

RESEARCH ARTICLE

Transient synchrony among populations of five foliage-feeding Lepidoptera

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Abstract

1. Studies of transient population dynamics have largely focused on temporal changes in dynamical behaviour, such as the transition between periods of stability and instability. This study explores a related dynamic pattern, namely transient synchrony during a 49-year period among populations of five sympatric species of forest insects that share host tree resources. The long time series allows a more comprehensive exploration of transient synchrony patterns than most previous studies. Considerable variation existed in the dynamics of individual species, ranging from periodic to aperiodic.
2. We used time-averaged methods to investigate long-term patterns of synchrony and time-localized methods to detect transient synchrony. We investigated transient patterns of synchrony between species and related these to the species' varying density dependence structures; even species with very different density dependence exhibited at least temporary periods of synchrony. Observed periods of interspecific synchrony may arise from interactions with host trees (e.g., induced host defences), interactions with shared natural enemies or shared impacts of environmental stochasticity.
3. The transient nature of synchrony observed here raises questions both about the identity of synchronizing mechanisms and how these mechanisms interact with the endogenous dynamics of each species. We conclude that these patterns are the result of interspecific interactions that act only temporarily to synchronize populations, after which differences in the endogenous population dynamics among the species acts to desynchronize their dynamics.

KEYWORDS

forest pest, Moran effect, population dynamics, sympatric species, time-series analysis

1 | INTRODUCTION

Community dynamics have received attention from ecologists for decades. Investigations of patterns and mechanisms of community

composition from year to year have resulted in, for example, the neutral theory (Hubbell, 2001). This theory assumes that in the presence of limited resources the community biomass will be stable, despite yearly variations in community composition. Community

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processes would then lead to compensation in the densities of individual species in response to increases in densities of others (Huisman & Weissing, 1999). This leads to the expectation of negative covariance and asynchrony in the population fluctuations of individual species, which generally does not frequently appear in natural systems (Gonzalez & Loreau, 2009). In addition, within communities, long-term synchronous population fluctuations have been observed among species in several different communities (e.g., Huitu, Norrdahl, & Korpimäki, 2004; Ims & Fuglei, 2005; Loreau & de Mazancourt, 2008). Within communities lateral and trophic interactions determine relationships between species in a direct or indirect manner (Agrawal et al., 2007), shaping the eventual observed patterns in population fluctuations and often synchronized dynamics. For example, many species share fluctuating food resources (Bock & Lepthien, 1976; Jones, Doran, & Holmes, 2003; Koenig, 2001) and this sometimes drives synchronization among species, such as insectivorous bird populations feeding on fluctuating insect populations (Jones et al., 2003; Koenig & Liebhold, 2005) or among seed predators feeding on mast-seeding plants (Curran & Webb, 2000; Schaubert et al., 2002). Specialist predator populations may track prey populations with a lag of one or more generations (Murdoch, Briggs, & Nisbet, 2013). Numerous empirical examples confirm such linkages between consumer and resource populations, and these characteristically result in phase-locking between predator and prey populations (e.g., Korpimäki, Norrdahl, Klemola, Pettersen, & Stenseth, 2002; Stenseth et al., 1998). Alternative prey species that share a common predator, a situation referred to as “apparent competition,” may be forced into synchrony (Bulmer, 1975; Raimondo, Liebhold, Strazanac, & Butler, 2004; de Roos, McCauley, & Wilson, 1998; Small, Marcstrom, & Willebrand, 1993). Some species exhibit lagged synchrony, where oscillations of one species lead the other, and such patterns potentially could be caused by trophic linkages (Tenow, Nilssen, Bylund, & Hogstad, 2007).

In addition to endogenous dynamics, exogenous forcing has been recognized as an important factor in population dynamics and population synchronization. Synchrony has been observed among populations of sympatric species (e.g., sympatric herbivorous forest insects) and has been hypothesized to arise independently of trophic linkages (Hawkins & Holyoak, 1998; Miller & Epstein, 1986; Myers, 1998). In these and other cases, synchrony may be caused by shared exogenous stochastic effects (e.g., weather), analogous to the “Moran effect,” which is a known source of synchrony among spatially disjoint populations of the same species (Hudson & Cattadori, 1999; Liebhold, Koenig, & Bjørnstad, 2004). Due to exogenous forcing, populations might exhibit short bouts of synchronous dynamics as has been shown for the dynamics of different algae species after environmental disturbance (Keitt, 2008).

Although it is clear that either shared exogenous effects or trophic linkages are capable of synchronizing the dynamics of sympatric populations, one question that remains is how differences in the endogenous dynamics may affect that synchronization. A key assumption of Moran's (1953) original work is that synchronized populations exhibit identical patterns of density dependence.

However, theoretical analyses indicate that differences in the endogenous dynamics of two populations can strongly affect the extent to which they can be synchronized via external forcing (Goldwyn & Hastings, 2009; Liebhold, Johnson, & Bjørnstad, 2006).

