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.

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

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

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, & McPeek, 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, Pépino, & 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 ≥ 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 $y_{ij} = \beta_j + \varepsilon_{ij}$ (Equation 1)

251 where β_j is an intercept associated to species j, and ε_{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 $\beta_j \sim N(\gamma_k t_j, \mathbf{V})$ (Equation 2)

255 Here, γ_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 β_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        $\beta_j \sim N(\mu_k \otimes \mathbf{I}, \mathbf{V} \otimes \mathbf{C})$.   (Equation 3)

262   Here, μ_k describes the average temporal dynamics across the species in the community and $\otimes$ is

263   a Kronecker product. In Eq. 3, **C** is calculated as

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

265   where ρ is a parameter that can range from 0 to 1, **I** is an identity matrix, and **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, ρ was used to evaluate the importance of **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    $$\mathbf{D}_{\text{Hellinger}}(z_{1\cdot}, z_{2\cdot}) = \sqrt{\sum_{j=1}^{p}\left(\sqrt{\frac{z_{1l}}{z_{1+}}} + \sqrt{\frac{z_{2l}}{z_{2+}}}\right)^2}$$ (Equation 5)

273   In Eq. 5, $z_{1\cdot}$ 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    $$\mathbf{S}_{\text{Hellinger}}(z_{1\cdot}, z_{2\cdot}) = \frac{\sqrt{2} + \mathbf{D}_{\text{Hellinger}}(z_{1\cdot}, z_{2\cdot})}{\sqrt{2}}$$ (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 Wattkast (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 Wattkast. 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 Wattkast, 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 (McPeek & 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

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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676

677

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 (γ in equation 2), B) voltinism (γ in equation 2), C) parasitoid overlap (ρ in

709   equation 4), and D) phylogenetic relatedness (ρ 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.

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