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1 **Predator-vole interactions in northern Europe: the role of small mustelids revised**

2

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19

20 Keywords: population cycles; population dynamics; population growth rate; density
21 dependence

22

23 **Summary**

24 The cyclic population dynamics of vole and predator communities is a key phenomenon
25 in northern ecosystems, and it appears to be influenced by climate change. Reports of
26 collapsing rodent cycles have attributed the changes to warmer winters, which weaken
27 the interaction between voles and their specialist subnivean predators. Using population
28 data collected throughout Finland during 1986-2011, we analyse the spatiotemporal
29 variation in the interactions between populations of voles and specialist, generalist, and
30 avian predators, and investigate by simulations the roles of the different predators in the
31 vole cycle. We test the hypothesis that vole population cyclicity is dependent on predator-
32 prey interactions during winter. Our results support the importance of the small mustelids
33 for the vole cycle. However, weakening specialist predation during winters, or an
34 increase in generalist predation, was not associated with the loss of cyclicity.
35 Strengthening of delayed density dependence coincided with strengthening small
36 mustelid influence on the summer population growth rates of voles. In conclusion, a
37 strong impact of small mustelids during summers appears highly influential to vole
38 population dynamics, and deteriorating winter conditions are not a viable explanation for
39 collapsing small mammal population cycles.

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41 **Key index words:** population cycles; population dynamics; population growth rate;
42 density dependence

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45 **1. Introduction**

46

47 Trophic interactions have a profound impact on population dynamics (1). Population
48 cycles, in particular, are commonly thought to arise from trophic interactions, which can
49 introduce a delay in the regulation of population growth (1). Boreal voles of Eurasia are a
50 well-studied example of species in which predation can cause delayed density
51 dependence of population growth, and cyclic population dynamics (2, 3). Voles are often
52 the most abundant mammals in boreal and subarctic regions, and an indispensable food
53 source for numerous avian and mammalian predators (4, 5). The interaction between the
54 vole and the predator communities, and the cyclic population dynamics observed in both,
55 are key phenomena in northern Eurasian ecosystems.

56 During recent years there have been reports of collapsing rodent cycles with
57 potentially detrimental effects on the predator community (6, 7). The loss of cyclicity has
58 been attributed to milder and shorter winters, which are thought to increase density-
59 independent winter mortality, and decrease the influence of delayed density dependence
60 (6, 7). However, we recently showed that mild winters are not associated with collapsing
61 cyclicity among boreal vole populations (8). Furthermore, it is not known how the
62 interactions between voles and predators vary temporally and geographically, so the
63 attribution of causality to altered predator-vole interactions is far from clear.

64 Practically all terrestrial carnivores in northern Europe consume voles at least
65 occasionally, and the following predators show a clear preference for voles: the small
66 mustelids (9), the red fox (10), the pine marten (11) and several owl and raptor species
67 (12, 13). The small mustelids, the least weasel, *Mustela nivalis nivalis*, and the stoat,

68 *Mustela erminea*, are key predators in the boreal vole cycle (2). They are small and
69 highly adapted to prey on voles even in their nests and under the snow cover, and can be
70 the main cause of mortality in vole populations (14). They depend almost exclusively on
71 voles (9), but have a much lower intrinsic growth rate than their prey, and hence a strong
72 but delayed numerical response to vole densities, resulting in delayed density-dependent
73 predation pressure on vole populations (9, 15). Of the two species, the stoat is considered
74 to be more of a generalist than the least weasel (9).

75 Generalist predators, exploiting a variety of food sources, are thought to have a
76 stabilizing effect on the prey populations, preying on voles during the peak phase of the
77 cycle, and switching to alternative prey when vole densities are low (16, 17). Because of
78 this, the generalists have the ability to transmit the cyclic population dynamics of voles to
79 their alternative prey populations (18, 19). According to diet analyses, the red fox (*Vulpes*
80 *vulpes*) and the pine marten (*Martes martes*) are generalist predators in Fennoscandia (10,
81 11). They are thus expected to have a cycle-dampening effect (17).

82 Birds of prey may dampen or enhance cyclicity in their prey. Nomadic species are
83 able to travel long distances and nest where vole densities are high, i.e. have a direct
84 numerical response and dampen the vole cycle (13, 20); on the other hand, migratory
85 birds are not able to survey vole densities during the winter, and may rely on last season's
86 information to decide where to nest (21). The reproductive effort and success of the
87 resident raptors is dependent on current vole densities (22, 23). Therefore, avian
88 predators might respond to vole densities of the previous autumn (decision on where to
89 nest, recruitment of last year's young), spring (reproductive effort) or the current summer
90 (survival of fledglings).

