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**Running head:** Temporal community dynamics

# **Title:** Related herbivore species show similar temporal dynamics

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## Abstract

1. Within natural communities, different taxa display different dynamics in time. Why this is the case we do not fully know. This thwarts our ability to predict changes in community structure, which is important for both the conservation of rare species in natural communities and for the prediction of pest outbreaks in agriculture.
2. Species sharing phylogeny, natural enemies and/or life history traits have been hypothesized to share similar temporal dynamics. We operationalized these concepts into testing whether feeding guild, voltinism, similarity in parasitoid community, and/or phylogenetic relatedness explained similarities in temporal dynamics among herbivorous community members.
3. Focusing on two similar data sets from different geographical regions (Finland and Japan), we used asymmetric eigenvector maps as temporal variables to characterize species- and community-level dynamics of specialist insect herbivores on oak (*Quercus*). We then assessed whether feeding guild, voltinism, similarity in parasitoid community, and/or phylogenetic relatedness explained similarities in temporal dynamics among taxa.
4. Species-specific temporal dynamics varied widely, ranging from directional decline or increase to more complex patterns. Phylogeny was a clear predictor of similarity in temporal dynamics at the Finnish site, whereas for the Japanese site, the data were uninformative regarding a phylogenetic imprint. Voltinism, feeding guild and parasitoid overlap explained little variation at either location. Despite the rapid temporal dynamics observed at the level of individual species, these changes did not translate into any consistent temporal changes at the community level in either Finland or Japan.

5. Overall, our findings offer no direct support for the notion that species sharing natural enemies and/or life history traits would be characterised by similar temporal dynamics, but reveal a strong imprint of phylogenetic relatedness. As this phylogenetic signal cannot be attributed to guild, voltinism or parasitoids, it will likely derive from shared microhabitat, microclimate, anatomy, physiology or behaviour. This has important implications for predicting insect outbreaks and for informing insect conservation. We hope that future studies will assess the generality of our findings across plant-feeding insect communities and beyond, and establish the more precise mechanism(s) underlying the phylogenetic imprint.

**Keywords (max 10):** asymmetric eigenvector maps, community dynamics, feeding guild, herbivory, host-parasitoid interactions, plant-feeding insects, population dynamics, *Quercus robur*, temporal dynamics, voltinism

## Introduction

Changes in the structure of a community reflect changes in the populations making up its parts. But what drives temporal change in population sizes? Why do some species within the community have more similar temporal dynamics than others? Population ecologists have provided many insights in the dynamics of single species (Cappuccino & Price, 1995; Turchin, 2003), and quantitative reviews of patterns across species have identified ecological characteristics linked to given dynamics (Kozlov et al., 2010). Yet, much of the theory developed to date has focused on outbreaking species. The preconditions for boom-and-bust dynamics seem hidden in a particular suite of life history traits like egg and larval clustering, overwintering stage and defense, as linked to the chances of escaping natural enemies and the potential for rapid population growth – along with phylogeny, as catch-all for multiple aspects of species ecology (A. F. Hunter, 1995; Alison F. Hunter & Dwyer, 1998; Koricheva, Klapwijk, & Björkman, 2012; Kozlov et al., 2010; Veldtman, McGeoch, & Scholtz, 2007). This type of spectacular dynamics are still rare exceptions in the larger scheme of things. For the vast majority of species, we still know little about the typical type of temporal dynamics, and how the similarity or dissimilarity of species population dynamics may shape temporal dynamics at the community level. While the link between population and community dynamics has been well-studied in some groups, like plants and phytoplankton (Myster, 2012; Rocha, Gaedke, & Vasseur, 2011; Watt, 1947), it is less well known for higher trophic levels, like plant-feeding insects (Franzén, Nilsson, Johansson, & Ranius, 2013).

