

# *Related herbivore species show similar temporal dynamics*

Article

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1 **Running head:** Temporal community dynamics

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

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4 F. G. Blanchet<sup>1</sup>, T. Roslin<sup>2,3</sup>, M. T. Kimura<sup>4</sup>, T. Huotari<sup>3</sup>, R. Kaartinen<sup>5</sup>, S. Gripenberg<sup>6</sup>, A. J. M.  
5 Tack<sup>7\*</sup>

6

7 <sup>1</sup> Département de biologie, Faculté des sciences, Université de Sherbrooke, 2500 Boulevard  
8 Université, Sherbrooke, Québec, Canada, J1K 2R1

9 <sup>2</sup> Department of Ecology, Swedish Univ. of Agricultural Sciences, Box 7044, SE-750 07  
10 Uppsala, Sweden

11 <sup>3</sup> Department of Agricultural Sciences, PO Box 27, (Latokartanonkaari 5), FI-00014 University  
12 of Helsinki, Finland

13 <sup>4</sup> University Museum, Hokkaido University, Sapporo, Hokkaido 060-0810, Japan

14 <sup>5</sup> School of Biological Sciences, University of Edinburgh, Ashworth laboratories, Charlotte  
15 Auerbach Road, Edinburgh EH9 3FL, United Kingdom

16 <sup>6</sup> Department of Zoology, University of Oxford, Oxford OX1 3PS, United Kingdom

17 <sup>7</sup> Department of Ecology, Environment and Plant Sciences, Stockholm University, Svante  
18 Arrhenius väg 20A, Stockholm

19

20 \* Corresponding author; e-mail: [ayco.tack@su.se](mailto:ayco.tack@su.se); phone: +46-(0)70 4942557

21 **Abstract**

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

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

52

53

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

57 **Introduction**

58 Changes in the structure of a community reflect changes in the populations making up its parts.  
59 But what drives temporal change in population sizes? Why do some species within the  
60 community have more similar temporal dynamics than others? Population ecologists have  
61 provided many insights in the dynamics of single species (Cappuccino & Price, 1995; Turchin,  
62 2003), and quantitative reviews of patterns across species have identified ecological  
63 characteristics linked to given dynamics (Kozlov et al., 2010). Yet, much of the theory developed  
64 to date has focused on outbreaking species. The preconditions for boom-and-bust dynamics seem  
65 hidden in a particular suite of life history traits like egg and larval clustering, overwintering stage  
66 and defense, as linked to the chances of escaping natural enemies and the potential for rapid  
67 population growth – along with phylogeny, as catch-all for multiple aspects of species ecology  
68 (A. F. Hunter, 1995; Alison F. Hunter & Dwyer, 1998; Koricheva, Klapwijk, & Björkman, 2012;  
69 Kozlov et al., 2010; Veldtman, McGeoch, & Scholtz, 2007). This type of spectacular dynamics  
70 are still rare exceptions in the larger scheme of things. For the vast majority of species, we still  
71 know little about the typical type of temporal dynamics, and how the similarity or dissimilarity  
72 of species population dynamics may shape temporal dynamics at the community level. While the  
73 link between population and community dynamics has been well-studied in some groups, like  
74 plants and phytoplankton (Myster, 2012; Rocha, Gaedke, & Vasseur, 2011; Watt, 1947), it is less  
75 well known for higher trophic levels, like plant-feeding insects (Franzén, Nilsson, Johansson, &  
76 Ranius, 2013).

77 In natural systems, the temporal dynamics of species are oftentimes more complex than  
78 an increase or decrease in abundances through time (Tack, Mononen, & Hanski, 2015). Overall,  
79 the temporal dynamics of individual species can be characterized by the degree of temporal

80 autocorrelation, and the occurrence of cycling and chaotic dynamics (Pierre Legendre &  
81 Gauthier, 2014). Indeed, for a long time naturalists have observed that temporal dynamics are  
82 more predictable for some species than for others (Cooke & Lorenzetti, 2006; see K. Heliövaara,  
83 Väisänen, & Simon, 1994; Williams & Simon, 1995). However, while the temporal dynamics for  
84 single species and pairwise trophic interactions (like predator-prey and host-parasitoid  
85 interactions) have been frequently described, discussed and modelled (Elton, 1924; Moran,  
86 1953), we lack comprehensive descriptions of the temporal dynamics of larger sets of species  
87 occupying the same higher trophic level within a natural community (Pierre Legendre &  
88 Gauthier, 2014). Deriving such insights for plant-feeding insects is particularly relevant, as they  
89 frequently exhibit outbreaks, are major agricultural and forestry pests, and play a key role in  
90 structuring terrestrial communities (Price, 1984).