Different population and community processes often take place at characteristic time-scales. Disturbance (i.e., exogenous forcing) often results in responses on fast time-scales, whereas movement along a population equilibrium takes place at slow time-scales (Hastings, 2004). Theoretical explorations of population dynamics often investigate dynamics at the slow scale, whereas empirical studies of population processes often investigate short time-scale, thus capturing fast scale dynamics. Disturbances result in dynamics at the fast time-scale that may shift the dynamics that are ongoing at the slow time-scale, that is the behaviour of a dynamic system that is not the long-term or final behaviour, coined transient (Hastings, 2001, 2004, 2010). Because disturbances can cause rapid changes in species abundances (Ostfeld & Keesing, 2000) and may lead to temporary synchrony among populations of different species in a community (Keitt, 2008; Vasseur & Gaedke, 2007), temporary bouts of synchrony, that is transient synchrony, might be a common occurrence in natural communities. Most of the literature investigating transient dynamics in insect populations investigate either the transition phases between different patterns of dynamics in populations of a single species (Friedenberg, Powell, & Ayres, 2007) following Hastings (2001), or transient dynamics among spatially structured populations of a single species (Hastings & Higgins, 1994; Ranta, Kaitala, & Lundberg, 1998; Saravia, Ruxton, & Coviella, 2000). Some studies explore transient synchrony in predator-prey interactions in spatially structured populations (Kidd & Amarasekare, 2012; Tobin & Bjørnstad, 2003); they find that transient dynamics in the short term can affect the stability of predator-prey interactions.

We present a study of the dynamics of five sympatric species to investigate relationships among species that share resources, and using long time series we can consider both fast and slow dynamics in interspecific synchrony. Here, we analyse five 49-year-long population time series to quantify time-varying patterns in synchrony among sympatric populations of five oak-feeding Lepidoptera: gypsy moth (*Lymantria dispar* L.; Erebidae), browntail moth (*Euproctis chrysorrhoea* L.; Erebidae), green leafroller moth (*Tortrix viridana* L.; Tortricidae), oak processionary moth (*Thaumetopoea processionea* L.; Notodontidae) and lackey moth (*Malacosoma neustria* L.; Lasiocampidae). All five of these species share hosts, mainly different oak species (*Quercus* spp.), as well as many natural enemies, that is birds, small mammals and generalist arthropod natural enemies, such as parasitoids. The five species here exhibit marked differences in their density dependence and population dynamics, varying from periodic to totally aperiodic. We find that differences among species in their dynamics are associated with diminished interspecific synchrony but we also find evidence for transient synchronization, particularly among populations exhibiting periodic dynamics where periods and strength of periodicity may vary among species.

2 | MATERIALS AND METHODS

2.1 | Data collection

Data analysed here consist of annual records of area defoliated by five species feeding on broadleaf trees in Hungary. The total forest area in Hungary is 1,831,000 ha, of which 1,338,000 ha are comprised of hardwood forests and 306,000 ha are softwood forests (*Populus*, *Salix*, etc.) (NÉBIH: Erdőleltár (Forest Inventory)—webpage). Area damaged by insect outbreaks is reported annually by forest companies, private forest owners and forest managers following specific survey procedures specified by the Department of Forest Protection of the Hungarian Forest Research Institute. The surveys are carried out by experts in forest protection that are trained to recognize the common forest pest species. Using field guides (Csóka, Hirka, Koltay, & Kolozs, 2013; Hirka & Csóka, 2006), the defoliating agent is recorded either by recognizing larvae, which are very distinct for each of the species, or by identifying remnants of feeding activity made by larvae or other species-specific signs (egg masses/pupal remnants—gypsy moth; larval nests—browntail moth/lackey moth/oak processionary moth; leaf rolls—green leafroller moth). When two species have been reported for the same area, visual reports of larval densities were used to attribute the damage according to species density. Entomological specialists employed by the Department of Forest Protection of the Hungarian Forest Research Institute validate these reports; if there is any ambiguity in the reported data, they travel to the area and assess the damage caused by each of the species based on visual surveys of the area. The time series analysed here are comprised of annual values of total (across all Hungary) of forest areas with defoliation exceeding 20% reduction of all foliage. It has been found that such measurements of area damaged correlates well with measures of population abundance (e.g., light trap data) and can therefore be used as proxies for population density (Leskó, Szentkirályi, & Kádár, 1994, 1995, 1997). Furthermore, area of defoliation is a commonly used metric used in analyses of large-scale population dynamics and spatial synchrony (e.g., Allstadt, Haynes, Liebhold, & Johnson, 2013; Haynes, Liebhold, & Johnson, 2012; Liebhold et al., 2006; Williams & Liebhold, 2000).

Damage is reported for the five Lepidoptera species historically causing the most damage: gypsy moth, browntail moth, green leafroller moth, oak processionary moth and lackey moth. All five species are sympatric, univoltine insects with larvae feeding on the foliage of broadleaf trees during late spring to early summer.

The gypsy moth is a notorious pest insect with a large native distribution over most of Eurasia and Northern Africa. Through most of its range, it exhibits periodic outbreaks with periods of approximately 8–12 years (Johnson, Liebhold, Bjørnstad, & McManus, 2005). In Hungary, the species feeds primarily on oaks, especially, Austrian oak (*Quercus cerris*), pedunculate oak (*Q. robur*) and sessile oak (*Q. petraea*) as well as hornbeam (*Carpinus betulus*), alder (*Alnus* spp.), aspen (*Populus* spp.) and willow (*Salix* spp.). The species feeds solitarily and overwinters as neonate larvae inside the egg. The

dynamics of gypsy moth populations are believed to be influenced by interactions with pathogens, parasitoids and small mammals (Elkinton & Liebhold, 1990; Hoch, Zubrik, Novotny, & Schopf, 2001).

Like the gypsy moth, the browntail moth is highly polyphagous, feeding on at least 26 plant genera ranging from oak to roses. It is a univoltine, solitary species that overwinters as a first instar and adults emerge in July. Although extensive information about its dynamics is lacking, parasitoids appear to play a key role in its dynamics (Elkinton, Preisser, Boettner, & Parry, 2008; Frago, Pujade-Villar, Guara, & Selfa, 2011).