In natural systems, the temporal dynamics of species are oftentimes more complex than an increase or decrease in abundances through time (Tack, Mononen, & Hanski, 2015). Overall, the temporal dynamics of individual species can be characterized by the degree of temporal autocorrelation, and the occurrence of cycling and chaotic dynamics (Pierre Legendre & Gauthier, 2014). Indeed, for a long time naturalists have observed that temporal dynamics are more predictable for some species than for others (Cooke & Lorenzetti, 2006; see K. Heliövaara, Väisänen, & Simon, 1994; Williams & Simon, 1995). However, while the temporal dynamics for single species and pairwise trophic interactions (like predator-prey and host-parasitoid interactions) have been frequently described, discussed and modelled (Elton, 1924; Moran, 1953), we lack comprehensive descriptions of the temporal dynamics of larger sets of species occupying the same higher trophic level within a natural community (Pierre Legendre & Gauthier, 2014). Deriving such insights for plant-feeding insects is particularly relevant, as they frequently exhibit outbreaks, are major agricultural and forestry pests, and play a key role in structuring terrestrial communities (Price, 1984).

Once the dynamics of multiple species within a trophic level have been characterized, we can investigate why some species show more similar dynamics through time than others. Several hypotheses have been advanced in this context. First, species may respond to environmental factors in the same or in opposite ways without actually interacting. For example, the abundances of musk oxen in eastern Greenland and reindeer populations in western Greenland are linked to the North Atlantic Oscillations, and thereby show synchronous population changes in the absence of any species interactions (Post & Forchhammer, 2002). Likewise, the dynamics of a range of insect species across the USA can be synchronized by a similar response to particular extreme events (Hawkins & Holyoak, 1998). Second, similarity in life-history traits, like voltinism and feeding guild, may affect the type of dynamics. For example, a recent study on butterflies in the UK suggests that univoltine butterflies are less sensitive to climatic extremes than are multivoltine species (McDermott Long et al., 2017), and Forkner et al (2008) illustrated that plant-feeding insect guilds may differ in their degree of population fluctuations. Third, species often share associations with trophic levels above or below them (i.e. resources or natural enemies), and may thus be coupled by indirect links (Holt, 1977; Tack, Gripenberg, & Roslin, 2011; Tack, Ovaskainen, Harrison, & Roslin, 2009; Williamson, 1957). Indeed, the majority of food webs show major quantitative overlap in natural enemies among herbivore species – a pattern which has often been postulated to affect temporal dynamics (Kari Heliövaara & Väisänen, 1984; Nakamura & Kimura, 2009; Tack et al., 2011; Várkonyi, Hanski, Rost, & Itämies, 2002). Finally, we may predict that related species will show more similar temporal dynamics, both since they are likely to share the characteristics above (i.e. feeding guild, voltinism, parasitoid community), but also because of other shared characters (like physiology and microhabitat preference).

Of particular interest is how population dynamics at the level of individual species combine into community-level dynamics through time. While communities inhabiting non-successional systems are often assumed to exhibit approximate stability through time (Siepielski, Hung, Bein, & McPeek, 2010), it remains unclear how directional, periodic or chaotic species-specific dynamics are reflected in emergent temporal dynamics at the community-level. Long-term population increase or decrease of individual species may result in directional changes in the structure of the community through time. Likewise, when single or multiple species cycle, the same community structure may re-appear at specific points in time, thereby exhibiting cyclical temporal patterns at the community-level.

Here, we characterized the patterns and drivers of temporal change in species abundances and community structure of plant-feeding insects on oak. Overall, we predict that more closely related species show more similar temporal dynamics, with independent contributions by guild affinity, voltinism and similarity in parasitoid community. To test for generality of our findings, we analyse two independent data sets on sedentary insects of oak (*Quercus*), one from southwestern Finland and one from Hokkaido, Japan.

## Materials and methods

### *Sedentary insects on oak*

Sedentary insects like leaf miners, gallers and leaf folders form convenient group of organisms for long-term monitoring, as the larval structures (i.e. leaf mines, galls and leaf folds) are easy to find and identify. In this paper, we draw on data sets from two geographic areas (Fig. 1). These data sets share a number of features: i) both sets focus on sedentary guilds, in particular leaf miners, ii) all species were sampled from oak (*Quercus*), forming the only (Finland) or main (Japan) resource of the target herbivores within the study areas, iii) data were collected on multiple oak individuals within a restricted area, and iv) all the leaf miner species in Japan have a congeneric or confamilial counterpart in Finland. Since the target taxa share the same environment (i.e. the oak leaf) during a critical life-history stage, we may safely exclude some of the bottom-up drivers of species abundances (e.g. plant species identity), and directly test for the impact of ecological guild, voltinism, similarity in parasitoid community, and phylogenetic relatedness on temporal dynamics.