91       Once the dynamics of multiple species within a trophic level have been characterized, we  
92 can investigate why some species show more similar dynamics through time than others. Several  
93 hypotheses have been advanced in this context. First, species may respond to environmental  
94 factors in the same or in opposite ways without actually interacting. For example, the abundances  
95 of musk oxen in eastern Greenland and reindeer populations in western Greenland are linked to  
96 the North Atlantic Oscillations, and thereby show synchronous population changes in the  
97 absence of any species interactions (Post & Forchhammer, 2002). Likewise, the dynamics of a  
98 range of insect species across the USA can be synchronized by a similar response to particular  
99 extreme events (Hawkins & Holyoak, 1998). Second, similarity in life-history traits, like  
100 voltinism and feeding guild, may affect the type of dynamics. For example, a recent study on  
101 butterflies in the UK suggests that univoltine butterflies are less sensitive to climatic extremes  
102 than are multivoltine species (McDermott Long et al., 2017), and Forkner et al (2008) illustrated

103 that plant-feeding insect guilds may differ in their degree of population fluctuations. Third,  
104 species often share associations with trophic levels above or below them (i.e. resources or natural  
105 enemies), and may thus be coupled by indirect links (Holt, 1977; Tack, Gripenberg, & Roslin,  
106 2011; Tack, Ovaskainen, Harrison, & Roslin, 2009; Williamson, 1957). Indeed, the majority of  
107 food webs show major quantitative overlap in natural enemies among herbivore species – a  
108 pattern which has often been postulated to affect temporal dynamics (Kari Heliövaara &  
109 Väisänen, 1984; Nakamura & Kimura, 2009; Tack et al., 2011; Várkonyi, Hanski, Rost, &  
110 Itämies, 2002). Finally, we may predict that related species will show more similar temporal  
111 dynamics, both since they are likely to share the characteristics above (i.e. feeding guild,  
112 voltinism, parasitoid community), but also because of other shared characters (like physiology  
113 and microhabitat preference).

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

123         Here, we characterized the patterns and drivers of temporal change in species abundances  
124 and community structure of plant-feeding insects on oak. Overall, we predict that more closely  
125 related species show more similar temporal dynamics, with independent contributions by guild



126 affinity, voltinism and similarity in parasitoid community. To test for generality of our findings,  
127 we analyse two independent data sets on sedentary insects of oak (*Quercus*), one from  
128 southwestern Finland and one from Hokkaido, Japan.

129

130

## 131 **Materials and methods**

### 132 *Sedentary insects on oak*

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

145

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

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

149 (60°11'35N, 21°37'58"E) in southwestern Finland (Fig. 1). Given the lack of congeneric oak  
150 species in Finland, all the species are specialists of the pedunculate oak in the study area. Each  
151 year, data on species abundances were collected by sampling twenty shoots on each of five  
152 branches from a set of twenty oak trees located in an area of *c.* 400 × 100 m, with the same five  
153 branches per tree sampled every year (Gripenberg, Salminen, & Roslin, 2007; Roslin et al.,  
154 2006). Surveys were conducted every September from 2003 to 2013 (n = 11 years). Leaves  
155 sampled were located 1-4 m above the ground. A quantitative host-parasitoid interaction matrix  
156 was constructed for 17 of the 21 herbivore species using data from Kaartinen and Roslin (2011,  
157 2012).

