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Outbreaking forest insect drives phase synchrony among sympatric folivores: Exploring potential mechanisms

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Abstract

We explore a common feature of insect population dynamics, interspecific synchrony, which refers to synchrony in population dynamics among sympatric populations of different species. Such synchrony can arise via several possible mechanisms, including shared environmental effects and shared trophic interactions, but distinguishing the relative importance among different mechanisms can be challenging. We analyze interannual time series of population densities of the larch budmoth, *Zeiraphera griseana* (Lepidoptera: Tortricidae), along with six sympatric larch-feeding folivores from a site in the European Alps 1952–1979. These species include five lepidopterans, *Exapate duratella*, *Ptycholomoides aeriferana*, *Spilonota laricana*, *Epirrita autumnata* and *Teleiodes saltuum*, and one hymenopteran sawfly *Pristiphora laricis*. We document that the highly regular oscillatory behavior (period 9–10 years) of *Z. griseana* populations is similarly evident in the dynamics of most of the sympatric folivores. We also find that all of the sympatric species are phase synchronized with *Z. griseana* populations with half of the sympatric species exhibiting nonlagged phase synchrony and three of the species exhibiting 2–5 year lags behind *Z. griseana* populations. We adapt a previously developed tritrophic model of *Z. griseana* dynamics to explore possible mechanisms responsible for observed phase synchronization. Results suggest that either shared stochastic influences (e.g., weather) or shared parasitoid impacts are likely causes of nonlagged phase synchronization. The model further indicates that observed patterns of lagged phase synchronization are most likely caused by either shared delayed induced host plant defenses or direct density-dependent effects shared with *Z. griseana*.

KEYWORDS

folivore, interspecific synchrony, outbreak, population dynamics, trophic

1 | INTRODUCTION

Recent reports of dramatic decreases in insect numbers (Hallmann et al., 2017; Leather, 2018) have increased the awareness of the importance of insects in ecosystems. Other recent reports and predictions of increased damage from insect pests as a consequence of climate change are equally alarming (Estay, Lima, & Labra, 2009; Weed, Ayres, & Hicke, 2013). These apparently conflicting reports may seem paradoxical but highlight the lack of knowledge on the population dynamics of communities of insects. There is a strong need to better understand connections, not only between species at different trophic levels, but also among species at the same trophic level. For example, several processes are known to produce periodic behavior in insect folivore populations, but little is known on how these processes may interact among sympatric folivore populations.

The ability of trophic interactions to produce periodic behavior is well known (Elton & Nicholson, 1942; Varley, Gradwell, & Hassell, 1974). For example, in the classic Lotka–Volterra model, both predator and prey populations cycle with peaks in predator populations lagging one-quarter-cycle length behind that of prey populations (Bulmer, 1976). In nature, there is a plethora of evidence of such oscillatory dynamics in predator and parasitoid populations linked to oscillations of their hosts (Bayliss & Choquenot, 2002). One ubiquitous characteristic of such predator–prey cycles is the existence of temporal lags between cycles of predators and prey.

While linkages between oscillating prey and predator populations are well-studied, less is known about mechanisms driving linkages in the dynamics of sympatric consumer populations. Populations of consumer species may track fluctuating patterns in shared food resources, contributing to synchrony in their dynamics. For example, several studies have documented that fluctuating abundance of shared seed or insect populations can drive synchrony among populations of seed-eating or insectivorous birds (Bock & Lepthien, 1976; Jones, Doran, & Holmes, 2003). However, many consumer populations exhibit oscillatory dynamics, and little is known about how cycles among populations of different consumer species are related.

One group of consumer species for which interspecific synchrony is known to commonly occur is in foliage-feeding forest insects (Kawatsu, Yamanaka, Patoèka, & Liebhold, 2019; Klapwijk et al., 2018; Miller & Epstein, 1986; Myers, 1998; Raimondo, Liebhold, Strazanac, & Butler, 2004; Raimondo, Turcáni, Patoèka, & Liebhold, 2004). Several explanations have been proposed to explain synchrony among these folivore populations. Shared influences of interannual variability in weather is one of these proposed mechanisms (Miller & Epstein, 1986; Myers, 1998). Others have suggested synchronization via shared trophic interactions, such as predators and parasitoids (Marcström, Kenward, & Engren, 1988; Raimondo, Turcáni, et al., 2004) or shared host plants (Baltensweiler, 1991; Klapwijk et al., 2018).

The phenomenon of interspecific synchrony is in some ways analogous to the phenomenon of spatial synchrony, which refers to synchrony in the dynamics of spatially disjunct populations of the same species (Liebhold, Koenig, & Bjørnstad, 2004). Like interspecific synchrony, several different processes are capable of producing spatial synchrony; these include stochastic influences (e.g., weather) which are synchronous across space (the "Moran effect"), dispersal of individuals among populations and dispersal of predators among habitat patches (Liebhold et al., 2004; Walter et al., 2017). Unfortunately, all three of these mechanisms are capable of producing identical patterns of synchrony and therefore it is characteristically difficult to dissect the cause of spatial synchrony from spatiotemporal patterns alone. Analysis of interspecific synchrony has received less attention and it is not clear if it is similarly difficult to identify the drivers of interspecific synchrony.

Here, we analyze patterns of interspecific synchrony in a highly periodic system. Specifically, we quantify periodicity and phase dependency among populations of six foliage-feeding insect species feeding sympatrically with the larch budmoth, *Zeiraphera griseana*, in the European Alps. Population oscillations of this insect are widely recognized as one of the most regular of all animal species (Baltensweiler, Benz, Bovey, & Delucchi, 1977; Varley et al., 1974). During population peaks, populations in optimal habitats reach very high densities, often more than 300 larvae per kg of foliage (ca. 120,000 larvae per tree), causing massive defoliation of European larch (*Larix decidua*). The very regular oscillations in *Z. griseana* populations are hypothesized to result from a combination of delayed density-dependent response by hosts and by parasitoids (Turchin 2003, Turchin et al., 2003). The year following defoliation, host larches produce needles shorter in length and larvae feeding on this foliage perform more poorly resulting in decreased fecundity in females (Benz, 1974). Moreover, needle flush is delayed relative to the timing of egg hatch, causing extensive mortality in early-emerging budmoth larvae (Benz, 1974). Sympatric larch folivores have never been observed to reach larval densities similar to those of *Z. griseana* populations but may peak at around 18 larvae per kg of larch foliage (Baltensweiler, 1991). While nothing is known about the induced effect of *Z. griseana* defoliation on foliage quality for other insects, it seems likely that changes in the physical and chemical property of larch foliage would also adversely affect sympatric populations of other insect species feeding on foliage. Thus, it is possible that *Z. griseana* exerts a synchronizing influence on sympatric larch-feeding folivores via direct competition for foliage, induced changes in foliage quality or from mutual numerical interactions of shared parastioids species. We apply a model to simulate these interactions and compare patterns of phase synchronization with observed patterns to infer underlying mechanisms driving interspecific synchrony.