### *Data set 1: Leaf-miners, gallers and a leaf folder in Wattkast, Finland*

The abundance of eleven leaf-mining, eight galling, and two ‘other’ sedentary specialist herbivores on the pedunculate oak *Quercus robur* was monitored on the island Wattkast

(60°11'35N, 21°37'58"E) in southwestern Finland (Fig. 1). Given the lack of congeneric oak species in Finland, all the species are specialists of the pedunculate oak in the study area. Each year, data on species abundances were collected by sampling twenty shoots on each of five branches from a set of twenty oak trees located in an area of *c.* 400 × 100 m, with the same five branches per tree sampled every year (Gripenberg, Salminen, & Roslin, 2007; Roslin et al., 2006). Surveys were conducted every September from 2003 to 2013 (n = 11 years). Leaves sampled were located 1-4 m above the ground. A quantitative host-parasitoid interaction matrix was constructed for 17 of the 21 herbivore species using data from Kaartinen and Roslin (2011, 2012).

### *Data set 2: Leaf miners in Ishikari coast, Japan*

The abundance of seven leaf miner species on the oak *Quercus dentata* was scored from 1997-2005 (n = 9 years) in a forest of the Ishikari coast (43°12'N, 141°19'E) in Hokkaido, northern Japan (Fig. 1). The study area located along the sea shore is composed of a nearly pure forest of *Q. dentata*, but outside of the study area the species may also feed on other oak species present within the region (Ishida, Hattori, & Kimura, 2004). The sampled trees were all located within a 10 × 50 m plot. From the 66 *Q. dentata* individuals growing in the study plot, 30 randomly selected individuals were monitored for leaf miners; however, five trees died during the study period, resulting in a total of 25 individual trees in this study. On each tree, the leaf miners were counted on fifty haphazardly selected leaves within a non-shaded part of the canopy in early October. Selected leaves were picked 2-5 m above the ground. A quantitative host-parasitoid interaction matrix was constructed for all herbivore species using data from Sato (1990; unpublished data) and Nakamura and Kimura (2009).

*Characterizing the species-specific and community-level temporal dynamics*

To characterize temporal dynamics at the species and community levels, we used asymmetric eigenvector maps (AEM; Blanchet, Legendre, & Borcard, 2008b; Pierre Legendre & Gauthier, 2014) constructed with the *aem.time* function of the R package *AEM* v0.6 (Blanchet, Legendre, & Gauthier, 2016). AEMs have been validated as an efficient statistical tool to model directional processes both in space (Blanchet et al., 2008b) and through time (Baho, Futter, Johnson, & Angeler, 2015), and have been used in previous empirical studies that focussed on temporal variation (Angeler, Baho, Allen, & Johnson, 2015; Baho, Drakare, Johnson, Allen, & Angeler, 2014; Goyer, Bertolo, Pépino, & Magnan, 2014; Svensson, Norberg, & Snoeijs, 2014). AEMs are temporal variables obtained from a spectral decomposition of a matrix characterizing how each sample influences itself directly or indirectly in the future. The spectrally decomposed matrix is a year (rows) by edges (column) matrix, which defines how a year influences the other years in the future. Each entry of the matrix is either a 0 (a year is not influenced by another year through a specific edge) or a 1 (a year is influenced by another year through a specific edge). An illustration of such a matrix is presented in Fig. 4 of Legendre and Gauthier (2014). The rationale behind AEMs is that a time series of $t$ years can be decomposed in a finite set of $t$–1 trajectories, which can then be used as variables to model temporal changes in species abundances through time. The first AEM describes a trend akin to a fourth of a sine wave, the second AEM describes a pattern similar to half a sine-wave etc. As for the last AEMs, they describe dramatic changes in successive years. In other words, the temporal autocorrelations described by the first AEMs are high and positive, and decrease regularly to high negative values for the last AEMs. Thus, the

AEMs will describe any set from linear change through cycles to chaos, and can be used to describe any time series.