91 The interactions between the vole and the predator communities of northern Europe
92 have been studied with mechanistic models and phenomenological time-series analyses
93 (e.g. 2, 17, 24) and large-scale, yet local, manipulative experiments (reviewed by 25, 26),
94 but they are not well described on a large temporal and geographic scale, let alone using
95 observational data. Predator-vole interactions are likely to depend on environmental
96 conditions and may thus be subject to spatial and temporal variation: e.g. snow cover may
97 influence the availability of voles to avian and larger mammalian predators (23),
98 temperatures may affect the energy requirements of predators (23, 27); and food
99 availability to voles will influence the relative contribution of predation on vole
100 population growth rates (28).

101 In the present study we aim to characterize the interactions between voles and the
102 specialist mammalian, the generalist mammalian, and the avian predators using animal
103 population monitoring data collected throughout Finland during 23 years. We will
104 estimate the time lags in the predator responses to vole densities as well as the predator
105 effects on vole population growth rates. Specifically, we test the hypothesis that
106 weakening vole-specialist predator interactions during winters are associated with the
107 collapse of the vole cycle. Finally, we use the data-derived parameter estimates to
108 simulate vole population dynamics under a number of scenarios to gauge the roles of
109 different predators in the boreal vole cycle.

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111

112

113

114 **Methods**

115

116 Vole population data

117 Vole populations were censused using biannual snap trapping [in spring before the
118 reproductive season of voles in mid-March to mid-June, and in autumn after the
119 reproductive season in mid-August to mid-October (both times dependent upon
120 geographic location and seasonal phenology)] in forest and old-field habitats in 32
121 locations during 1986-2011 (Fig. 1, Fig. S1). Voles of the genera *Microtus* and *Myodes*
122 were included in the analyses. On average each trapping session included 289 trap nights
123 (range 30-1800). Trapping was conducted with standard metal mouse snap traps. At each
124 location, a mean of 50–100 traps were set either a) in a line, in clusters of three traps with
125 an inter-trap distance of 1–2m and an inter-cluster distance of 10–20m, or b) according to
126 the small quadrat method (29). Traps were set for 1–4 nights and checked and re-set if
127 necessary once a day. Regardless of the number of traps used per session, or the number
128 of consecutive trap nights, each trap effectively traps a standard-size area. Since the
129 density of traps (traps per unit area) does not change between sites or over time, our
130 trapping indices from different areas and times are comparable.

131 The vole data comprise the following species: *Microtus agrestis* (28%), *M. levis*
132 (5%) and *M. oeconomus* (6%), and *Myodes glareolus* (57%), *M. rutilus* (3%), and *M.*
133 *rufocanus* (1%). Density indices were calculated as $N = \log [(total\ number\ of\ voles$
134 $trapped + 1) / trap\ nights * 100]$. Seasonal vole population growth rates were calculated
135 as $S_t - A_{t-1}$ (winter) and $A_t - S_t$ (summer), where S denotes spring vole density, A autumn
136 vole density and t denotes year. Each vole time series was standardized to mean = 0 to

137 correct for potential trapping-site quality bias. We decided the pool all vole species
138 despite the ecological differences between *Myodes* and *Microtus* voles. We have analysed
139 the variation in the spatiotemporal dynamics separately for *Microtus* voles in their
140 principal habitat (old fields) and for *Myodes* voles in forests. The spatiotemporal patterns
141 in the population dynamics of the different genera parallel each other, and those obtained
142 with the pooled vole densities [see Table 1 in (8)]. Furthermore, the different species are
143 known to fluctuate in synchrony (8, 30) and be subject to predation by the same predators
144 (e.g. 31, 32). Therefore, the pooled data allow us to answer the study questions more
145 clearly than the genus-specific results would.