The green leafroller moth is a polyphagous herbivore on oak. This species is univoltine, and larvae are solitary feeders on buds. It hibernates in the egg stage. Outbreaks have been recorded with a period of eight to 10 years (Schroeder & Degen, 2008). The dynamics of green leafroller are strongly influenced by interactions with its host plant (Hunter, Varley, & Gradwell, 1997; Kapeller, Schroeder, & Schueler, 2011).

The oak processionary moth is a gregarious specialist on oak. The species overwinters in the egg stage. After hatching in spring, larvae live in “nests” spun with silken thread. While occasional outbreaks have been recorded, they do not occur with any regularity. There is some indication that the frequency of outbreaks by this insect have recently increased in certain parts of Europe (Meurisse, Hoch, Schopf, Battisti, & Gregoire, 2012). The species is distributed throughout Europe. Natural enemies are the main cause of mortality in oak processionary moth during the egg and larval stages (Wagenhoff & Veit, 2011).

The lackey moth, another polyphagous species, is known to feed on fruit trees (*Malus* spp., *Pyrus* spp. and *Prunus* spp.), willow (*Salix* spp.), hornbeam (*Carpinus* spp.), lime (*Tilia* spp.) and oak (*Quercus* spp.) and is distributed across Europe, Asia and North Africa. The larvae spin silken tents, which they mostly use for thermoregulation. The species overwinters in the egg stage. The larvae feed from April through June. Relatively little is known about the dynamics of this species although parasitism is believed to be an important source of mortality (Özbek & Coruh, 2010).

Time series of area defoliated by each species were \log_{10} -transformed, then de-trended and centralized yielding a series with mean of zero and a standard deviation of one prior to analyses (Cazelles et al., 2008). These transformations are commonly applied prior to application of wavelet analysis and eliminate non-stationarity prior to AR analysis. The lackey moth series contained a missing value in 1968. To keep the series complete, the missing value was replaced with a value estimated using linear interpolation from the preceding and following values.

2.2 | Time-series analyses

2.2.1 | Characteristics of individual time series

To assess similarity in density dependence among the five species, we fit a second-order autoregressive [AR(2)] model to the transformed and standardized time series (AR—stats-package in R;

Percival & Walden, 1993). The values of the AR(2) coefficients indicate the type of (delayed) feedback in populations as described (on a logarithmic scale) by $R_t = a_1 X_t + a_2 X_{t-1} + \mu_t$. Here, R_t represents the population growth rate at time t , X_t represents the log population density at time t , X_{t-1} represents the log population density at time $t - 1$, a_1 and a_2 represent the first- and second-order autoregression parameter, and μ_t represents the perturbation effect (an identical distributed random number with a mean of zero) (Royama, 1992, p. 93–96).

To characterize periodicity and evaluate the presence of changes in periodicity over time, wavelet analysis (Cazelles et al., 2008) was applied to the transformed and standardized time series of area damage for each species (Torrence & Compo, 1998). The continuous wavelet transform is a common tool for analysing localized intermittent oscillations in time series (Grinsted, Moore, & Jevrejeva, 2004); in other words, wavelet analysis can be used to analyse time series that contain non-stationary power at many different frequencies (Daubechies, 1990). By decomposing a time series in time-scale (equivalently, time-frequency) space, one can determine the dominant mode of variability and the variation of these modes over time (Torrence & Compo, 1998). This method of analysing time series is increasingly applied to ecological time series (Cazelles et al., 2008; Haynes et al., 2012). The principle of the analysis is to measure the fit of wavelets (oscillating periodic functions) to a time series. The resulting wavelet transform is a complex matrix giving the strength and phase of oscillations, indexed by time and time-scale. The wavelet power spectrum, corresponding to the strength of oscillations, is a matrix of period (number of years) by time (year) and can be plotted in a contour plot to visualize the periodic behaviour of the time series (Torrence & Compo, 1998). Wavelet spectra can be affected by the lack of data at the beginning and end of series; therefore, when the spectrum is plotted, a cone of influence is drawn to show the regions (outside the cone of influence) where such time-series edge effects are most influential. These effects are more important for time series with less regular fluctuations compared to time series with cyclic behaviour (Torrence & Compo, 1998). We used the continuous Morlet wavelet transform (Farge, 1992; Grenfell, Bjornstad, & Kappey, 2001) to calculate the wavelet spectrum of each time series (Cazelles et al., 2008). Differences between species in population fluctuations through time were quantified based on dissimilarity of wavelet transforms, as in Rouyer, Fromentin, Stenseth, and Cazelles (2008). To compare persistent vs. transient dynamics, the global wavelet power spectrum was calculated as the average over time of the power spectrum. Statistical significance of wavelet power at $\alpha = 0.05$ was determined by comparison with an AR(1) process. All wavelet analyses were carried out using the package `BIWAVELET` version 0.20.11 (R platform for statistical computing; Gouhier, Grinsted, & Simko, 2016).