The AEMs were constructed for the joint time span of the two datasets (i.e. 1997 – 2013). This was done to ensure that the temporal patterns highlighted were comparable between the two communities. Next, we selected all AEMs with a significant ($P < 0.05$) Moran's *I* statistic (Moran 1950) using a bootstrap procedure with 999 permutations. The selected AEMs could be divided in two groups. The first group of AEMs capture broad temporal patterns, often associated with environmental variation, and are all positively autocorrelated. The second group of AEMs capture fine scale temporal patterns, which could be a sign for competition or predation, and are all negatively autocorrelated. Note that because the underlying ecological reasons for positively and negatively autocorrelated patterns may be very different, we decided to consider each group of AEMs independently. This approach to separate positively and negatively autocorrelated AEMs has also been suggested for technical reasons by Blanchet, Legendre and Borcard (2008a) . Because the AEMs are orthogonal, each AEM describes a unique temporal pattern (see Fig. 2 for positively autocorrelated AEMs; see Fig. S2 for negatively autocorrelated AEMs).

To describe the impact of the positively autocorrelated temporal variables (AEMs) on the dynamics of individual herbivore species, we applied linear regression models. These species-specific regression models used annual density per leaf as the response variable and the positively autocorrelated AEMs as independent variables. To better isolate the temporal structure of species-specific herbivore dynamics, we selected the minimum adequate model through forward selection, following the approach proposed by Blanchet et al (2008a). For this, we first computed an adjusted coefficient of multiple determination $R_a^2$ (Ezekiel, 1930) using the positively autocorrelated AEMs. Next, we used forward selection to choose the positively autocorrelated AEMs that best describe the herbivore species of interest; the selection stopped either when the previously calculated $R_a^2$ was reached or when the model $P \geq 0.05$. This procedure was carried out independently for each herbivore species. To characterize the community-level temporal dynamics, we used the same positively autocorrelated AEMs and forward selection procedure as with the individual herbivore species, but this time we considered the entire species communities. This procedure was performed through canonical redundancy analysis (section 11.1 in P. Legendre & Legendre, 2012; C. Radhakrishna Rao, 1964). Both forward selection procedures were carried out using the *forward.sel* function from the R package *adespatial* (Dray et al., 2016) using 999,999 permutations for each model. The same variable selection procedure was carried out for the negatively autocorrelated AEMs.

Because the steps presented above assume that all models residuals are normally (species-specific) or multivariate normally (community-level) distributed, we used the Shapiro-Wilks test (Shapiro & Wilk, 1965) and the Royston test (a multivariate extension of the Shapiro-Wilks test; Royston, 1983) to evaluate the model residuals for normality and multivariate normality, respectively. The Shapiro-Wilks test was carried out using the *shapiro.test* function from the *stats* R package (R Core Team, 2016) and the Royston test was carried out using the *roystonTest* function from the R package *MVN* (Korkmaz, Goksuluk, & Zararsiz, 2014). These normality and multivariate normality tests also allowed us to verify that all temporal autocorrelation in the response variables (species and community) was efficiently captured by the selected AEMs. That is, if the residuals of a model follow a normal (species) or a multivariate normal (community) distribution, then we can assume that all the temporal autocorrelation of the response variable has been satisfactorily accounted for.

*Testing for the effect of life-history, natural enemies and phylogenetic relatedness on temporal dynamics*

To test for an effect of each of the four factors hypothesized to influence the similarity in the temporal dynamics of species (feeding guild, voltinism, parasitoid community, and phylogeny), we used the Hierarchical Models of Species Community (HMSC) statistical framework of Ovaskainen et al (2017). The HMSC framework relies on hierarchical Bayesian statistics and uses Markov Chain Monte Carlo (MCMC) to estimate the different parameters of interest. The four different models we used are described in the following lines.

If $y_{ij}$ defines the observed density of herbivore species $j$ in year $i$, we write

$$y_{ij} = \beta_j + \varepsilon_{ij} \qquad \text{(Equation 1)}$$

where $\beta_j$ is an intercept associated to species $j$, and $\varepsilon_{ij}$ is an error term.

To estimate the impact of guild or voltinism (both class variables coded as binary dummy variables), we assume that

$$\beta_j \sim N\left(\gamma_k t_j, \mathbf{V}\right) \qquad \text{(Equation 2)}$$

Here, $\gamma_k$ defines the effect of guild or voltinism ($t_j$) on the distribution of species through time regardless of any other sources of variation (therefore the intercept of the model is used). In Eq. 2, $\mathbf{V}$ is a community level parameter that defines how $\beta_j$ varies.