2 | METHODS

Time series of *Z. griseana* and six sympatric larch-feeding folivores were collected from 1952–1979 by Dr. Christian Auer (Department of Entomology, ETH Zürich, Switzerland) as part of a rigorous, labor-intensive and statistically robust sampling plan (Auer, 1977). Sampling was conducted from early to late June depending on the season, when the first *Z. griseana* larvae were observed to have reached the fourth instar. At that point, all *Zeiraphera* eggs were considered to have hatched. All *Z. griseana* and other larvae were counted on branches selected using a stratified random sampling scheme, which involved taking samples from several hundreds of trees with samples consisting of 1 kg of twigs with foliage. Samples were cut from three branches selected at three levels within the crown of each tree; foliage was searched, and densities were expressed as larvae per kg of foliage. Sampling was conducted at five sites across the European alps 1952–1979 but we limited our analysis to data from the subalpine forests of the Upper Engadine Valley (Kanton Graubunden, Switzerland) which had the longest period of continuous sampling (1952–1979). Time series from all sites were published in Baltensweiler (1991) and the Engadine Valley series is included here as Table S1.

The six most common species of foliage-feeding insects occurring sympatrically with *Z. griseana* on larch during the study period were the lepidopterans *Exapate duratella* (Lepidoptera: Tortricidae), *Epirrita autumnata* (Lepidoptera: Geometridae), *Ptycholomoides aeriferana* (Lepidoptera: Tortricidae), *Spilonota laricana* (Lepidoptera: Tortricidae), *Teleiodes saltuum* (Lepidoptera: Tortricidae) and the hymenopteran sawfly *Pristiphora laricis* (Hymenoptera: Tenthredinidae). These species vary in both their taxonomic and phenotypic similarity to *Z. griseana* as shown in Table 1. We also searched the literature, summarizing information about parasitoids that share *Z. griseana* and one or more of these species (Table S2).

In order to quantify periodicity in time series of annual density, we calculated autocorrelation functions (ACFs) and wavelet spectra for each of the seven species using the "acf" function in base R and the "biwavelet" R library (Cazelles et al., 2008; Gouhier, Grinsted, & Gouhier, 2018; Turchin & Taylor, 1992). To quantify phase synchrony of Z. *griseana* with each of the six other insect species, we estimated cross-correlation functions (CCFs) using the "ccf" function in base R.

To explore the potential for shared host plant interactions or shared natural enemy interactions to synchronize sympatric species, we modeled the dynamics of *Z. griseana*, populations along with those of a hypothetical sympatric folivore. These simulations were based on a tritrophic model of *Z. griseana* dynamics developed by Turchin (2003) and Turchin et al. (2003). The model uses a modified Ricker model to represent moth population dynamics and incorporates delayed density dependence arising from both a numerical response by parasitoids and from decreased foliage quality following host tree defoliation. The model consists of three equations describing the density of *Z. griseana* (N_t), the density of parasitoids (P_t) and larch host quality (Q_t):

$$N_{t+1} = N_t \exp\left\{ r_0 \left(1 - \exp\left[-\frac{Q_t}{\delta} \right] \right) - \frac{r_0}{k} N_t - \frac{\alpha P_t}{1 + awP_t} \right\} \tag{1}$$

$$P_t = N_t \left\{ 1 - \exp\left[\frac{\alpha P_t}{1 + \alpha w P_t} \right] \right\} \tag{2}$$

$$Q_t = (1 - \beta) + \beta Q_t - \frac{cN_t}{d + N_t} \tag{3}$$

Equation (1) represents the dynamics of *Z. griseana* populations, incorporating direct density dependence as well as delayed density dependence arising both from mortality caused by parasitoids and induced host defenses that reduce population growth. Equation (2) represents the dynamics of parasitoid populations and incorporates their numerical response to *Z. griseana* populations. Equation (3) represents the dynamics of host quality that is depressed by

TABLE 1 Seven larch-feeding folivores sampled in the Upper Engadin Valley, Switzerland 1952–1979

Species	Order	Family	Host specificity	Life cycle
Zeiraphera griseana	Lepidoptera	Tortricidae	Oligophagous	Univoltine
Exapate duratella	Lepidoptera	Tortricidae	Polyphagous	Univoltine
Epirrita autumnata	Lepidoptera	Geometridae	Polyphagous	Univoltine
Ptycholomoides aeriferana	Lepidoptera	Tortricidae	Oligophagous	Univoltine
Spilonota laricana	Lepidoptera	Tortricidae	Monophagous	Univoltine
Teleiodes saltuum	Lepidoptera	Gelechiidae	Oligophagous	Biennial
Pristiphora laricis	Hymenoptera	Tenthredinidae	Monophagous	Bivoltine

Z. griseana populations. The model was implemented in the R language (code provided in SI1).

To model *Z. griseana*, we adopted Turchin's default parameters $\delta = 0.25$, $c = 0.9$, $\alpha = 2.5$, $r_0 = 2.3$, $w = 0.17$, $d = 100$, $\beta = .5$ (Table S3). We used one set of equations to represent *Z. griseana* per host tree per parasitoid dynamics and another set of the same equations and mostly the same parameter values to represent the dynamics of a hypothetical sympatric larch-feeding folivore. Taking into account the approximate maximum values observed for densities of the seven folivores (Table S1), we assumed a default carrying capacity of $k = 250$ larvae per kg of foliage for *Z. griseana* but a $k = 10$ for the hypothetical sympatric species so that while *Z. griseana* would periodically reach outbreak levels, the sympatric folivore would not. Preliminary simulations indicated that the dynamics of the model were relatively insensitive across a range of values of k. To represent a common host tree foliage effect we replaced folivore density, N_t, in Equation (2) with the sum of both *Z. griseana* and the sympatric folivore densities, $N1_t + N2_t$, assuming that both species cause a comparable per capita decrease in host quality and that their populations are equally affected by foliage quality. To represent a shared numerical response by parasitoids, we assumed that in each generation there was a 10% "dispersal" of parasitoids among the guilds attacking each host folivore.

For each of the four scenarios described above, we simulated the dynamics of *Z. griseana* and the hypothetical sympatric folivore across 2,500 generations. The final 50 generations were used to calculate ACFs for each species and CCFs to quantify lagged synchrony between species.

3 | RESULTS

Time series of *Z. griseana* densities, as well as those of the six sympatric larch folivores are shown in Figure 1.