2.2.2 | Interspecific synchrony

We used wavelet coherence to assess the time-varying pair-wise synchrony between the species (Grinsted et al., 2004). Values of wavelet coherence between a pair of time series are relatively high

when the time series have similar periodicity and consistent phase differences through time. The consistency of phase differences is a key quality because it implies some sort of causal relationship between the time series (Sheppard, Bell, Harrington, & Reuman, 2016); for example, unrelated population time series could oscillate at the same frequency because their underlying dynamics are similar, but without a synchronizing mechanism such as shared environmental fluctuations, competition or trophic linkage, the time series would have consistent phase differences only by chance. Like the wavelet power spectrum, wavelet coherence can be considered as a matrix indexed by time and time-scale or averaged over time (i.e., global wavelet coherence). Statistical significance was assessed by comparison with distributions of wavelet coherences arising from a null model. We considered wavelet coherence to be statistically significant when it exceeded the 95th percentile of the coherence of 1,000 pairs of surrogate time series that have identical variance and serial autocorrelation properties to the original data, but have the phase of oscillations randomized to eliminate any expected coherence between the signals. Surrogates were generated using a Fourier transform with randomized phases (Sheppard, Hale, Petkoski, McClintock, & Stefanovska, 2013; Sheppard et al., 2016). This method produces surrogate series reproducing exactly the (time-averaged) power spectrum of the empirical time series, but having no consistent phase relationship through time, and oscillations are consistent throughout the time series (i.e., are non-transient). Consequently, the method provides an appropriate null hypothesis against which to test for transient synchrony.

For comparison with our wavelet-based results, we also calculated the cross-correlation function (CCF—stats-package in R; Venables & Ripley, 2013) for each combination of species and identified the maximum (positive or negative) correlation between the species and the lag it occurs at (Table S1 in Appendix S1).

3 | RESULTS

3.1 | Characteristics of individual time series

Raw and transformed damage time series for each species is shown in Figure 1. Each series showed episodes of abrupt changes in damage but they also exhibited periods of multi-year outbreaks. Across all series, gypsy moth damage reached the highest levels; damage values in 2005 were more than 100 times greater than the highest levels reached by any of the other species in any year (Figure 1). This gypsy moth outbreak during 2003–2006 also coincided with a spike in damage by the browntail moth and the oak processionary moth.

Estimation of the AR(2) coefficients for each species (Table 1) indicated that both browntail moth and gypsy moth exhibit stable (non-explosive) oscillatory dynamics (Zellner, 1971; Figure 2) with periods ≈ 9 and ≈ 7 years, respectively (calculated following Bjornstad, Liebhold, & Johnson, 2008, p. 381). The green leafroller exhibits dynamics that are on the border between oscillatory and non-oscillatory, whereas oak processionary moth and lackey moth

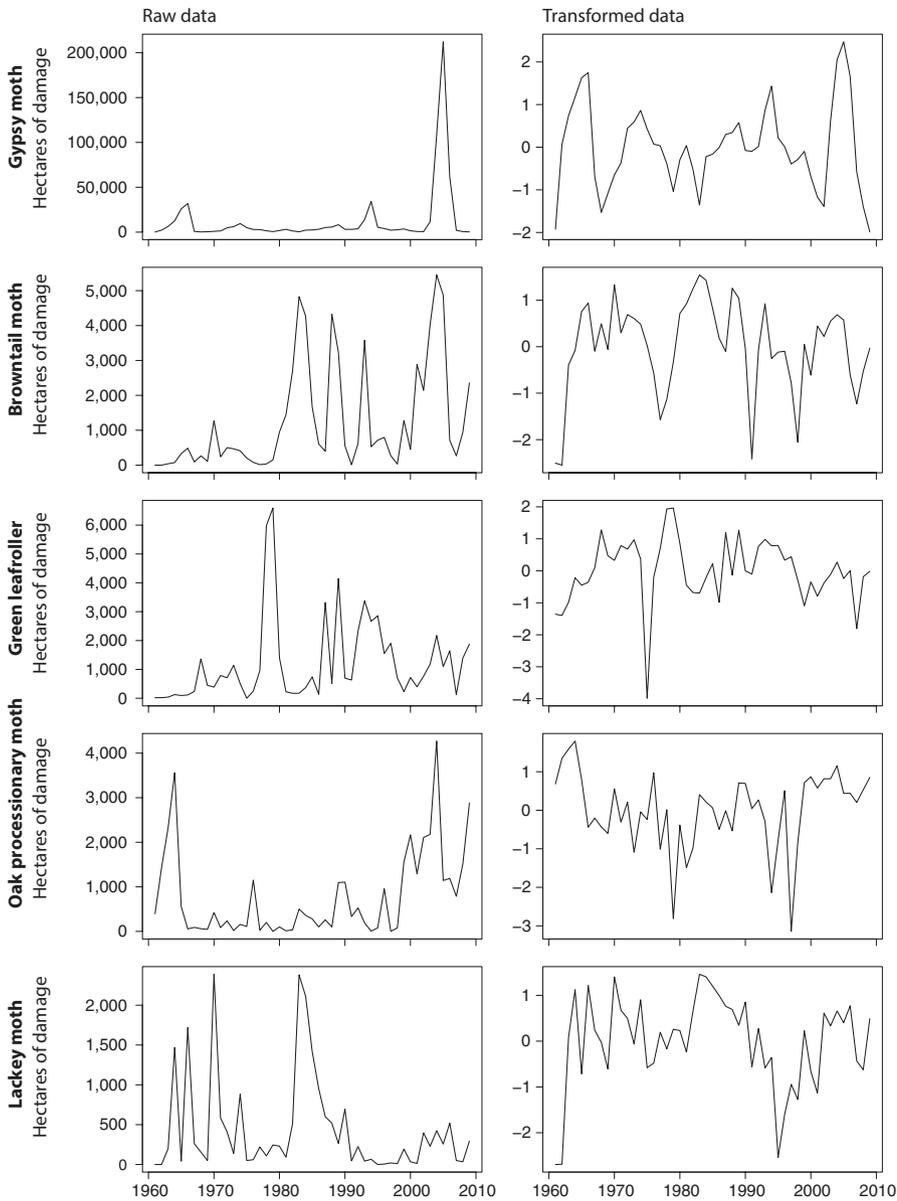


FIGURE 1 Raw and standardized data series for the five forest Lepidoptera species. Time series of area defoliated (ha) by each species was \log_{10} -transformed, then de-trended and centralized yielding a series with mean of zero and a standard deviation of one prior to analyses (Cazelles et al., 2008)