146

147 Mammalian predator data

148 We obtained density indices for the mammalian predators from the Finnish Game and
149 Fisheries Research Institute (33). Mammalian predator densities were monitored by
150 counting snow tracks on previously marked transects in winter (mid-January to mid-
151 March) during 1989-2011. Triangles consisting of three 4-km transects were surveyed
152 and all mammal tracks crossing the transect were counted and identified to species one or
153 two days after a pre-check or snowfall. Annually ca. 800 triangles are monitored (Fig. 1
154 and S1). As weather conditions could influence the visibility of the snow tracks, the
155 protocol set by the Finnish Game and Fisheries Research Institute rigorously defines the
156 environmental circumstances under which the snow track counts may be conducted.
157 Firstly, the transect must be walked or skied twice - first to mark all existing tracks, then
158 at least 24 hours later to count all new tracks. This time of track accumulation cannot
159 include extreme cold temperatures, heavy winds or snowfall. Alternatively, tracks may be

160 counted without a preliminary marking round, 24-48 hours after a snowfall. In both cases,
161 the snow cover must be fine and soft enough to enable the smallest recordable animals,
162 least weasels, to leave identifiable tracks. These strict guidelines ensure that the weather
163 conditions during the snow track count are geographically and temporally consistent. The
164 degree of detectability of tracks is thus unlikely to differ between geographic areas.

165 The density index for a given species is calculated as $\log[(n_{i,t} + n_{\min})/d]$, where
166 the $n_{i,t}$ is the number of tracks observed per 10 km of survey route at location i and year
167 t , n_{\min} is the minimum observed non-zero n , and d is the number of days during which
168 the tracks accumulated. We included the densities of four mammalian predators and
169 aggregated the predator species into two groups based on their behaviour and
170 morphology: the small mustelids (the least weasel and the stoat) formed the specialist
171 predator group, and the larger mammalian predators (the red fox and the pine marten) the
172 generalist predator group (17). Density indices of both groups were calculated for each
173 vole trapping location by distance-weighted averaging (using all data points, with weight
174 decreasing by distance²). The mammalian predator data were globally standardized to
175 mean = 0 to render the values of the different predator groups comparable.

176

177 Avian predator data

178 The data for avian predators were obtained from the Finnish Museum of Natural History
179 (34). The monitoring scheme is organized in 25 areas (Fig. 1, Fig. S1), which together
180 cover all of Finland. In each area, all known raptor territories are visited each spring and
181 summer, and checked for nests from which eggs and later the chicks are counted. Raptor
182 monitoring data were available from 1986 to 2011. We included data on the following

183 species, which prey on voles and which are relatively abundant in our study area: the
184 nomadic or migratory species *Asio flammeus*, *Asio otus*, *Aegolius funereus*, *Glaucidium*
185 *passerinum*, *Falco tinnunculus*, *Circus cyaneus*, and *Buteo lagopus*; and the resident
186 species *Strix uralensis*, *Strix aluco*, *Bubo bubo*, and *Buteo buteo*. Although it is known
187 that these species react slightly differently to vole abundances and differ in their
188 specialization in voles, their densities showed strong correlations ($r > 0.8$), which
189 justified the calculation of a total avian predator density index as $\log\left[\frac{n_{i,t}c_{i,t}+2n_{i,t}}{s_{i,t}}\right]$, where
190 $n_{i,t}$ refers to the number of nesting pairs in area i and year t , $c_{i,t}$ to the average number of
191 chicks per nest in area i and year t , and $s_{i,t}$ to the number of territories surveyed in area i
192 and year t . The avian predator density index was calculated for each vole-trapping site by
193 averaging over all raptor-monitoring areas within a 50 km distance. Prior to combining
194 the avian time series, they were de-trended, as some showed potentially artificial
195 increasing trends due to increased nest-box availability. The avian predator density was
196 calculated for each vole-trapping site by averaging over all raptor-monitoring areas
197 within a 50 km distance.

198

199 Influence of predators on vole population growth rates

200 To estimate the spatial and temporal variation in the impact of the different predator
201 groups on vole populations, we modelled vole population growth rates during winter
202 (Model 1) and summer (Model 2) as a function of vole and predator indices. Mammalian
203 predator indices were measured in winter, and avian predator indices in summer. We
204 assumed the linear models

205

206 $Y_{1,t} = S_t - A_{t-1} = a_1 + b_1A_{t-1} + c_1A_{t-2} + d_1P_{1,t} + e_1P_{2,t} + f_1P_{3,t-1} + \varepsilon_{1,t}$ (Model 1)
207 $Y_{2,t} = A_t - S_t = a_2 + b_2S_t + c_2S_{t-1} + d_2P_{1,t} + e_2P_{2,t} + f_2P_{3,t} + \varepsilon_{2,t}$ (Model 2)
208

209 where P_1 refers to the density index of the small mustelids, P_2 to the generalist
210 mammalian predators, and P_3 to the avian predators.