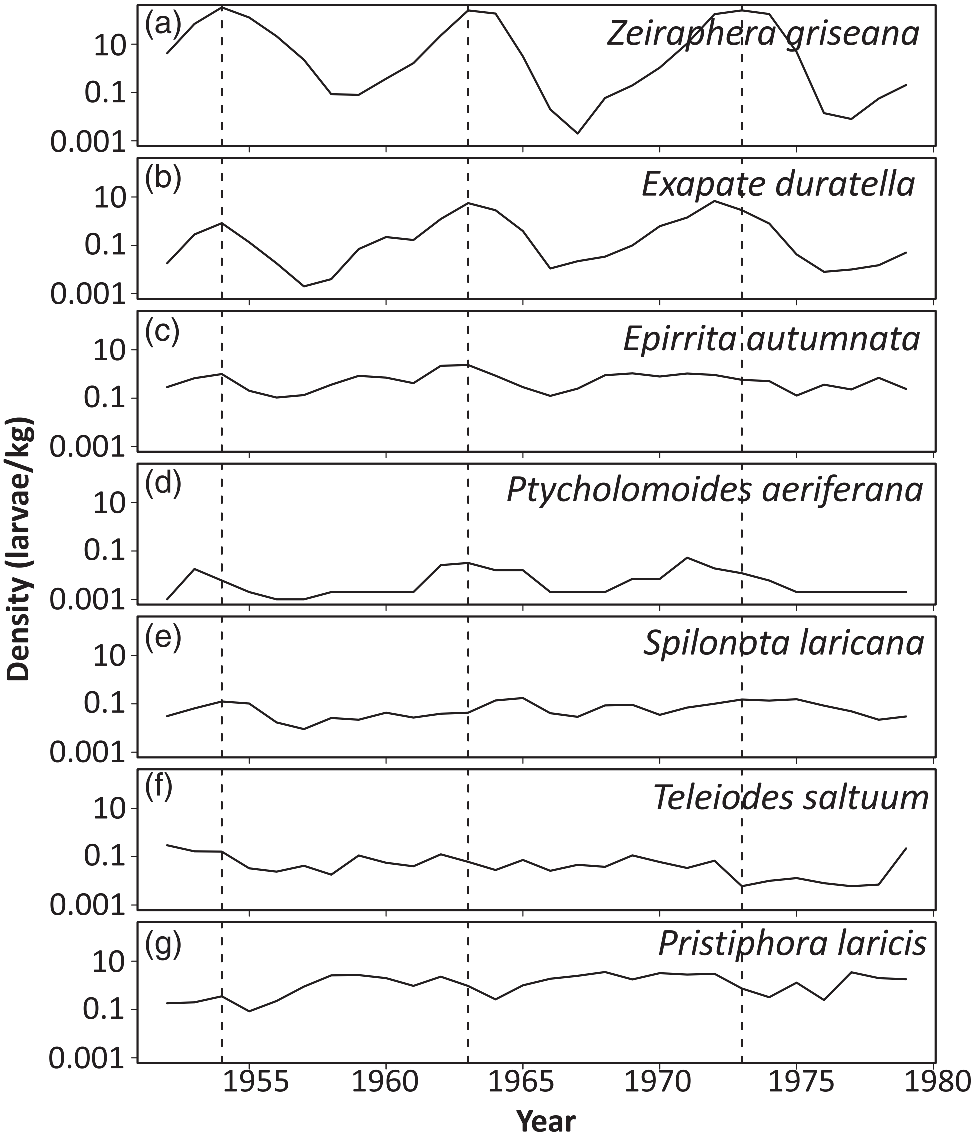

FIGURE 1 Time series (1952–1979) of log density of seven sympatric larch-feeding folivores plotted on a common logarithmic scale. Dashed vertical lines are shown at *Zeiraphera griseana* population peaks of 1954, 1963 and 1973

Dynamics of *Z. griseana* populations are clearly oscillatory and densities fluctuate through several orders of magnitude. Time series for *E. duratella* and *P. aeriferana* also appear oscillatory and somewhat synchronous with those of *Z. griseana*. The dynamics of the other four species do not appear clearly oscillatory and though some population peaks do appear coincident, there is less visual evidence of their synchrony with that of *Z. griseana*.