TABLE 1 First- and second-order autoregression parameters (a_1 and a_2) estimated for the five species and the variance (σ^2) explained by the model fit to the data

	a_1	a_2	σ^2
Gypsy moth	1.0684	-0.6426	0.6897
Browntail moth	0.6228	-0.1581	0.3815
Green leafroller	0.3252	-0.0228	0.7548
Oak processionary moth	0.2570	0.2042	0.8795
Lackey moth	0.4508	0.1295	0.8413

exhibit explosive non-oscillatory dynamics. In other words, the gypsy moth and browntail moth (to a lesser extent because of the low explained variance) exhibit population dynamics that fluctuate in a regular manner between low and high densities. The green leafroller borders on regular fluctuations in its long-term dynamics. Both

oak processionary and lackey moth do not show clear periodicity in their long-term dynamics but occasionally rapidly increase their densities in a relatively unpredictable way.

Wavelet power spectra show that each species exhibits periods of transient periodicity (Figure 3). The gypsy moth time series shows significant power at periods of c. 8 years both from 1960 to 1970 and then again from 1997 to 2010 (Figure 3a), which is observed near the edges of the time series. However, in the case of periodic time series, edge effects and the connected cone of influence in the figure are of less significance in time series with cyclic dynamics (Torrence & Compo, 1998). The browntail moth time series show significant power at periods of 4 and 7 years during a single period of 1985–1995 (Figure 3b). The green leafroller shows high power at 2, 4 and 8 years from 1970 to 1985 (Figure 3c). The oak processionary moth exhibits significant power at periods of 2 and 3 years from 1978 to 1981 and again 1991 to 1999 (Figure 3d). And lackey moth exhibits its significant power at periods of 3 years

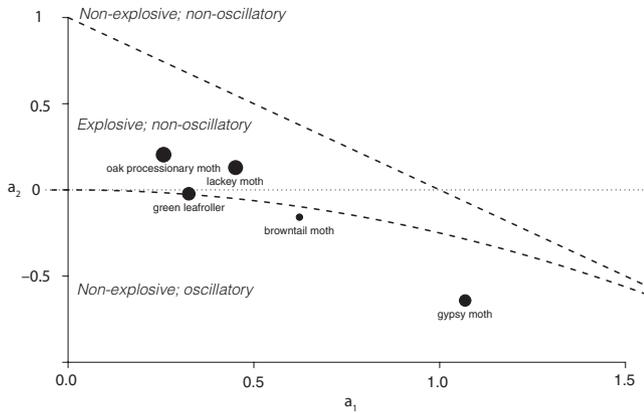


FIGURE 2 Plot of the autoregression parameters (a_1 on x-axis, a_2 on y-axis) estimated for each species. The lines in the graphs indicate the borders between the dynamics associated with different combinations of the a_1 and a_2 parameters (Royama, 1992). For each area in the graph, the corresponding dynamics are given. The size of the points indicates the variance explained by the estimated autoregressive models. (based on Zellner (1971) figure 7.1, on p. 196)

from 1960 to 1969 (Figure 3e). None of the species exhibited persistent periodicity throughout the entire time series from 1961 to 2009.

A comparison of the wavelet spectra for all species shows that the lowest dissimilarity is found between gypsy moth and browntail moth (Figure 4). All species tended to have more similar wavelet spectra to the gypsy moth than to any other species, except for the pairing of lackey moth and browntail moth as indicated by the values calculated for the dissimilarity (Table S2 in Appendix S1).

3.2 | Interspecific synchrony

Most pairs of species exhibited significant wavelet coherence, that is, were synchronized, over some times and time-scales (Figure 5a–j), but the size of these regions in time–time–scale space, and at what time and time-scale interspecific synchrony occurred varied among species pairs. Phase differences also varied among species pairs and among regions in time–frequency space of significant synchrony. For example, the browntail moth and the green leafroller show dynamics that are approximately in phase over 4- to 5-year time-scales from 1985 to 1995 but over a period around year 2000 at periods of 2–3 years, the dynamics are approximately antiphase (Figure 5e). Similarly, there often were lags in synchrony between pairs of species. The assessment of the global (time-averaged) synchrony (Figure 5—line plots) shows that apart from the gypsy moth and lackey moth, none of the species combinations are significantly coherent at any period, confirming the lack of persistent long-term synchrony in the dynamics. Cross-correlation analyses were largely consistent with wavelet analyses in that they detected significant associations between species pairs that were often lagged in time (Table S1 in Appendix S1).