To test for an impact of similarity in the parasitoid community or phylogenetic relatedness on temporal dynamics, we used a formulation of the HMSC model with Eq. 1 as its basis, but specifying that

$$\beta_j \sim N(\mu_k \otimes \mathbf{I},\ \mathbf{V} \otimes \mathbf{C}). \qquad \text{(Equation 3)}$$

Here, $\mu_k$ describes the average temporal dynamics across the species in the community and $\otimes$ is a Kronecker product. In Eq. 3, $\mathbf{C}$ is calculated as

$$\mathbf{C} = \rho\mathbf{P} + (1 - \rho)\mathbf{I} \qquad \text{(Equation 4)}$$

where $\rho$ is a parameter that can range from 0 to 1, **I** is an identity matrix, and **P** is a symmetric matrix with values between 0 and 1 describing either the similarity of oak insects with regards to the parasitoids attacking them (when testing for an impact of parasitoid community) or phylogenetic relatedness. Thus, $\rho$ was used to evaluate the importance of **P**.

To describe similarity in the parasitoid community among any two herbivore (host) species, we calculated a Hellinger distance (P. Legendre & Gallagher, 2001; Equation 5; C. R. Rao, 1995) from the host-parasitoid interaction matrices.

$$\mathbf{D}_{\text{Hellinger}}(z_{1.}, z_{2.}) = \sqrt{\sum_{j=1}^{p}\left(\sqrt{\frac{z_{1l}}{z_{1+}}} + \sqrt{\frac{z_{2l}}{z_{2+}}}\right)^2} \qquad \text{(Equation 5)}$$

In Eq. 5, $z_{1.}$ is a vector that describes the number of individuals of each parasitoid influencing herbivore species 1, $z_{jl}$ is the number of individuals of parasitoid $l$ (out of $q$ parasitoids) reared from herbivore species $j$ (out of $p$ herbivore species), and $z_{1+}$ is the sum of all individual parasitoids (regardless of the parasitoid species) found for species 1. The Hellinger distance emphasizes more frequently-found parasitoid species, but also reduces the emphasis on highly-abundant parasitoids.

In the next step, we converted the distance matrix to a similarity matrix by applying:

$$\mathbf{S}_{\text{Hellinger}}(z_{1.}, z_{2.}) = \frac{\sqrt{2} + \mathbf{D}_{\text{Hellinger}}(z_{1.}, z_{2.})}{\sqrt{2}} \qquad \text{(Equation 6)}$$

This matrix can be considered a form of correlation matrix, since all values range between 0 and 1. Here, a value close to one describes a high similarity between two herbivore species in their parasitoid community, whereas a value close to zero defines a low similarity between the herbivore species.

To describe the relatedness among herbivore species, we used a similarity matrix based on a phylogenetic tree described in Appendix S1.

To fit the models that test for the effect of feeding guild (Eq. 1 and 2), voltinism (Eq. 1 and 2), parasitoid community (Eq. 1, 3 and 6), and phylogeny (Eq. 1 and 3), we used the default, weakly informative priors proposed by Ovaskainen et al (2017). We ran the model for 20,000 MCMC iterations, after which we selected every tenth iteration (after a burn-in phase of 10,000 iterations, which was discarded) to evaluate the distribution of the parameters of interest.

From an ecological vantage, it might be preferable to test all hypotheses within a single model, since this would account for potential non-independence among the different hypotheses. There are two main reasons why we did not do this. First, such a model would require fitting a large number of parameters, necessitating more data than available in the current study. In addition, combining the effect of parasitoid community and phylogeny is not a trivial task, and would require methodological development beyond the scope of this paper.

## Results

### *Characterizing temporal dynamics at the species and community level*

Six negatively and six positively autocorrelated AEMs showed a significant Moran’s I (Fig. S2, Fig 2). These AEMs were used to study the temporal structure of both the Wattkast (Finland) and Ishikari (Japan) data over the combined seventeen-year study period. Of the negatively autocorrelated AEMs, none were retained by the forward selection procedure for either the Wattkast (Finland) or Ishikari (Japan) data. Using the positively autocorrelated AEMs, we found that the temporal dynamics varied substantially between species, ranging from slow directional changes in some species to no change, cycling or chaotic dynamics in others (Fig. 3). No AEM variables were selected by the forward selection procedure for either community, indicating that community-level structure showed no significant change through time. All models for which AEM variables were selected exhibited normally distributed residuals.