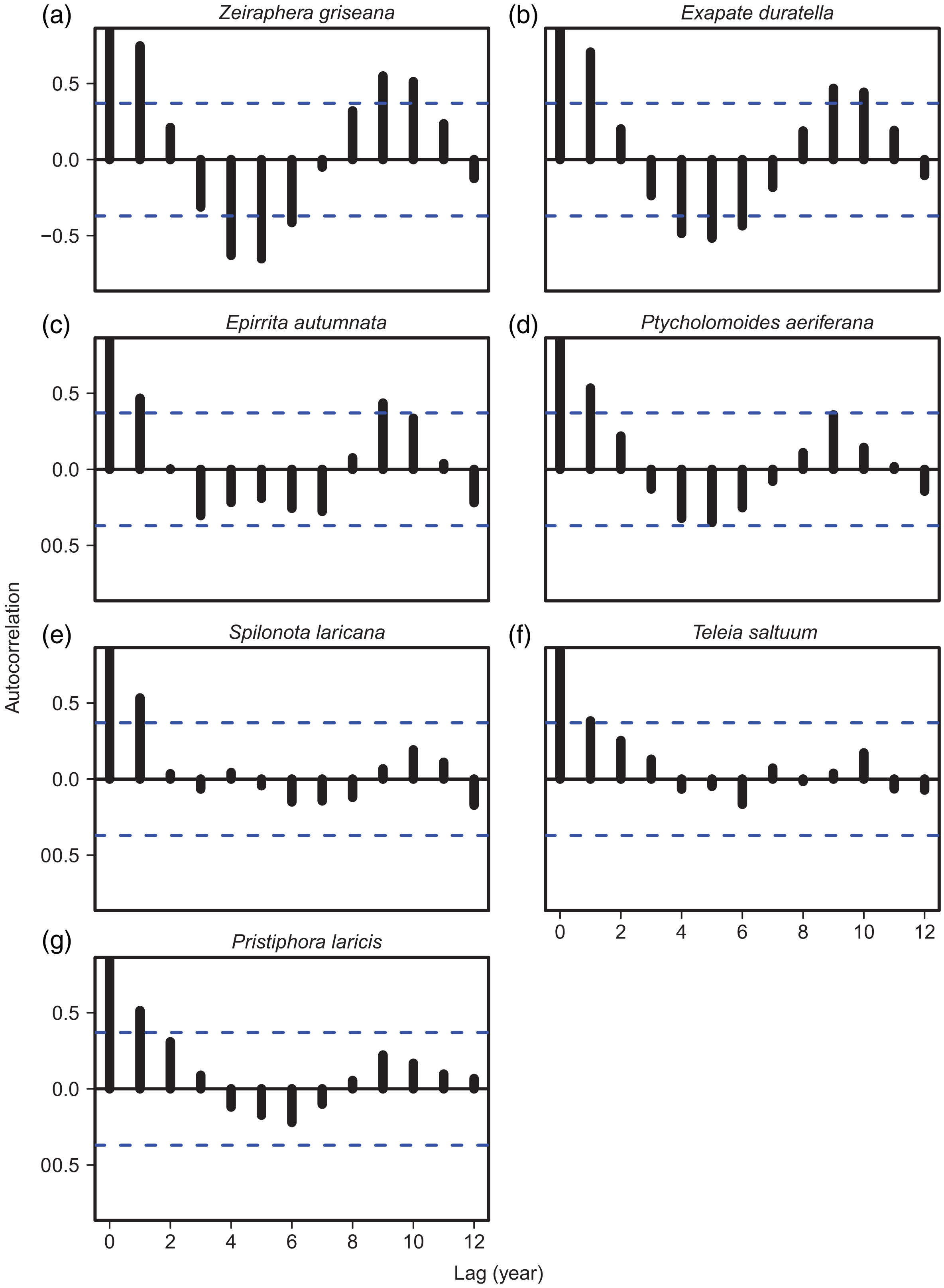

FIGURE 2 Autocorrelation functions of time series of each of the seven sympatric larch-feeding folivore species [Color figure can be viewed at wileyonlinelibrary.com]

The ACFs for *Z. griseana*, *E. duratella* and *P. aeriferana* series all had significantly positive values at Lags 9 or 10, indicating periodicity (Figure 2). The ACF for *P. laricis* showed a similar pattern but none of the lagged ACF values were significant. Global wavelet spectra (Figure S1) confirm that both *Z. griseana* and

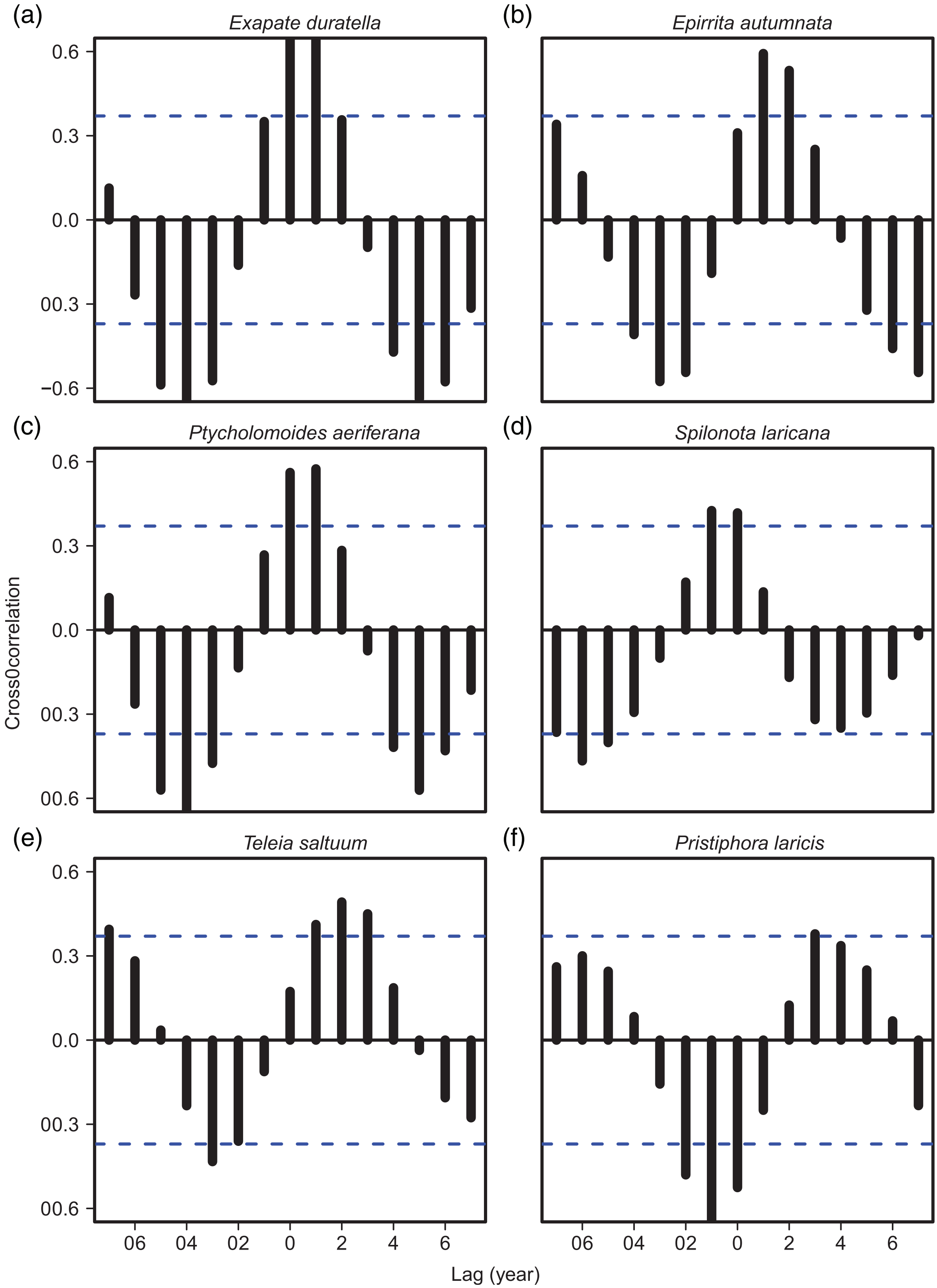

FIGURE 3 Cross-correlations of *Zeiraphera griseana* with each of the six sympatric larch-feeding folivore species [Color figure can be viewed at wileyonlinelibrary.com]

E. duratella exhibit a strong periodic population behavior with a dominant period of 9 years. The species *E. autumnata* and *P. aeriferana* also exhibited significantly oscillatory behavior at period 9 but only during part of the 1952–1979 interval and were not significantly globally periodic. The species *E. autumnata* and *S. laricana* exhibited oscillatory behavior at a 5-year period but this was only significant during part of the 1952–1979 interval and not globally significant.

All of the six sympatric foliage-feeding insects exhibited significant cross-correlation with *Z. griseana* though the lag associated with peak cross-correlation varied somewhat among species (Figure 3, Table 2). *Exapate duratella* and *P. aeriferana* both had significant cross-correlations at Lags 0 and 1. Cross-correlation with *S. laricana* was somewhat similar with significant lags at −1 and 0 while peaks in *E. autumnata* appeared to lead those of *Z. griseana* slightly by 1–2 years. The most strongly out of phase behavior was seen in *T. saltuum* which had peak correlations at Lags 1, 2 and 3 and *P. laricis* which lead *Z. griseana* by 3–4 years.