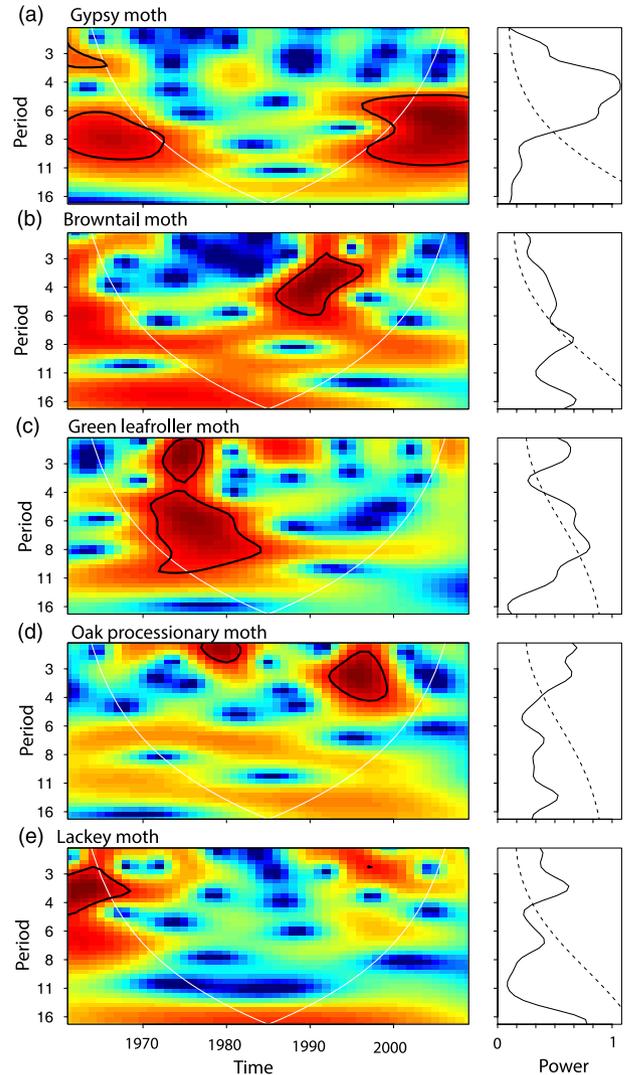


FIGURE 3 Wavelet power spectra and associated global significance for the individual species over time. For the global significance, the average wavelet spectrum is calculated, and the dashed line is the significance of the wavelet period (Cazelles et al., 2008) using the *wt.sig-biwavelet* in R (Gouhier et al., 2016). Spectra are shown for the (a) gypsy moth; (b) browntail moth; (c) green leafroller; (d) oak processionary moth; (e) lackey moth. The colours of the contour indicate the power of the wavelet spectrum, the colour “red” indicates high power the increasingly “colder” colours indicate reduced power. The white line (V-shaped) is the so-called cone of influence, and this is the area of the analysis where time-series edge effects become important (Torrence & Compo, 1998). The black lines in the graph circle areas where the power of the spectrum was found to be significant

4 | DISCUSSION

We analysed damage data collected for five sympatric Lepidoptera species and found that over the long term, species’ dynamics were unrelated to one another, but on fast time-scales, the species exhibited intermittently coherent dynamics. During the five decades spanned by the damage data analysed here, the gypsy moth was

the dominant defoliator, defoliating more than 100 times the area of any other species; most of this damage occurred during a single year, 2005. The damage series of the gypsy moth also exhibited

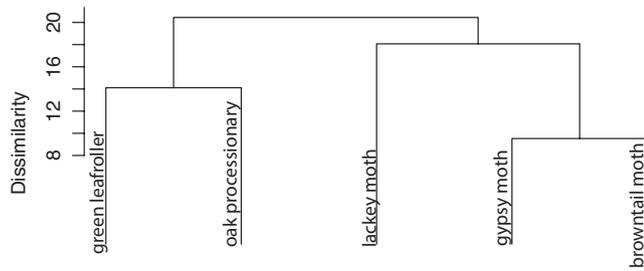


FIGURE 4 Dendrogram indicating dissimilarity among the wavelet spectra of the five species. Dissimilarity values are given in Table S2 of Appendix S1

the strongest pattern of periodicity, exhibiting 7- to 8-year oscillations (with a break in cyclicity from 1985 to 1995, Figure 1), with the strongest periodicity towards the beginning and end of the 50-year study period (Figures 1 and 3), which is included in the cone of influence. Because of known cyclic behaviour of the gypsy moth populations of approximately every 5–10 years (Johnson et al., 2005), time-series edge effects represented by the cone of influence are of minor importance (Torrence & Compo, 1998). Periodicity was less evident in the other four species, although they each went through at least brief phases during which they exhibited periodic behaviour.

Although population dynamics among the five species were not consistently synchronized through time, there is evidence of transient synchrony for shorter bouts of time (Figure 5). In particular, gypsy moth damage was intermittently synchronized with other