158

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

160 The abundance of seven leaf miner species on the oak *Quercus dentata* was scored from 1997-  
161 2005 (n = 9 years) in a forest of the Ishikari coast (43°12'N, 141°19'E) in Hokkaido, northern  
162 Japan (Fig. 1). The study area located along the sea shore is composed of a nearly pure forest of  
163 *Q. dentata*, but outside of the study area the species may also feed on other oak species present  
164 within the region (Ishida, Hattori, & Kimura, 2004). The sampled trees were all located within a  
165 10 × 50 m plot. From the 66 *Q. dentata* individuals growing in the study plot, 30 randomly  
166 selected individuals were monitored for leaf miners; however, five trees died during the study  
167 period, resulting in a total of 25 individual trees in this study. On each tree, the leaf miners were  
168 counted on fifty haphazardly selected leaves within a non-shaded part of the canopy in early  
169 October. Selected leaves were picked 2-5 m above the ground. A quantitative host-parasitoid  
170 interaction matrix was constructed for all herbivore species using data from Sato (1990;  
171 unpublished data) and Nakamura and Kimura (2009).

172

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

174 To characterize temporal dynamics at the species and community levels, we used asymmetric  
175 eigenvector maps (AEM; Blanchet, Legendre, & Borcard, 2008b; Pierre Legendre & Gauthier,  
176 2014) constructed with the *aem.time* function of the R package *AEM* v0.6 (Blanchet, Legendre,  
177 & Gauthier, 2016). AEMs have been validated as an efficient statistical tool to model directional  
178 processes both in space (Blanchet et al., 2008b) and through time (Baho, Futter, Johnson, &  
179 Angeler, 2015), and have been used in previous empirical studies that focussed on temporal  
180 variation (Angeler, Baho, Allen, & Johnson, 2015; Baho, Drakare, Johnson, Allen, & Angeler,  
181 2014; Goyer, Bertolo, P epino, & Magnan, 2014; Svensson, Norberg, & Snoeijs, 2014). AEMs  
182 are temporal variables obtained from a spectral decomposition of a matrix characterizing how  
183 each sample influences itself directly or indirectly in the future. The spectrally decomposed  
184 matrix is a year (rows) by edges (column) matrix, which defines how a year influences the other  
185 years in the future. Each entry of the matrix is either a 0 (a year is not influenced by another year  
186 through a specific edge) or a 1 (a year is influenced by another year through a specific edge). An  
187 illustration of such a matrix is presented in Fig. 4 of Legendre and Gauthier (2014). The rationale  
188 behind AEMs is that a time series of  $t$  years can be decomposed in a finite set of  $t-1$  trajectories,  
189 which can then be used as variables to model temporal changes in species abundances through  
190 time. The first AEM describes a trend akin to a fourth of a sine wave, the second AEM describes  
191 a pattern similar to half a sine-wave etc. As for the last AEMs, they describe dramatic changes in  
192 successive years. In other words, the temporal autocorrelations described by the first AEMs are  
193 high and positive, and decrease regularly to high negative values for the last AEMs. Thus, the

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

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

210         To describe the impact of the positively autocorrelated temporal variables (AEMs) on the  
211 dynamics of individual herbivore species, we applied linear regression models. These species-  
212 specific regression models used annual density per leaf as the response variable and the  
213 positively autocorrelated AEMs as independent variables. To better isolate the temporal structure  
214 of species-specific herbivore dynamics, we selected the minimum adequate model through  
215 forward selection, following the approach proposed by Blanchet et al (2008a). For this, we first  
216 computed an adjusted coefficient of multiple determination  $R_a^2$  (Ezekiel, 1930) using the

217 positively autocorrelated AEMs. Next, we used forward selection to choose the positively  
218 autocorrelated AEMs that best describe the herbivore species of interest; the selection stopped  
219 either when the previously calculated  $R_a^2$  was reached or when the model  $P \geq 0.05$ . This  
220 procedure was carried out independently for each herbivore species. To characterize the  
221 community-level temporal dynamics, we used the same positively autocorrelated AEMs and  
222 forward selection procedure as with the individual herbivore species, but this time we considered  
223 the entire species communities. This procedure was performed through canonical redundancy  
224 analysis (section 11.1 in P. Legendre & Legendre, 2012; C. Radhakrishna Rao, 1964). Both  
225 forward selection procedures were carried out using the *forward.sel* function from the R package  
226 *adespatial* (Dray et al., 2016) using 999,999 permutations for each model. The same variable  
227 selection procedure was carried out for the negatively autocorrelated AEMs.