Not surprisingly, when populations of *Z. griseana* and a hypothetical sympatric larch folivore species were simulated with no linkages, the populations behaved independently; populations of *Z. griseana* were oscillatory with a 9–10 year period but populations of the hypothetical sympatric folivore exhibited dampened 2-year oscillations toward equilibrium levels and there were no significant cross-correlations between the series (Figure 4). In contrast, when the hypothetical folivore shared direct density dependence with *Z. griseana*, both populations exhibited the same 9-year period though oscillations of the sympatric folivore did not show the same smooth sinusoidal oscillatory behavior seen in *Z. griseana* (Figure 5). Furthermore, oscillations of the two populations were slightly out of phase with peak *Z. griseana* populations leading those of the sympatric folivore by about 1 year (Figure 5). Simulation with a shared induced-delayed host plant effect again yielded periodic behavior (period of 10 years) in both populations; oscillations were out of phase again with the sympatric folivore leading *Z. griseana* populations by 1–3 years (Figure 6). Finally, simulations with 10% sharing of parasitoids yielded oscillatory patterns in both species though with a slightly shorter period of 8–9 years. The two populations oscillated slightly out of phase with the sympatric folivore slightly leading *Z. griseana* populations and significant cross-correlations at lags of 0–2 years (Figure 7).

TABLE 2 Summary of significant positive lag cross-correlations of *Zeiraphera griseana* with six sympatric larch folivores or with hypothetical folivores linked by three different mechanisms

Linkage/species	Mechanism linking populations with *Z. griseana*	Maximum lag cross-correlation with *Z. griseana*
Hypothetical sympatric folivore	Density dependence	1 (but out of phase at Lag 0)
Hypothetical sympatric folivore	Induced host effect	1, 3
Hypothetical sympatric folivore	Parasitoid populations	0, 2
Exapate duratella	Parasitoid populations, weather generalist predators?	0, 1
Epirrita autumnata	Induced host effect or density dependence?	1, 2
Ptycholomoides aeriferana	Parasitoid populations, weather generalist predators?	0, 1
Spilonota laricana	Parasitoid populations, weather generalist predators?	−1, 0
Teleiodes saltuum	Induced host effect or density dependence?	1, 2, 3
Pristiphora laricis	Induced host effect or density dependence?	3, 4

4 | DISCUSSION

Several explanations have been proposed to explain synchrony among herbivore populations. One hypothesis is that interannual variation in weather affects populations of different species in a common way, driving synchronous increases and decreases in abundance (Miller & Epstein, 1986; Myers, 1998). Raimondo, Turcáni, et al. (2004) used a simple population model to show that a shared functional response of generalist predators can synchronize multiple prey populations. Similarly, there is evidence that the numerical response of shared predators can synchronize prey herbivore populations (Marcström et al., 1988). Finally, Baltensweiler (1991) and Klapwijk et al. (2018) suggested that forest folivore populations may be synchronized when one species reaches outbreak levels causing a reduction in either quantity or quality of a shared foliar resource.

In the system studied here, a single species, *Z. griseana*, exhibits high amplitude and high periodic population oscillations and appears to impart its characteristic cyclicity on several sympatric folivores. Populations of

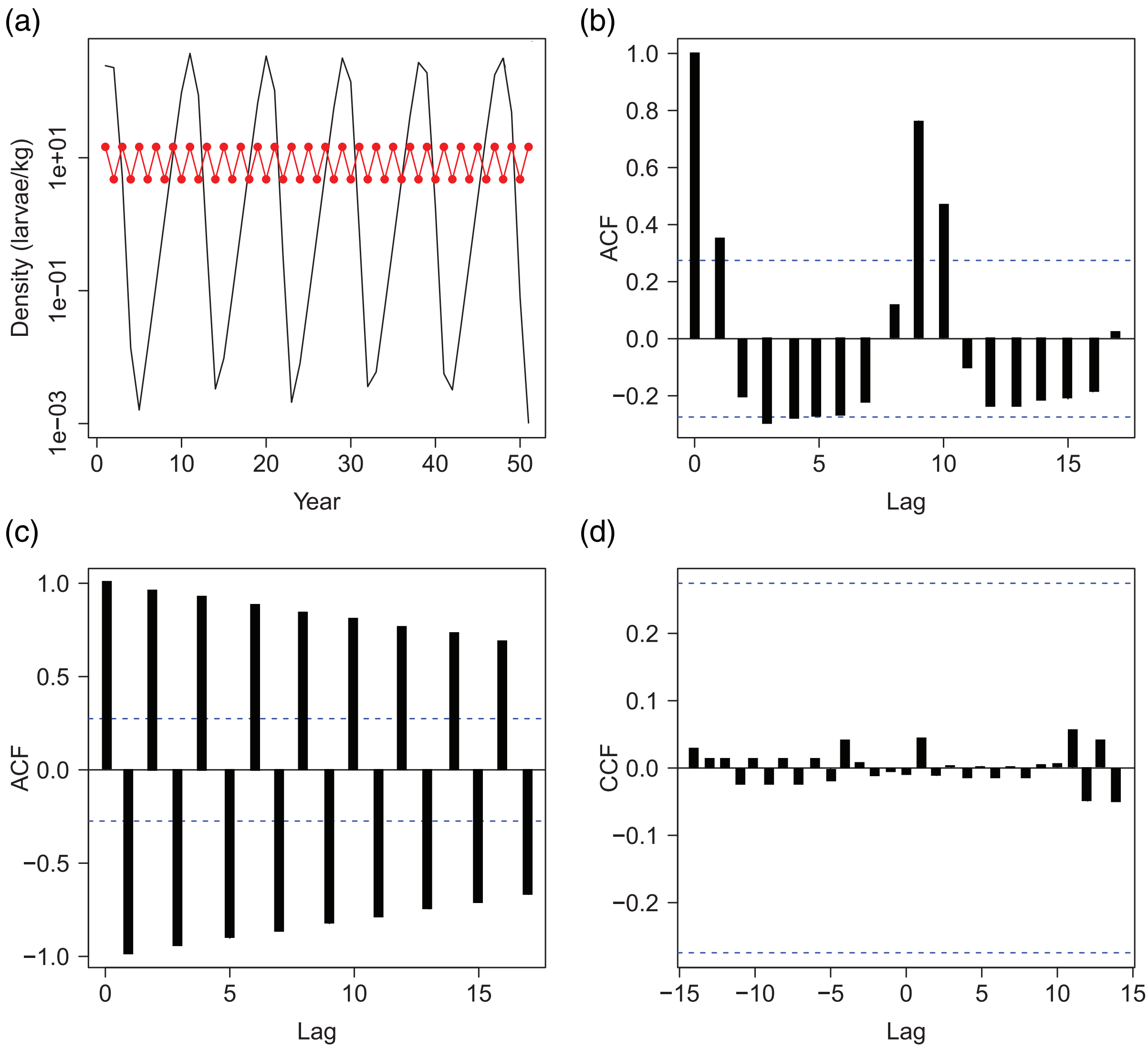

FIGURE 4 Simulation of populations of *Zeiraphera griseana* and a hypothetical sympatric larch-feeding folivore species sharing no linkages. (a) Time series of simulated populations. Black line is *Z. griseana* and red line is sympatric folivore. (b) Autocorrelation function (ACF) of *Z. griseana*. (c) ACF of the sympatric folivore. (d) Cross-correlogram between *Z. griseana* and sympatric folivore. CCF = cross-correlation function [Color figure can be viewed at wileyonlinelibrary.com]

E. duratella, *E. autumnata* and *P. aeriferana* exhibit oscillatory behavior of periods 9–10 years almost identical to that of *Z. griseana* (Figure 2), while the same 9–10 year periodicity is weakly evident in the dynamics of the other three sympatric species (Figure S1).

