of synchrony (prior to extensive climate change and human modifications), either an increase or a decrease in synchrony, often imposes costs on ecosystem functioning and services. Active management with the goal of maintaining or restoring ecological synchrony could alleviate such costs.
3. Climate change and human activities interact to influence (a)synchrony, often with climate change acting as broad-scale, top-down drivers and human activities as local-scale, bottom-up drivers.
4. There exist 'cascades of ecological synchrony' through cross-scale interaction and cross-scale emergence. For example, changes in the emergence between pest individuals on a population level might scale up to changes in the interaction between pest and host plant phenology on the community level (Gulke, 2011), and further to the pace of nutrient input and uptake on the ecosystem level (Grüning et al., 2017). As a result, human disturbance or management on a single scale can alter synchrony on other scales.

To make ecological synchrony an explicit consideration in sustainable management, despite current knowledge gaps, we suggest a set of guiding questions. These questions can be used with stakeholders to clarify and refine synchrony-related management goals.

1. Identify the key ecological synchrony in the system being managed. What variables are included? What scale (spatial, temporal, level of organization) is this synchrony on?
2. Compare the current synchrony with a historical baseline of synchrony. Has the synchrony of interest increased or decreased in magnitude? Has the form (e.g. with or without time lag) or parameters (e.g. time lag) of this synchrony changed? Has the spatial scale of synchrony changed? In the absence of suitable historical data, comparison along a gradient of human modification could be an alternative.
3. Describe the effects of synchrony on key ecosystem services. Is higher synchrony beneficial or harmful to the total amount of ecosystem services? How does it affect the stability of ecosystem services over space and time? How does it affect the distribution of ecosystem services?
4. Infer and predict the impacts of planned management on synchrony. How have similar management practices influenced synchrony in other study systems? Considering the (dis)similarities in social-ecological context, what changes in synchrony can we expect?
5. Explore interacting drivers and unintended consequences. Are there social-ecological variables that could enhance and diminish the effect of the planned management on synchrony, possibly through cross-scale interaction? Does modification of the synchrony of interest have spillover effects to other locations, ecological systems, or social systems, possibly through cross-scale emergence?

The collection and publication of big data, from observatory networks, remote sensing, and citizen and community science projects, provides opportunities to answer these questions on large spatiotemporal scales and cross-discipline collaborations (Reuman et al., 2025). Examples of such observatory networks include the National Ecological Observatory Network (NEON) (Loescher et al., 2016), the Long-term Agroecosystem Research Network (LTAR) (Spiegel et al., 2018), the Long-Term Ecological Research Network (LTER) (Vanderbilt & Gaiser, 2017), and the Critical Zone Observatories (CZO) (Guo & Lin, 2016).

#### AUTHOR CONTRIBUTIONS

All authors collectively conceived and designed the study. Yiluan Song developed and drafted the theoretical framework. Yiluan Song, Mallory Barnes, Kyla M. Dahlin, Travis McDevitt-Galles, Stephan B. Munch, Casey Youngflesh, and Kai Zhu conducted data analyses for case studies and drafted corresponding sections. Yiluan Song, K. Ann Bybee-Finley, Guillermo E. Ponce-Campos, and Benjamin Zuckerberg wrote parts of the introduction and synthesis. The manuscript received substantial input and review from all authors.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

We used published and publicly available raw data in all case studies. Daymet data version 3 (Thornton et al., 2016) are available from ORNL Distributed Active Archive Center (ORNLDAAC): <https://doi.org/10.3334/ORNLDAAC/1328>, here downloaded using the 'daymet' R package (Hufkens et al., 2018). AmeriFlux BASE data product was retrieved from AmeriFlux: <https://ameriflux.lbl.gov/> (Chu et al., 2023). Breeding Bird Survey data (Robbins et al., 1986) are available from USGS ScienceBase: <https://doi.org/10.5066/P97WAZE5>, here downloaded using the 'bbsBayes' R package (Edwards & Smith, 2021). Human footprint data (Venter et al., 2018a) were downloaded from NASA Socioeconomic Data and Applications Center (SEDAC) at <https://doi.org/10.7927/h46t0jq4>. NEFSC Fall Bottom Trawl Survey data (Azarovitz, 1981) are available from Data.gov: <https://catalog.data.gov/dataset/fall-bottom-trawl-survey1>. Mosquito sampling data (NEON, 2021) are available from NEON (National Ecological Observatory Network) data portal: <https://doi.org/10.48443/c7h7-q918>. Processed data and novel code are permanently archived on Zenodo: <https://doi.org/10.5281/zenodo.18852863>.

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## SUPPORTING INFORMATION

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

**Table S1.** List of marine species studied in case study C.

**Figure S1.** Comparing the spatial correlation of managed and unmanaged marine species on the continental shelf of northeastern United States from 1973 to 2016 in terms of the mean correlation among all pairs of sites (mean), the maximum correlation at a short distance (upper), the minimum correlation at a long distance (lower), and the distance where correlation decays to half (range) (km).

**Text S1.** Preprocessing mosquito population dynamics data.

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