211 Because we had no *a priori* knowledge of the geographic and temporal variation in
212 predator-vole interactions, we began with a very flexible model, and then simplified the
213 model based on the data. Initially, we allowed the parameters $a - f$ to vary with time and
214 space by including a latitude*longitude*(year + year²) interaction. After fitting these
215 models, we simplified the models using AIC (Akaike Information Criterion, 35): all
216 terms whose elimination would have resulted in an increase in AIC were retained in the
217 final model.

218 We validated the models by dividing the data set randomly into a training set (50%
219 of the data points) and a test set (50%), refitting the models to the training data, and using
220 these models to predict the test data; this was repeated 50 times (Fig. S2). In addition, we
221 assessed the performance of the models by simulating vole and predator dynamics using
222 parameter estimates from the models; adequate models should be able to create realistic
223 dynamics.

224 Based on the models, we calculated the relative contributions of the different
225 predator groups and of the non-predation-attributable density dependence to the variation
226 in vole population growth rates for each trapping site and year as a fraction of the total
227 variation. To do so, we decomposed the total variance (example for Model 1) as
228

$$\begin{aligned}
\text{Var}(Y_{1,t}) = & b^2\text{Var}(A_{t-1}) + c^2\text{Var}(A_{t-2}) + d^2\text{Var}(P_1) + e^2\text{Var}(P_2) + f^2\text{Var}(P_3) \\
& + 2bc\text{Cov}(A_{t-1}, A_{t-2}) + 2bd\text{Cov}(A_{t-1}, P_1) + 2be\text{Cov}(A_{t-1}, P_2) \\
& + 2bf\text{Cov}(A_{t-1}, P_3) + 2cd\text{Cov}(A_{t-2}, P_1) + 2ce\text{Cov}(A_{t-2}, P_2) \\
& + 2cf\text{Cov}(A_{t-2}, P_3) + 2de\text{Cov}(P_1, P_2) + 2df\text{Cov}(P_1, P_3) \\
& + 2ef\text{Cov}(P_2, P_3) + \sigma^2,
\end{aligned}$$

229

230 where the variances and co-variances are calculated from the whole data set, σ^2 is the
231 variance of the residual term ε , and the model parameter values $a - f$ depend on
232 sampling location and year.

233 To simplify the interpretation of the results, rather than considering the relative
234 contributions of co-variances separately, we decided to treat the co-variances by
235 assigning half of the co-variances to each of the terms involved. As an example, the
236 variance explained by the small mustelids was calculated as

237

$$\begin{aligned}
\text{Var}_{P_1} = & (d^2\text{Var}(P_1) + bd\text{Cov}(A_{t-1}, P_1) + cd\text{Cov}(A_{t-2}, P_1) + de\text{Cov}(P_1, P_2) \\
& + df\text{Cov}(P_1, P_3)) / \text{Var}(Y_{1,t})
\end{aligned}$$

238

239 These values were summarized to represent three regions by averaging over the trapping
240 locations in each: northern Finland (above the 66th latitude), southwestern (<64th latitude
241 and < 25th longitude) and eastern (> 27th longitude) Finland (Fig. 1).

242

243

244

245 Influence of vole population densities on predator abundance indices

246 Using the same initial spatiotemporal structure as in Models 1 and 2, we modelled the
247 predator indices as a function of current and past vole densities to determine the
248 magnitude of and the time lags in the predators' responses:

249

250
$$Y_{3,t} = a_3 + b_3A_{t-1} + c_3S_{t-1} + d_3A_{t-2} + \varepsilon_{3,t}, \text{ (Model 3a: Mammalian predators)}$$

251
$$Y_{3,t} = a_3 + b_3S_t + c_3A_{t-1} + d_3S_{t-1} + \varepsilon_{3,t} \text{ (Model 3b: Avian predators)}$$

252

253 We did not include previous predator densities in the predator models because after
254 accounting for the vole-cycle-attributable autocorrelation, no temporal autocorrelation
255 was left in the predator time series. AIC-determined model reduction was performed as
256 explained above. The relative contributions of vole densities at different time lags to the
257 predator densities were calculated as