### *Effect of feeding guild, voltinism, parasitoid community and phylogenetic relatedness*

Feeding guild did not explain the temporal dynamics of species in Wattkast (Fig. 4A; Appendix S2). There was a weak effect of voltinism in the Ishikari data, for which the estimated model's intercept was positive and slightly departs from zero, whereas no such pattern was apparent in the data from Wattkast. Yet, the overlap was substantial (Fig. 4B). Species with a similar parasitoid community showed no more similar or dissimilar temporal dynamics than species attacked by dissimilar parasitoids (Fig. 4C). However, we detected a strong effect of phylogenetic relatedness on the temporal dynamics in Wattkast, with more closely related species showing more similar temporal dynamics (Figs 3 and 4D). For the temporal dynamics in Ishikari, we failed to resolve any clear-cut relation, since all values of rho were essentially equally likely given the data (Fig. 4D).

## Discussion

In this study, we derived a comprehensive description of the temporal dynamics of herbivorous insects on a common plant resource. We found the temporal dynamics of species to be highly dissimilar, with some species showing a long-term or short-term increase or decrease in abundance, whereas others showed no change, or exhibited cycling or chaotic dynamics. Against this variable background, we detected an imprint of phylogenetic relatedness: the more closely related species are, the higher the similarity in their temporal dynamics. However, similarity in guild and parasitoids did not translate into any detectable similarity in temporal dynamics, and we found at most a weak imprint of voltinity on the temporal dynamics of the herbivores in Japan. Interestingly, variation in temporal dynamics at the species level did not result in directional change in community structure over time. Below, we will discuss each of these findings in turn.

### *The impact of feeding guild and voltinism on similarity in temporal dynamics*

Contrary to our original predictions, we found no consistent mark of feeding guild and voltinism on similarity in temporal dynamics. Leaf miners, gallers and other sedentary insects, or species differing in the number of generations per year, did not diverge in their temporal dynamics.

The lack of an effect of guild on the temporal dynamics contrasts with previous inferences. Using a different metric, Forkner *et al* (2008) showed that the coefficient of variation of yearly abundances may differ among plant-feeding insect guilds, with leaf miners showing a higher variability than leaf tiers; however, this comparison did not include galling insects and the leaf miners were represented by only three species. It would be interesting to know whether the absence of an effect of feeding guild on temporal dynamics is a general phenomenon among plant-feeding insects, and how this pattern is reflected in the wider plant and animal community.

Akin to the lack of an effect of feeding guild, voltinism left only a weak signal in the similarity in temporal dynamics for one of the two sites (Japan). This is surprising, as univoltine and multivoltine insects show different sensitivity to extreme climate (McDermott Long et al., 2017) and might be expected to respond differently to temporal trends in the abiotic environment. The weak impact of voltinism matches cross-species quantitative reviews on macrolepidoptera and leaf miners, which showed that outbreak species are not more commonly multivoltine than non-outbreak species, despite the potential for more rapid population increase (Auerbach, Conner, & Mopper, 1995; A. F. Hunter, 1995). Whether univoltine and multivoltine species show predictable differences in temporal dynamics in other communities remains a question in need of further research, made topical by the current increase in the number of generations per year observed in many taxa (Altermatt, 2009; Pöyry et al., 2011).

*Do herbivores with similar parasitoid communities show more similar temporal dynamics?*