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

240

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

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

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

$$250 \quad y_{ij} = \beta_j + \varepsilon_{ij} \quad \text{(Equation 1)}$$

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

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

$$254 \quad \beta_j \sim N(\gamma_k t_j, \mathbf{V}) \quad \text{(Equation 2)}$$

255 Here,  $\gamma_k$  defines the effect of guild or voltinism ( $t_j$ ) on the distribution of species through time  
256 regardless of any other sources of variation (therefore the intercept of the model is used). In Eq.  
257 2,  $\mathbf{V}$  is a community level parameter that defines how  $\beta_j$  varies.

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

$$261 \quad \beta_j \sim N(\mu_k \otimes \mathbf{I}, \mathbf{V} \otimes \mathbf{C}). \quad \text{(Equation 3)}$$

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

$$264 \quad \mathbf{C} = \rho \mathbf{P} + (1 - \rho) \mathbf{I} \quad (\text{Equation 4})$$

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

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

$$272 \quad \mathbf{D}_{\text{Hellinger}}(z_1, z_2) = \sqrt{\sum_{j=1}^p \left( \sqrt{\frac{z_{1l}}{z_{1+}}} + \sqrt{\frac{z_{2l}}{z_{2+}}} \right)^2} \quad (\text{Equation 5})$$

273 In Eq. 5,  $z_1$  is a vector that describes the number of individuals of each parasitoid influencing  
 274 herbivore species 1,  $z_{jl}$  is the number of individuals of parasitoid  $l$  (out of  $q$  parasitoids) reared  
 275 from herbivore species  $j$  (out of  $p$  herbivore species), and  $z_{1+}$  is the sum of all individual  
 276 parasitoids (regardless of the parasitoid species) found for species 1. The Hellinger distance  
 277 emphasizes more frequently-found parasitoid species, but also reduces the emphasis on highly-  
 278 abundant parasitoids.

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

$$280 \quad \mathbf{S}_{\text{Hellinger}}(z_1, z_2) = \frac{\sqrt{2} + \mathbf{D}_{\text{Hellinger}}(z_1, z_2)}{\sqrt{2}} \quad (\text{Equation 6})$$

281 This matrix can be considered a form of correlation matrix, since all values range between 0 and  
 282 1. Here, a value close to one describes a high similarity between two herbivore species in their

283 parasitoid community, whereas a value close to zero defines a low similarity between the  
284 herbivore species.

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

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

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

298

## 299 **Results**

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

301 Six negatively and six positively autocorrelated AEMs showed a significant Moran's I (Fig. S2,  
302 Fig 2). These AEMs were used to study the temporal structure of both the Wattkast (Finland) and  
303 Ishikari (Japan) data over the combined seventeen-year study period. Of the negatively  
304 autocorrelated AEMs, none were retained by the forward selection procedure for either the  
305 Wattkast (Finland) or Ishikari (Japan) data. Using the positively autocorrelated AEMs, we found



306 that the temporal dynamics varied substantially between species, ranging from slow directional  
307 changes in some species to no change, cycling or chaotic dynamics in others (Fig. 3). No AEM  
308 variables were selected by the forward selection procedure for either community, indicating that  
309 community-level structure showed no significant change through time. All models for which  
310 AEM variables were selected exhibited normally distributed residuals.

311

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

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

323

#### 324 **Discussion**

325 In this study, we derived a comprehensive description of the temporal dynamics of herbivorous  
326 insects on a common plant resource. We found the temporal dynamics of species to be highly  
327 dissimilar, with some species showing a long-term or short-term increase or decrease in  
328 abundance, whereas others showed no change, or exhibited cycling or chaotic dynamics. Against

329 this variable background, we detected an imprint of phylogenetic relatedness: the more closely  
330 related species are, the higher the similarity in their temporal dynamics. However, similarity in  
331 guild and parasitoids did not translate into any detectable similarity in temporal dynamics, and  
332 we found at most a weak imprint of voltinity on the temporal dynamics of the herbivores in  
333 Japan. Interestingly, variation in temporal dynamics at the species level did not result in  
334 directional change in community structure over time. Below, we will discuss each of these  
335 findings in turn.