Virtually all of the sympatric folivores exhibit some degree of phase synchronization with *Z. griseana*. In some species (*E. duratella*, *P. aeriferana* and *S. laricana*), peak correlations are almost perfectly in phase with *Z. griseana* (Figure 3). However, in other species (*E. autumnata*, *T. saltuum* and *P. laricis*), population peaks lead those of *Z. griseana*.

Simulation conducted using a tritrophic model previously developed to represent the dynamics of *Z. griseana* (Turchin et al., 2003), indicates that if some fraction (10% in our simulations) of parasitoids move between populations parasitizing *Z. griseana* and those parasitizing a sympatric folivore then populations of the sympatric species would be synchronized with those of *Z. griseana* with little or no phase difference (Figure 7). This same nonlagged phase synchronization is seen in *E. duratella*, *P. aeriferana* and *S. laricana* (Figure 3) and suggests that shared parasitoid species could explain their synchrony with *Z. griseana* oscillations (Table 2). Analysis of the literature shows that roughly one-third of the 112 parasitoid species known to parasitize *Z. griseana* also utilize one or more of the six sympatric folivores studied here (Table S2). The three species known to share the highest numbers of parasitoid species were *S. laricana*, *E. duratella* and *P. aeriferana* which are exactly the same species that we

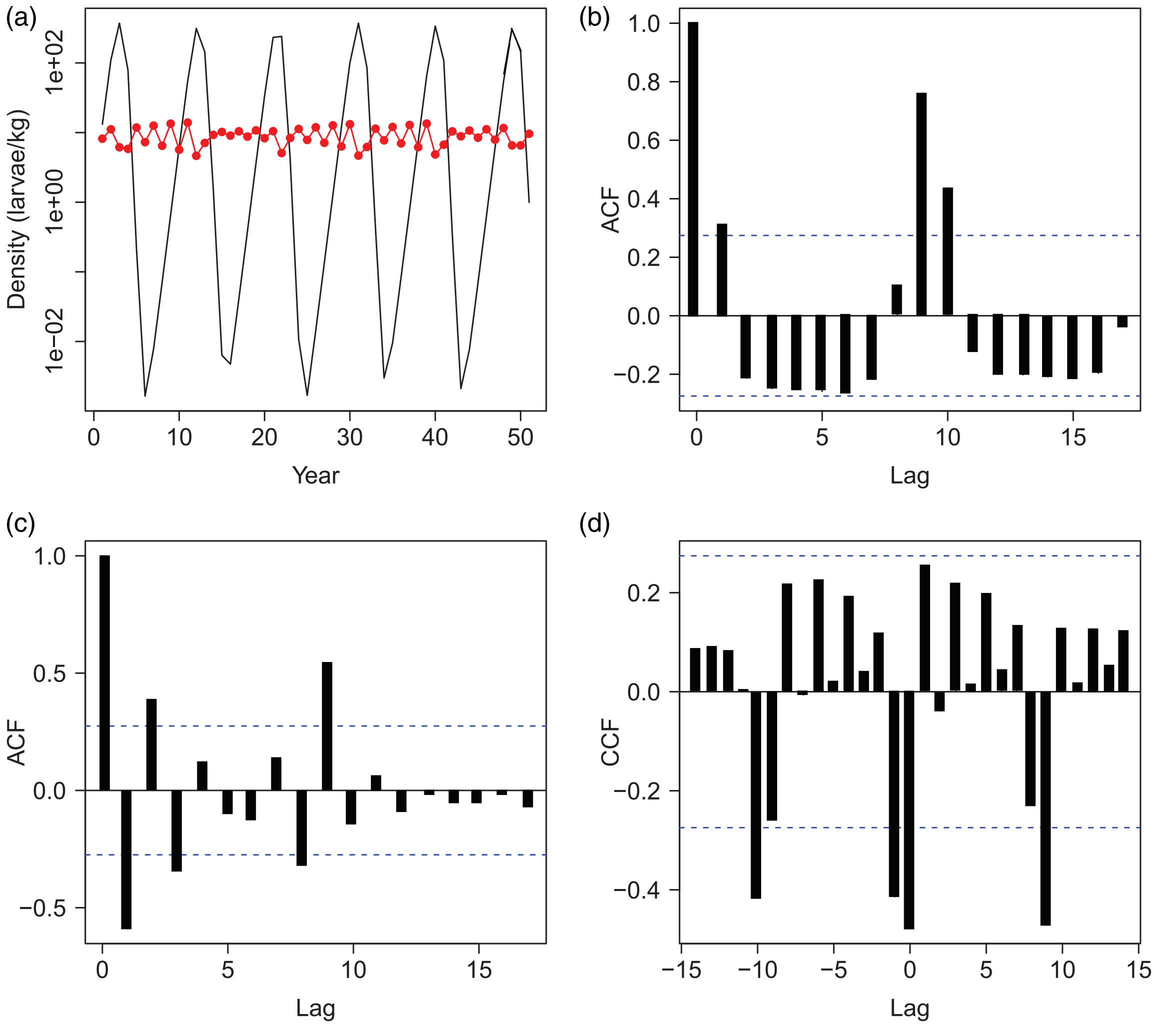

FIGURE 5 Simulation of populations of *Zeiraphera griseana* and a hypothetical sympatric larch-feeding folivore species sharing direct density dependence. (a) Time series of simulated populations. Black line is *Z. griseana* and red line is sympatric folivore. (b) Autocorrelation function (ACF) of *Z. griseana*. (c) ACF of the sympatric folivore. (d) Cross-correlogram between *Z. griseana* and sympatric folivore. CCF = cross-correlation function [Color figure can be viewed at wileyonlinelibrary.com]

found exhibited nonlagged phase synchrony (Figure 3, Table 2), supporting the possible role of shared parasitoids in driving phase synchronization in these species.