258

$$\begin{aligned} \text{Var}_{A_{t-1}} = & (b^2\text{Var}(A_{t-1}) + bc\text{Cov}(A_{t-1}, S_{t-1}) + bd\text{Cov}(A_{t-1}, A_{t-2})) / (b^2\text{Var}(A_{t-1}) \\ & + c^2\text{Var}(S_{t-1}) + d^2 \text{Var}(A_{t-2}) + 2bc\text{Cov}(A_{t-1}, S_{t-1}) \\ & + 2bd\text{Cov}(A_{t-1}, A_{t-2}) + 2cd\text{Cov}(S_{t-1}, A_{t-2}) + \sigma^2) \end{aligned}$$

259

260 The values were summarized to regions (Fig. 3) as explained above.

261

262 Roles of the different predators in the boreal vole cycle: simulation

263 We used the parameter estimates from models 1-3 to simulate vole and predator
264 population dynamics. The simulations were used both for model validation, i.e. to

265 confirm that the models were capable of reproducing the population dynamics observed
266 in different locations and time points, and for scenario simulations, i.e. to investigate the
267 roles of the different predators in vole population dynamics. We focused on three
268 geographic regions, which we had previously discovered to exhibit distinctly different
269 vole population dynamics: the north, the southwest, and the east (8). Using the parameter
270 estimates for the geographic locations and the year 2011 (the last available year with full
271 data records), we simulated 1000 years of vole and predator time series under eight
272 different scenarios in which one, two or all predator groups were removed by setting their
273 density to the minimum observed value in the data set.

274 We estimated the direct and delayed density dependence of vole population growth
275 rates in the simulated time series by regressing the seasonal vole population growth rates
276 against the current and the 1-year-lagged vole densities (8). To assess the variability in
277 the model predictions, we divided the 1000-year time series into 25-year sections, and
278 fitted autoregressive models to each section. Consensus density dependence values were
279 obtained by averaging over the results from the 40 sections, and annual density
280 dependence was calculated from the seasonal density dependence values as in (8). From
281 each 25-year section, we calculated the standard deviation of the population densities (s-
282 index) as an index of amplitude, and seasonality as the difference between the average
283 summer and average winter population growth rates, and averaged these over all sections.
284 The type of population dynamics was inferred from the density dependence values,
285 autocorrelation values, and from visual inspection of the time series. All statistical
286 analyses were conducted with R (36).

287

288 **Results**

289 Model validation

290

291 Our models performed well in model validation: they produced realistic predator-vole
292 dynamics capturing the spatial and temporal variation in vole population dynamics
293 (compare Fig. 4 to ref. 8). When refitted with 50% of the data points, they predicted the
294 remaining 50% fairly well (Fig. S2). Only the small mustelid model's performance was
295 somewhat unsatisfactory, as the correlation between the observed and the predicted small
296 mustelid indices was only 0.42. The final best models based on the model selection are
297 presented in Tables S1-S4.

298

299 Spatiotemporal variation in predator-vole interactions

300

301 The relative influences of the different predator groups on vole population growth rates
302 showed substantial variation over the years and regions (Fig. 2). In the north, the
303 influence of the small mustelids on vole populations showed an increasing temporal trend
304 during both seasons, and they are currently estimated to be the strongest force affecting
305 the winter population growth rates of voles (Fig. 2a, b). According to our models, the
306 generalist predators influenced vole populations only during summers in the north, and
307 the relative impact of the avian predators was declining, particularly during winters (Fig.
308 2a, b).

309 Predators were estimated to have a modest impact on the winter population growth
310 rates of voles in the southwest (Fig. 2c). However, the relative contribution of the small

311 mustelids on the summer population growth rates of voles appeared to have increased
312 considerably (Fig. 2d). The generalist predators were estimated to have very little impact
313 on vole populations in the southwest, and the avian predators to have a modest, and
314 possibly declining, impact during both seasons (Fig. 2c, d).

315 The factors affecting the winter population growth rates of voles in the east were
316 similar to those in the north: a strong avian predator influence substituted in the recent
317 years by a rapidly increasing small mustelid influence (Fig. 2e). However, during
318 summers the generalist and avian predators were estimated to be a stronger force than the
319 small mustelids (Fig. 2f).

320 The dependence of the predator indices on vole population densities tended to be
321 strongest, and the delays longest, in the north (Fig. 3). Particularly in the north and
322 southwest, there appeared to be a temporal trend of shortening delays in the numerical
323 responses of the predators. The small mustelids responded to all vole densities measured
324 during the previous 18 months, the longest delay being the weakest. The larger
325 mammalian predators responded to vole densities with a 10-month delay in the north, and
326 with a 5-month delay in the south. The avian predators responded to vole densities with a
327 time lag of 2-10 months.