336

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

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

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

348         Akin to the lack of an effect of feeding guild, voltinism left only a weak signal in the  
349 similarity in temporal dynamics for one of the two sites (Japan). This is surprising, as univoltine  
350 and multivoltine insects show different sensitivity to extreme climate (McDermott Long *et al.*,  
351 2017) and might be expected to respond differently to temporal trends in the abiotic

352 environment. The weak impact of voltinism matches cross-species quantitative reviews on  
353 macrolepidoptera and leaf miners, which showed that outbreak species are not more commonly  
354 multivoltine than non-outbreak species, despite the potential for more rapid population increase  
355 (Auerbach, Conner, & Mopper, 1995; A. F. Hunter, 1995). Whether univoltine and multivoltine  
356 species show predictable differences in temporal dynamics in other communities remains a  
357 question in need of further research, made topical by the current increase in the number of  
358 generations per year observed in many taxa (Altermatt, 2009; Pöyry et al., 2011).

359

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

361 Despite an overall imprint of phylogenetic relatedness, species with more similar parasitoid  
362 communities did not exhibit any more similar (or dissimilar) temporal dynamics than species  
363 attacked by distinct parasitoid assemblages. This is consistent with earlier work at the Finnish  
364 study site, where a previous multi-year experiment (Tack et al., 2011), as well as a natural  
365 experiment (Kaartinen & Roslin, 2013), failed to reveal any detectable impact of increased  
366 densities of herbivore species  $i$  in year  $t-1$  on the abundance of herbivore species  $j$  (sharing  
367 parasitoids with herbivore species  $i$ ) in year  $t$ . This contrasts with empirical field studies showing  
368 apparent competition in plant-feeding insects (Blitzer & Welter, 2011; Frost et al., 2016; Morris,  
369 Lewis, & Godfray, 2004). Indeed, while parasitism usually causes high mortality in plant feeding  
370 insects (Hawkins, Cornell, & Hochberg, 1997), studies have generally failed to find an impact of  
371 parasitoids on the pattern of herbivore cycling and outbreak dynamics (Hagen, Jepsen, Schott, &  
372 Ims, 2010; Schott, Hagen, Ims, & Yoccoz, 2010). Hence, that shared parasitism does not result in  
373 predictably similar temporal dynamics may be the rule rather than an exception. In the same  
374 vein, a study by Sanders et al. (2016) found context-dependence in the impact of a shared

375 parasitoid on temporal dynamics of three aphid species in a mesocosm: aphid coexistence varied  
376 with the identity of the aphid endosymbionts. Hence, the level of idiosyncrasy in the impact of  
377 parasitoids on the temporal population dynamics of the host species may be too large to leave a  
378 consistent, detectable signal in natural communities. Overall, our findings thus add further  
379 support against parasitoid similarity as a consistent driver of (dis)similarity of temporal dynamics  
380 within plant-feeding insect communities (but see Morris *et al.* 2004; Frost *et al.* 2016). These  
381 analyses do come with a caveat, which is that we used a single quantitative host-parasitoid  
382 matrix. One can imagine that such static matrix may fall short of representing the dynamical  
383 nature of host-parasitoid interactions across a longer time span, and thereby underestimates the  
384 importance of parasitoids for herbivore temporal dynamics. A challenging, necessary and  
385 promising avenue for future research may thus be to model and predict the long-term dynamics  
386 of host populations and communities by quantifying temporal variation in the quantitative host-  
387 parasitoid matrix. While not addressed in the current study, we also note that bottom-up effects –  
388 including temporal variation in host quality and quantity driven by the abiotic and biotic  
389 environment – may play an important role in structuring the temporal dynamics of herbivore  
390 communities (Ayres, 1993).