Though we did not explore it in simulations conducted here, it is also possible that such nonlagged phase synchronization could be caused by shared stochastic influences (Loreau & de Mazancourt, 2008), such as weather. Indeed, the ability of shared stochastic influences to synchronize spatially disjunct populations of the same species (the "Moran effect") has been well-studied (Bjørnstad, Ims, & Lambin, 1999; Liebhold et al., 2004; Royama, 2005). Spatial synchrony is analogous to the synchronization of sympatric populations of different species studied here and thus these studies suggest that shared stochastic effect could explain the observed nonlagged phase synchronization in these species. Though it is worth noting that the extent to which the Moran effect can synchronize dynamics depends on how similar the dynamics of the different species are (Hugueny, 2006; Liebhold, Johnson, & Bjørnstad, 2006). In addition, Raimondo, Turcáni, et al. (2004) showed that shared generalist predators can bring sympatric populations into nonlagged phase synchrony. Thus, the nonlagged synchrony observed between *Z. griseana* and *S. laricana*, *E. duratella* and *P. aeriferana* could be caused by shared parasitoid populations, shared effects of weather or shared effects of generalist predators (Table 2).

Phase synchronization of *Z. griseana* with the other three species (*E. autumnata*, *T. saltuum* and *P. laricis*), was consistently lagged by 1–4 years (Figure 3). Somewhat similar patterns of lagged phase synchronization were seen in simulations in which *Z. griseana* and a sympatric folivore either shared a common direct density-dependent response (Figure 5) or they shared a response

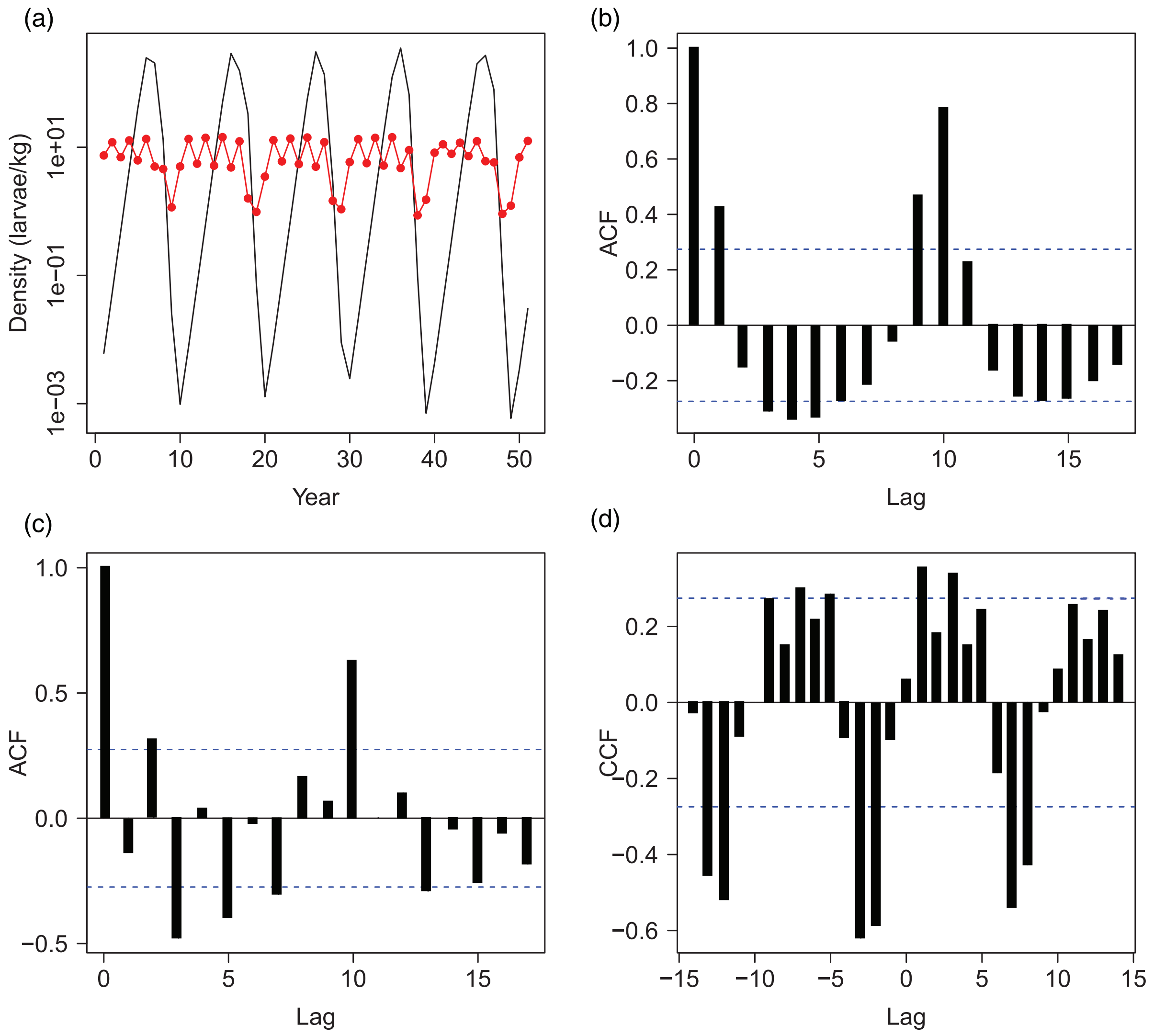

FIGURE 6 Simulation of populations of *Zeiraphera griseana* and a hypothetical sympatric larch-feeding folivore species sharing induced host defenses. (a) Time series of simulated populations. Black line is *Z. griseana* and red line is sympatric folivore. (b) Autocorrelation function (ACF) of *Z. griseana*. (c) ACF of the sympatric folivore. (d) Cross-correlogram between *Z. griseana* and sympatric folivore. CCF = cross-correlation function [Color figure can be viewed at wileyonlinelibrary.com]

to delayed induced host defenses (Figure 6). While there is ample evidence of a delayed induced host response in which performance of *Z. griseana* larvae is decreased when feeding on host larch foliage in the year after an outbreak (Baltensweiler, 1991; Baltensweiler et al., 1977; Baltensweiler & Fischlin, 1988), we are not aware of any evidence that this change in foliage quality also affects larvae of sympatric species feeding on larch. Similarly, while a breakage of the seasonal synchrony in the timing of egg hatch and larch needles flush is known to occur in *Z. griseana* the year following population peaks (Benz, 1974); no information exists about this for the other folivores overwintering as eggs (*E. duratella*, *E. autumnata*; Baltensweiler, 1991). Though the shared effects of induced plant defenses are a plausible explanation for the lagged phase synchrony seen in these three species, it is also possible that phase synchrony is driven in part by shared density dependence. Simulations (Figure 5) indicate that shared density dependence creates a strongly lagged phase synchrony. There are several processes that could potentially create shared density dependence but competition for larch foliage is one obvious such mechanism.