328

329 Is predation necessary for cyclic vole population dynamics?

330

331 Our model correctly predicted a regular, high-amplitude 5-year cycle in the North for the
332 year 2011 (Fig. 4a,b black symbol; Fig. S3). Removing either the small mustelids or the
333 avian predators weakened the delayed density dependence (Fig. 4a, pink and lightblue

334 symbols) and amplitude (Fig. 4b), and weakened the cycle (Fig. S3). The seasonality
335 disappeared in the absence of the small mustelids, regardless of which predators
336 remained (Fig. 4c, pink, orange, darkblue and gray symbols), suggesting that the major
337 cause of winter mortality in the north is predation by the small mustelids (Fig. 2a).
338 Removing both the avian predators and the small mustelids, with or without the larger
339 mammalian predators, weakened the delayed density dependence to the extent that the
340 vole cycle collapsed (Fig. 4a, orange and gray symbols; Fig. S3), and the amplitude was
341 clearly reduced (Fig. 4b). The generalist mammalian predators did not influence vole
342 population dynamics to a great extent in the north (Fig. 4a, b, c, yellow symbols).

343 The model predicted a 3-to-4-year cycle in southwestern Finland (Fig. 4d, black
344 symbol; Fig. S4), with a lower amplitude than in the north (Fig. 4e). The removal of the
345 small mustelids had a strong impact on vole population dynamics, regardless of whether
346 the predators remained present: both direct and delayed density dependence were
347 weakened to the extent that the vole cycle collapsed (Fig. 4d, pink, orange, darkblue, and
348 gray symbols; Fig. S4) into completely seasonal (Fig. 4f), high-amplitude dynamics (Fig.
349 4e). The small mustelids were capable of maintaining cyclic vole population dynamics in
350 the absence of the other predators: removing the generalist and the avian predators
351 increased the cycle period (Fig. 4d, red symbols; Fig. S4) and weakened the seasonality
352 (Fig. 4f).

353 The model predicted irregular dynamics in eastern Finland (Fig. 4g; Fig. S5).
354 Predator removal had no effect on the density dependence (Fig. 4g). Removing the small
355 mustelids reduced, and removing the generalist mammals increased the seasonality and

356 the amplitude (Fig. 4h, i, pink and yellow symbols); removing the avian predators had no
357 influence on vole population dynamics (Fig. 4h, i, lightblue symbols).

358

359 Changes within the predator community

360

361 A high relative abundance of the stricter vole specialist, the least weasel, in relation to the
362 semi-generalist stoat, coincided with cyclic vole dynamics (Fig. S6). In western Finland,
363 with continuously cyclic vole dynamics, the least weasel has been more abundant than
364 the stoat; in northern Finland the relative abundance of the least weasel was very low
365 during the non-cyclic period, and is currently increasing together with the strengthening
366 cycle. Most impressively, the relative abundance of the least weasel peaked in synchrony
367 with the vole density peaks in the north: the stoat dominated during cyclic lows, and the
368 least weasel when voles were abundant. A similar pattern was observed in the east,
369 although there the increasing relative abundance of the least weasel was evidently not
370 sufficient to strengthen the vole cycle. One possible explanation is the relative abundance
371 of the generalist mammalian predators, which in eastern Finland was in favor of the pine
372 marten, while the red fox was relatively more abundant in western Finland.

373

374 **Discussion**

375 We analysed predator-vole interactions comprehensively over a large geographic area
376 (ca. 300 000 km²) and a long time period (26 years), capturing the return of the high-
377 amplitude vole cycle in the north as well as the collapse of the cycle in the east. Our

378 results show that the predator-vole interactions vary temporally and geographically, and
379 that this variation explains many of the observed changes in vole population dynamics.

380 Not surprisingly, our model identified the small mustelids as key players in the
381 boreal vole cycle: their numerical response was estimated to be delayed and sufficiently
382 strong to cause negative delayed density dependence in vole populations, supporting
383 earlier results (e.g. 9, 15, 24). Earlier mechanistic modelling studies on vole-predator
384 interactions have suffered from the lack of predator time series to confirm the results. The
385 fact that very different approaches, based on different types of data and models, all lead
386 to the same conclusion offers strong support for the specialist predator hypothesis.