391

### 392 *The phylogenetic imprint on temporal dynamics*

393 Across the distant regions of Finland and Japan, phylogenetic relatedness left a mark on temporal  
394 population dynamics. Here, the evidence for a relation came mainly from Finland, with the data  
395 from Japan adding little evidence for and none against (see Fig. 4D). Nonetheless, since neither  
396 feeding guild, voltinism, or parasitoid overlap left any detectable signal (see above), the general  
397 consistency in temporal dynamics among closely related species must be sought elsewhere. Here,

398 similarity among related species in terms of microhabitat, anatomy, physiology, behaviour,  
399 spatial aggregation and ecological interactions emerge as potential explanations worthy of future  
400 assessment (Franzén et al., 2013; A. F. Hunter, 1995; Rocha et al., 2011). Overall, our data  
401 illustrated that the phylogenetic imprint on temporal patterns was not eroded by evolutionary  
402 processes like genetic drift, speciation following shifts in temporal dynamics (Kiss et al., 2011),  
403 or convergent selection pressures among unrelated species. Rather, phylogenetic relatedness  
404 provides a rough proxy for the type of dynamics to expect from a species. Per extension, this  
405 finding comes with implications for identifying herbivorous insect taxa prone to outbreak  
406 dynamics and for pest control – but also for predicting which species may be susceptible to  
407 temporal decline, as based on patterns detected in their relatives.

408

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

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

418         In the landscapes of Wattkast and Ishikari, the distribution of oaks is relatively stable  
419 (Nakamura, Hattori, Ishida, Sato, & Kimura, 2008; Pohjanmies et al., 2015), and no directional  
420 changes in climate have occurred during the sampling period (Nakamura et al., 2008). Yet, in

421 contrast to the stability of community structure that may be expected in such a setting, some  
422 species showed directional change – either positive or negative – without any clear link to  
423 specific climatic changes, habitat fragmentation and degradation. This suggests that unidentified  
424 abiotic and biotic environmental factors, or cycling or chaotic dynamics in the absence of  
425 exogenous forcing, are important in directional change of individual species across relatively  
426 short time scales. Yet, the changes in individual species did not result in significant changes at  
427 the community-level. In other words, the structure of the overall community was, as predicted,  
428 relatively constant, despite differential changes among its members.

429

### 430 *Conclusions*

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

443

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451

452 **Author contribution statement**

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

458

459 **Data accessibility statement**

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

461

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678 **Figure legends**

679

680 **Figure 1.** Study sites in Wattkast, Finland (green circle) and Ishikari coast, Japan (orange circle).

681 For each site, we show summary statistics (sampling period, number of leaf miner species,

682 number of leaves sampled) and key taxa as grouped by feeding guild (identified by background

683 colour). For each taxon, we show the silhouette of the imago, and identify its phylogenetic

684 affinity (Order and Family) and voltinism (number of generations per year; shown by number

685 next to silhouette). Genera represented at both the Finnish and the Japanese site are labelled by

686 shared colours.

687

688 **Figure 2.** Illustration of the six temporal eigenvectors (asymmetric eigenvector maps, AEMs)

689 that were used to describe the seventeen years spanning the two independent datasets in Wattkast

690 (Finland) and Ishikari coast (Japan). These AEMs were the ones with a positive and significant

691 ( $P < 0.05$ ) Moran's  $I$ . The name and period of each AEM is given in each panel. Note that the

692 temporal eigenvectors lack a specified y-axis, since their scale is relative rather than absolute.

693

694 **Figure 3.** Temporal dynamics of oak insect genera in Wattkast (Finland, blue) and Ishikari

695 (Japan, orange). Panels describe the temporal dynamics of species per genus. Densities are

696 standardized, with the maximum density recorded for any given species set to one (as such, there

697 are no “abundance” units associated with species density). The inset in each panel shows the

698 temporal eigenvectors (asymmetric eigenvector maps, AEMs) selected through forward

699 selection, as linked to individual species by the use of colour and boxes. Panels without any inset

700 describe genera where no temporal eigenvectors were selected by forward selection. Shown in

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

706

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

717