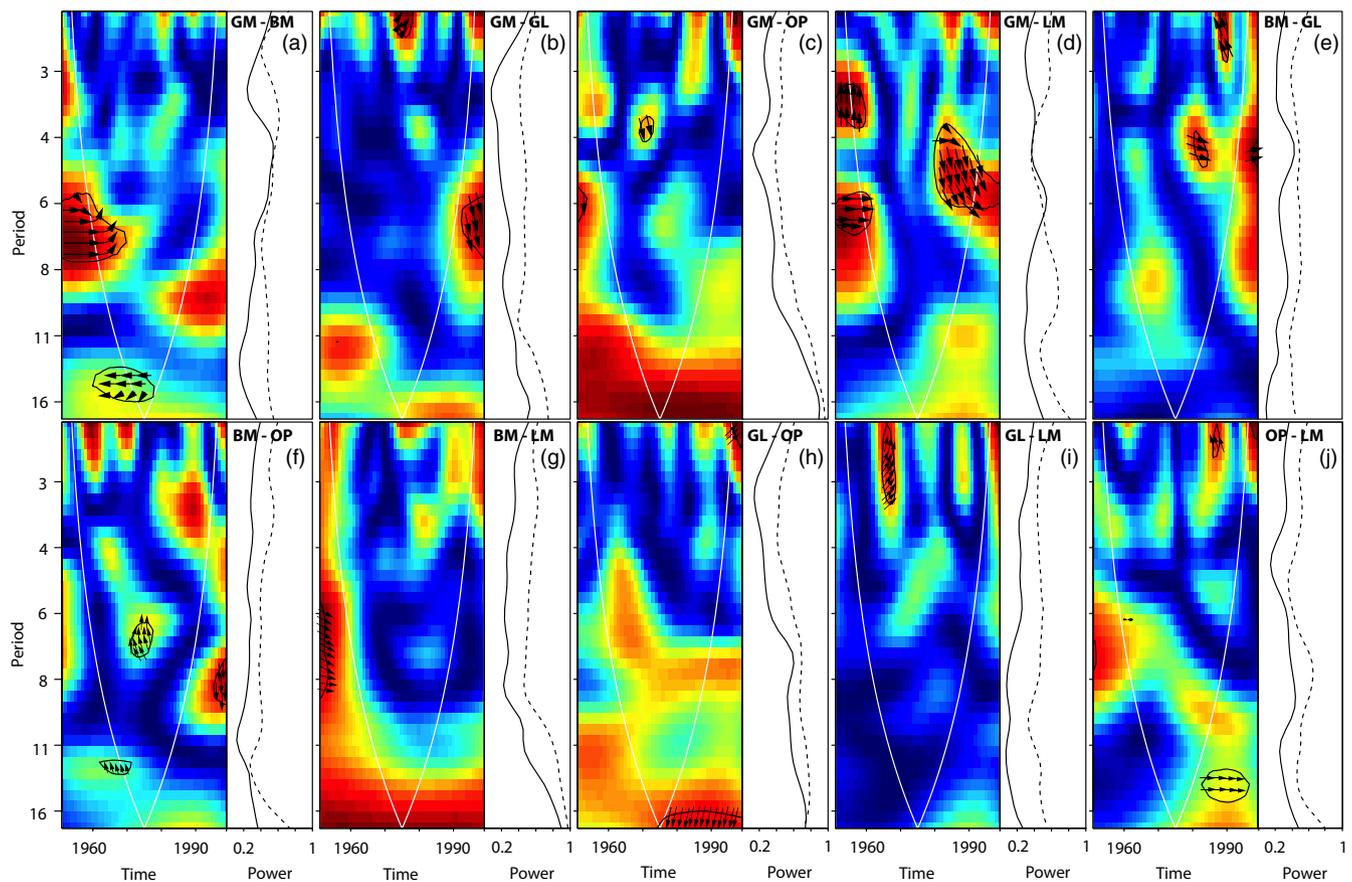


FIGURE 5 The wavelet coherence plots represent the magnitude by time and time-scale (period) for each species combination (in figure a–j; GM, gypsy moth; BM, browntail moth; GL, green leafroller moth; OP, oak processionary moth; LM, lackey moth). The directions of arrows in the plots indicate the phase in the correlation; arrows pointing to the right indicate that the two series are in phase. Arrows pointing to the left indicate that the series are in antiphase. Arrows pointing up indicate that the second series leads the first by $\pi/2$. Arrows pointing down mean that the first series leads the second by $\pi/2$ (biwavelet in R; Gouhier et al., 2016). The global (time-averaged) significance of the wavelet coherence for each species combination is given in the small plot right of the contour plot. When the solid line exceeds the dashed line (95th percentile of surrogates), the time series are coherent at that period. The absence of significance indicates the absence of long-term periodicity in the correlation between the dynamics of the species and thus confirms transient dynamics opposite to re-occurring synchrony. The colours indicate the strength of the coherence; red represents strong coherence; the colours orange, yellow and green represent reduced coherence; blue represents low/no coherence. Regions outlined in black indicate statistically significant wavelet coherence. The white line (V-shaped) is the so-called cone of influence, and this is the area of the analysis where time-series edge effects become important (Torrence & Compo, 1998)

species such as browntail moth and lackey moth (Figure 5a,d), particularly during periods when their densities were high. Damage caused by these other species appears to lag the gypsy moth outbreaks. Also, browntail moth is followed by the oak processionary moth during a period of damage increase (Figure 5f).

Several different mechanisms could be responsible for synchrony between populations of sympatric species, as observed here. Top-down trophic linkages, such as shared predators or parasitoids, can synchronize sympatric foliage-feeding Lepidoptera (e.g., Raimondo, Turceni, Patoeka, & Liebhold, 2004). Additionally, for herbivore species that share host plants, induced host defences may synchronize outbreaks of two or more sympatric species (Dormont, Baltensweiler, Choquet, & Roques, 2006). Alternatively, shared stochastic influences (e.g., weather) can synchronize populations in a manner similar to the Moran effect, that is widely recognized as an important cause of intraspecific spatial synchrony (Hudson & Cattadori, 1999; Liebhold et al., 2004; Myers, 1998). Such synchronizing effects of stochastic weather may act indirectly on herbivore populations via either top-down or bottom-up effects. As is the case for intraspecific spatial synchrony, differentiating between potential causes of interspecific synchrony may be difficult because they may produce similar effects. However, some key aspects of the time series analysed here and aspects of the life histories of the included species may give indications about potentially important mechanisms.