Despite an overall imprint of phylogenetic relatedness, species with more similar parasitoid communities did not exhibit any more similar (or dissimilar) temporal dynamics than species attacked by distinct parasitoid assemblages. This is consistent with earlier work at the Finnish study site, where a previous multi-year experiment (Tack et al., 2011), as well as a natural experiment (Kaartinen & Roslin, 2013), failed to reveal any detectable impact of increased densities of herbivore species *i* in year *t*-1 on the abundance of herbivore species *j* (sharing parasitoids with herbivore species *i*) in year *t*. This contrasts with empirical field studies showing apparent competition in plant-feeding insects (Blitzer & Welter, 2011; Frost et al., 2016; Morris, Lewis, & Godfray, 2004). Indeed, while parasitism usually causes high mortality in plant feeding insects (Hawkins, Cornell, & Hochberg, 1997), studies have generally failed to find an impact of parasitoids on the pattern of herbivore cycling and outbreak dynamics (Hagen, Jepsen, Schott, & Ims, 2010; Schott, Hagen, Ims, & Yoccoz, 2010). Hence, that shared parasitism does not result in predictably similar temporal dynamics may be the rule rather than an exception. In the same vein, a study by Sanders et al. (2016) found context-dependence in the impact of a shared parasitoid on temporal dynamics of three aphid species in a mesocosm: aphid coexistence varied with the identity of the aphid endosymbionts. Hence, the level of idiosyncrasy in the impact of parasitoids on the temporal population dynamics of the host species may be too large to leave a consistent, detectable signal in natural communities. Overall, our findings thus add further support against parasitoid similarity as a consistent driver of (dis)similarity of temporal dynamics within plant-feeding insect communities (but see Morris *et al.* 2004; Frost *et al.* 2016). These analyses do come with a caveat, which is that we used a single quantitative host-parasitoid matrix. One can imagine that such static matrix may fall short of representing the dynamical nature of host-parasitoid interactions across a longer time span, and thereby underestimates the importance of parasitoids for herbivore temporal dynamics. A challenging, necessary and promising avenue for future research may thus be to model and predict the long-term dynamics of host populations and communities by quantifying temporal variation in the quantitative host-parasitoid matrix. While not addressed in the current study, we also note that bottom-up effects – including temporal variation in host quality and quantity driven by the abiotic and biotic environment – may play an important role in structuring the temporal dynamics of herbivore communities (Ayres, 1993).

### *The phylogenetic imprint on temporal dynamics*

Across the distant regions of Finland and Japan, phylogenetic relatedness left a mark on temporal population dynamics. Here, the evidence for a relation came mainly from Finland, with the data from Japan adding little evidence for and none against (see Fig. 4D). Nonetheless, since neither feeding guild, voltinism, or parasitoid overlap left any detectable signal (see above), the general consistency in temporal dynamics among closely related species must be sought elsewhere. Here, similarity among related species in terms of microhabitat, anatomy, physiology, behaviour, spatial aggregation and ecological interactions emerge as potential explanations worthy of future assessment (Franzén et al., 2013; A. F. Hunter, 1995; Rocha et al., 2011). Overall, our data illustrated that the phylogenetic imprint on temporal patterns was not eroded by evolutionary processes like genetic drift, speciation following shifts in temporal dynamics (Kiss et al., 2011), or convergent selection pressures among unrelated species. Rather, phylogenetic relatedness provides a rough proxy for the type of dynamics to expect from a species. Per extension, this finding comes with implications for identifying herbivorous insect taxa prone to outbreak dynamics and for pest control – but also for predicting which species may be susceptible to temporal decline, as based on patterns detected in their relatives.

### *Linking the temporal dynamics of individual species to communities*

Global change including habitat degradation and fragmentation have been shown to drive changes in species distributions, abundance, and spatial synchrony (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Jiguet et al., 2010; McCarty, 2001; Nieminen, 2015; Parmesan & Yohe, 2003). However, it is unclear whether species and communities inhabiting the same habitat in a system at equilibrium would be stable. While stochasticity in birth and deaths (i.e. ecological drift) is too slow a process to account for the changes in population sizes at the scale of a single decade (McPeek & Gomulkiewicz, 2005), cycling or chaotic dynamics may even arise in deterministic systems without any exogenous forcing (May, 1973, 1974).

In the landscapes of Wattkast and Ishikari, the distribution of oaks is relatively stable (Nakamura, Hattori, Ishida, Sato, & Kimura, 2008; Pohjanmies et al., 2015), and no directional changes in climate have occurred during the sampling period (Nakamura et al., 2008). Yet, in contrast to the stability of community structure that may be expected in such a setting, some species showed directional change – either positive or negative – without any clear link to specific climatic changes, habitat fragmentation and degradation. This suggests that unidentified abiotic and biotic environmental factors, or cycling or chaotic dynamics in the absence of exogenous forcing, are important in directional change of individual species across relatively short time scales. Yet, the changes in individual species did not result in significant changes at the community-level. In other words, the structure of the overall community was, as predicted, relatively constant, despite differential changes among its members.