We raise one caveat concerning the model used here to explore synchronization between *Z. griseana* and its six sympatric folivores. While the tritrophic model does a good job of representing current knowledge of the primary drivers of *Z. griseana* population dynamics, we have no knowledge that it adequately represents the dynamics of the six lesser-known sympatric species. Another caveat

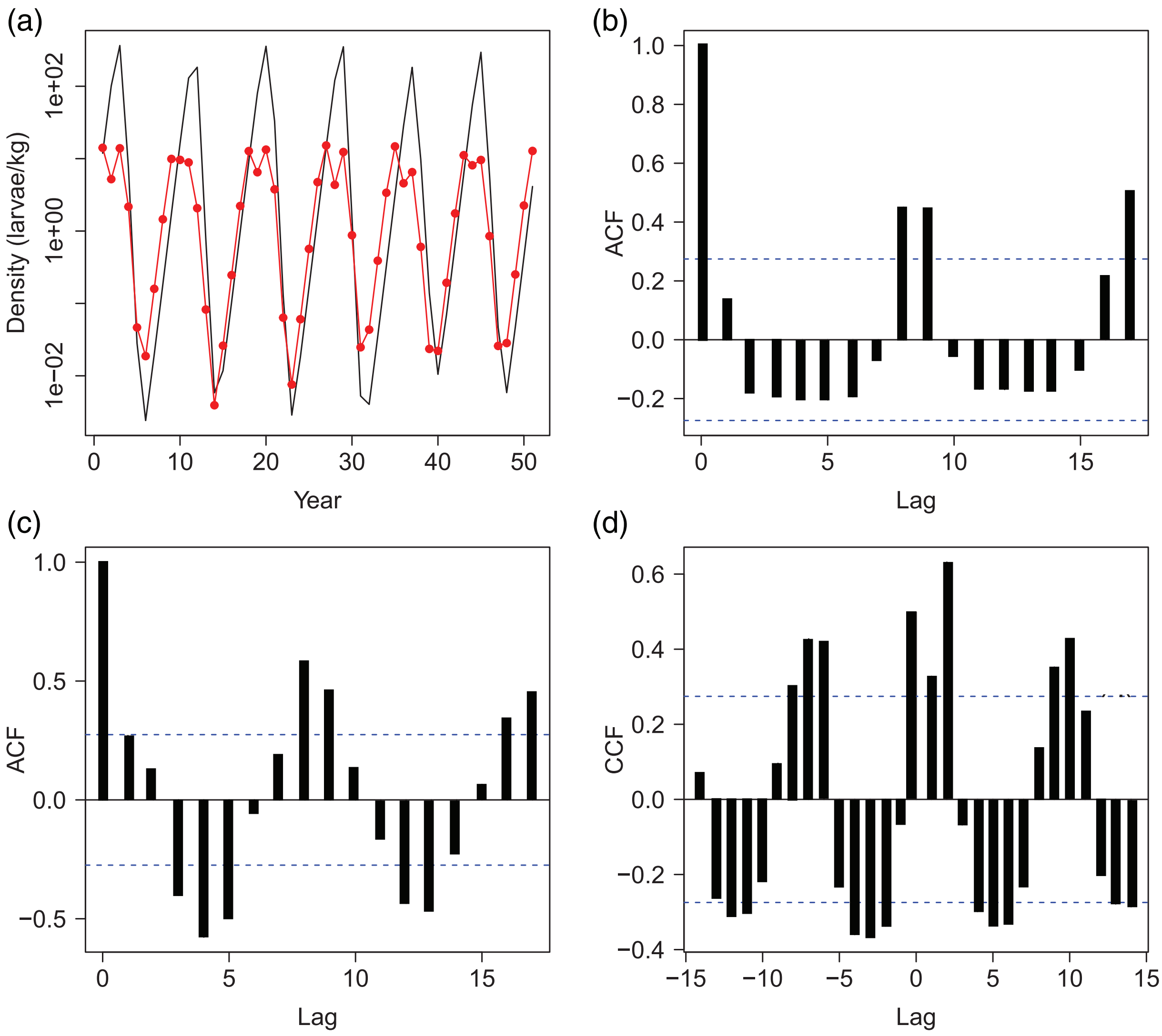

FIGURE 7 Simulation of populations of *Zeiraphera griseana* and a hypothetical sympatric larch-feeding folivore species partially sharing parasitoid populations. (a) Time series of simulated populations. Black line is *Z. griseana* and red line is sympatric folivore. (b) Autocorrelation function (ACF) of *Z. griseana*. (c) ACF of the sympatric folivore. (d) Cross-correlogram between *Z. griseana* and sympatric folivore. CCF = cross-correlation function [Color figure can be viewed at wileyonlinelibrary.com]

relates to the timing of larch branch sampling, which was designed specifically for the lifecycle of *Z. griseana*, but may not be ideal with respect to the timing of lifecycles of the other folivores (Baltensweiler, 1991). Specifically, it appears that when *Z. griseana* larvae reach the fourth instar, a large fraction of *S. laricana* larvae may have left branches for pupation and a large fraction of *P. laricis* eggs may not have hatched. Consequently, densities of these two species may have been systematically underestimated though the timing of sampling may have been adequate for survey of the other four species. Also, in exploring different synchronizing mechanisms via simulation, we did not consider various combinations of mechanisms or varying levels of intensity of these effects which possibly exist in nature.

While we were unable to identify specific mechanisms driving phase synchrony among folivores in this study system with precise certainty, we were able to reduce the number of possibilities by comparing observed patterns of lag correlations with those expected by theoretical models (Table 2). As is the case for spatial synchrony (Liebhold et al., 2004; Walter et al., 2017), identification of mechanisms responsible for observed interspecific synchrony is a challenge. Future research may provide new analytical methods for identifying the signature of different interspecific synchronizing mechanism in empirical data.

Patterns of synchrony among populations of different species within the same community have been implicated as playing an important role in determining community stability. When populations of different species fluctuate synchronously, this creates greater temporal variation in community-wide properties (e.g., total biomass) but population dynamics that is asynchronous among species results in greater stability of these properties through the "portfolio effect" (Gonzalez & Loreau, 2009; Loreau & de Mazancourt, 2008; Schindler, Armstrong, & Reed, 2015). Using this logic, the antisynchronous oscillations of species pairs such as *Z. griseana*/*P. laricis* should contribute to stability while synchrony of species pairs such as *Z. griseana*/*E. duratella* should destabilize the properties of the Alpine larch-feeding herbivore community. However, this is unlikely to be the case since the amplitude of *Z. griseana* oscillations vastly exceed those of other community members. However, while not explored here, it is possible that populations of sympatric folivores alter community-wide properties by stabilizing or destabilizing *Z. griseana* dynamics via indirect interactions.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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