The occurrence of a large gypsy moth outbreak in 2005 is perhaps the dominant feature of the 50-year time series (Figure 1). This outbreak appears to have had an influence on populations of the other species, which followed the gypsy moth outbreak with increases in their damage levels as well. The lagged synchrony between the lackey moth (and to a lesser extent the green leafroller) and the gypsy moth (Table S1 in Appendix S1) suggests that the synchrony may be driven by trophic linkages rather than stochastic influences (Berryman & Turchin, 2001), even though it might be a stochastic event disrupting one species and invoking synchrony (Keitt, 2008). If we speculate on possible mechanisms we can hypothesize that at peak gypsy moth densities, generalist natural enemies would likely be satiated by gypsy moth as prey. Predation pressure on the other species would then be reduced, allowing them to increase their densities in subsequent years. On the other hand, it could be argued that (with regards to the phase angles—Figure 5d) lackey moth dynamics follow gypsy moth dynamics with approx. 2-year lag, which could indicate positive host plant quality effects on the lackey moth, that is reduced defence chemicals due to previous year gypsy moth defoliation.

While natural enemy and host linkages may contribute to synchronization among herbivores, the species here appear to exhibit different patterns of direct density-dependent dynamics (a_1 in Table 1, Figure 2). This is in direct contradiction of the assumptions of Moran's theorem (Moran, 1953), which assumes identical density dependence among synchronized populations. The observed differences in density dependence likely work in opposition to synchronizing effects, as has been shown for synchrony among spatially disjoint populations of a single taxon (Liebhold et al., 2006), and may

explain why these five species spend most of their time fluctuating asynchronously. Consequently, it is possible that populations are only driven into synchrony when populations of one of the species reach very high levels, potentially due to exogenous forcing, thereby invoking linkages that overcome inherent differences in density dependence.

Species sharing a resource are more likely to influence each other's population dynamics through competition or facilitation (Agrawal et al., 2007; Hunter, 1998). Lackey moth dynamics are most strongly dissimilar to all other species but show coherence in parts of the time with all other species, more so than any of the other species. Lackey moth is also the species exhibiting the least area damaged during the study period. One of the explanations for this could be that the lackey moth population has the weakest direct density-dependent response (a_1 in Table 1; Figure 2) and therefore more inclined to be affected by the dynamics of other more abundant species, possibly benefitting, for example, from a release from generalist predators when one of the other species increases in abundance, allowing population increases of this species, too. This is illustrated by the phase arrows in Figure 5d, g, i and j which indicate that lackey moth tends to follow the dynamics of the other species, implying some indirect positive effect. As mentioned earlier, an alternative explanation could be that the plant defences are weakened by the damage caused by the first species, allowing the lackey moth to increase its performance and thus damage area.

Our results show that, even though populations of these species are fluctuating asynchronously most of the time, periods of transient synchrony do occur occasionally. As examples of transient dynamics have been observed for species in spatially structured environments (Hastings & Higgins, 1994; Ranta et al., 1998; Saravia et al., 2000) and in predator–prey interactions (Kidd & Amarasekare, 2012; Tobin & Bjornstad, 2003), resulting dynamics could lead to transient synchrony among competing or trophically linked species. We find that populations of sympatric species become coupled for short periods but over the long term, coupling breaks down and synchrony disappears. This could indicate that the dynamics might synchronize shortly after disturbance in the environment (Hastings, 2004; Keitt, 2008) or that changes in the dynamics in one species, possibly due to exogenous forcing, affects the trophic linkage with others, for example through predation (Raimondo, Turceni, et al., 2004).

While a great deal of attention has recently been directed towards intraspecific spatial synchrony, the phenomenon of interspecific synchrony has received less attention (but cf. Huitu et al., 2004; Ims & Fuglei, 2005; Loreau & de Mazancourt, 2008). From a community perspective, the observed dynamics do not indicate compensatory dynamics as the periods of temporal transient synchrony can have positive or negative directions (Gonzalez & Loreau, 2009). The outbreak-nature of the population dynamics of four of the five species indicates that the species do not operate at carrying capacity level but that there is much flexibility in the resource–consumer dynamics, leaving the possibility for species to follow fluctuations of other species. Another note that needs to be made with these species is that while all of them prefer oaks as their host,

only the oak processionary moth is relatively monophagous; even if resource availability could be a limiting factor in specialist insect communities, the polyphagous nature of these species will weaken the effect of direct competition on community dynamics.

Quantifying interspecific synchrony and inferring its causes may provide information useful for identifying the drivers of observed oscillations or other dynamics patterns in populations. This study illustrates the unique possibility to compare multiple species over a relatively long time-period, which allows the elucidation of patterns of temporal transient synchrony. The exceptional length of these time series allows for analysis of long-term patterns as well as more detailed analyses for shorter time periods as achieved with the wavelet coherence. Although quantifying global interspecific synchrony across long time series (e.g., Table S1 in Appendix S1) can provide useful insight, such analyses may actually mask more subtle relationships. More detailed analyses may indicate that insect populations exhibit both transient periodicity (Figure 3) and transient interspecific synchrony (Figure 5). Our results show that population dynamics of species can be synchronous for short periods of time. Within the framework of transient dynamics, short bouts of synchronous dynamics suggest that the synchronizing effects of species interactions or exogenous disturbances can act at different time-scales. Understanding the drivers of such transient dynamics, and the roles of endogenous and exogenous forcing, remains a challenge for the future analysis of population dynamics (Hastings, 2010).

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AUTHORS' CONTRIBUTIONS

M.J.K. and A.M.L. conceived the ideas and designed methodology; A.H. and G.C. collected the data; M.J.K., A.M.L. and J.A.W. analysed the data; M.J.K. and A.M.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.928c32c> (Klapwijk et al., 2018).

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SUPPORTING INFORMATION

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