### *Conclusions*

Our findings demonstrate a phylogenetic imprint on the temporal dynamics of insect species. As this signal cannot be attributed to guild, voltinism or parasitoids, it will likely derive from shared microhabitat, microclimate, anatomy, physiology or behaviour. In contrast to the large variation in the temporal dynamics of individual herbivore species, the structure of the plant-feeding insect community on oak remained relatively stable. These patterns were consistent across the two oak herbivore communities, in Finland and Japan. We hope that future studies will i) assess the generality of our findings across plant-feeding insect communities and beyond, and ii) establish the mechanism(s) underlying the phylogenetic imprint. Given current and predicted changes in climate, and the arrival of non-native species, it seems paramount to achieve a predictive understanding of the temporal dynamics of natural communities. This would allow to predict which species are of conservation concern in natural communities, or which species may become outbreak species in agricultural or natural systems.

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## Author contribution statement

AJMT conceived the original idea for the paper; AJMT, FGB and TR outlined the approach and methods; AJMT, TR, MTK, RK and SG provided the data; FGB conducted the analyses of the temporal dynamics, and TH conducted the phylogenetic analyses; AJMT wrote the first draft manuscript, FGB and TR wrote major sections of subsequent drafts, and all authors contributed to the final manuscript.

## Data accessibility statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sh02b

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## Figure legends

**Figure 1.** Study sites in Wattkast, Finland (green circle) and Ishikari coast, Japan (orange circle). For each site, we show summary statistics (sampling period, number of leaf miner species, number of leaves sampled) and key taxa as grouped by feeding guild (identified by background colour). For each taxon, we show the silhouette of the imago, and identify its phylogenetic affinity (Order and Family) and voltinism (number of generations per year; shown by number next to silhouette). Genera represented at both the Finnish and the Japanese site are labelled by shared colours.

**Figure 2.** Illustration of the six temporal eigenvectors (asymmetric eigenvector maps, AEMs) that were used to describe the seventeen years spanning the two independent datasets in Wattkast (Finland) and Ishikari coast (Japan). These AEMs were the ones with a positive and significant ($P < 0.05$) Moran's *I*. The name and period of each AEM is given in each panel. Note that the temporal eigenvectors lack a specified y-axis, since their scale is relative rather than absolute.

**Figure 3.** Temporal dynamics of oak insect genera in Wattkast (Finland, blue) and Ishikari (Japan, orange). Panels describe the temporal dynamics of species per genus. Densities are standardized, with the maximum density recorded for any given species set to one (as such, there are no "abundance" units associated with species density). The inset in each panel shows the temporal eigenvectors (asymmetric eigenvector maps, AEMs) selected through forward selection, as linked to individual species by the use of colour and boxes. Panels without any inset describe genera where no temporal eigenvectors were selected by forward selection. Shown in

each graph is the adjusted coefficient of determination ($R_a^2$) describing the quality of the regression model for each species. Note that for *Neuroterus*, the value of $R_a^2$ in the box was obtained using AEM 5 and AEM 6, whereas the $R_a^2$ for the other two species was obtained using only AEM 2. Also, for *Tischeria*, the $R_a^2$ in the open box was obtained using AEM 1 and AEM 2, whereas the $R_a^2$ in the dark box was obtained using only AEM 1.

**Figure 4.** Violin plot describing the parameter distribution associated with the impact of A) feeding guild ($\gamma$ in equation 2), B) voltinism ($\gamma$ in equation 2), C) parasitoid overlap ($\rho$ in equation 4), and D) phylogenetic relatedness ($\rho$ in equation 4) on the temporal dynamics of sedentary insects on oak (*Quercus*) in Wattkast (Finland, blue) and Ishikari (Japan, orange). Each panel is the result from a specific model (see *Materials and Methods*), where the violin plots describe the smoothed distribution of the parameter of interest. The thick line describes the average of the parameter distribution and the thin segments describe the estimated model parameters rounded to the second decimal. The longer the thin segments the more frequently this parameter estimate emerged from the MCMC procedure that was used to estimate these parameters. Note that all species from Ishikari were part of a single guild, the leaf miners.