387 In the north, the small mustelids were estimated to be currently the strongest force
388 affecting the winter population growth rates of voles. However, their influence on vole
389 populations appears not to be restricted to the winter season, but occurs, increasingly,
390 during summers, as well. The increase in summer impact coincides with increasing
391 summer precipitation in the north (8). In the coastal southwest, where winters are milder
392 and shorter than in the more continental east and in the north, the small mustelids appear
393 to exert their influence on vole populations mainly during summers. Hence, mild winters
394 appear not to weaken the overall impact of the specialist predators on vole populations.
395 Furthermore, as the vole cycle has collapsed in the east despite a strong relative influence
396 of the small mustelids during winters, it appears that predation by the small mustelids in
397 winter is alone not sufficient to create cyclic vole dynamics. Rather, a sufficient impact of
398 the small mustelids during summers may be an elemental part of the vole cycle,
399 contributing to the summer declines which characterize cyclic, but not non-cyclic, vole
400 populations (3, 37, 38). In addition to the small mustelids, the avian predators were found

401 to influence vole population dynamics, and to be an important source of delayed density
402 dependence in vole populations (see also 21).

403 Generalist predators are usually thought to dampen or inhibit cyclic dynamics in
404 their prey populations (17). However, the red fox is also considered strongly dependent
405 on voles, to the extent that the red fox game bag index has been used as a surrogate for
406 vole density (e.g., 39). Yet another view is that vole populations are not influenced by the
407 generalist predators, as previously shown for the red fox (18). According to our data, the
408 generalists did not depend strongly on voles, nor did they markedly influence vole
409 populations, especially in southern Finland. In the north, however, where alternative food
410 is scarce and where the climate is unfavourable for the red fox (27), the generalist
411 predator index responded occasionally quite strongly to the spring densities of voles and
412 influenced their summer population growth rates. This suggests that in unfavourable
413 environments, voles form a significant food source to fox cubs in their early life.
414 However, the overall impact of the generalists on vole population dynamics was weak.

415 All predators appear to be responding to vole densities with shortening time lags,
416 which may contribute to increasing direct, and weakening delayed density dependence in
417 vole populations. However, this may not unequivocally be the case. The predator
418 populations are monitored only once a year, which makes it difficult to estimate the time
419 lags in their responses and the timing of their impact on the vole populations. It is
420 possible for e.g. the small mustelids to be dependent on the spring densities of voles,
421 while influencing the vole populations during the following winter, or to be dependent on
422 the autumn densities of voles and to influence vole populations during the following
423 summer. In both cases, the impact on the density dependence of vole population growth

424 rates would be the same. The changes in the time lags of the predators' numerical
425 responses may also be due to temporal variations in the relative abundances of the
426 different species. Different raptor species respond to vole densities with different time
427 lags (40), and the stoat responds to vole densities with a shorter time lag than the least
428 weasel (15). Furthermore, the ability of the predators to track vole abundances and to
429 adjust their reproductive effort accordingly may depend on weather conditions, which
430 could lead to the observed temporal variation in the responses.

431 The reliability of the snow track indices is a matter of debate, especially with
432 respect to the small mustelids (discussed recently in 15, 42). Our results indicate a
433 marked amount of measurement error in the small mustelid index, as only ca. 50% of
434 variation in the index was attributable to the vole abundances, although these predators
435 are known to rely heavily on voles (9). Furthermore, a large fraction of the variation in
436 vole population growth rates was unexplained by the predator indices, although predation
437 has been shown to be a major cause of mortality in vole populations (14). The generalist
438 and avian predator indices are likely to be more accurate than the small mustelid index:
439 both indices behaved in our analyses as expected based on earlier studies, the generalists
440 cannot move under the snow cover, and the avian predator index is derived from counts
441 of the animals themselves. Measurement error in the predator indices is likely to weaken,
442 but not strengthen, the estimated interactions between voles and the predators; our
443 estimates are therefore conservative and the interactions may be stronger in reality.
444 Because of the unknown amount of measurement error in the predator indices, some of
445 the unexplained density dependence in vole population growth rates is most likely

446 attributable to predation, although undoubtedly other factors, such as food supply (28),
447 also influence vole populations.

448 According to our results, predation, by the small mustelids in the southwest and by
449 the whole predator guild in the north, is a necessary contributor to the regular, high-
450 amplitude vole cycle in northern Europe. The small mustelid-vole interaction is not
451 restricted to winters, confirming our previous finding that mild winters do not necessarily
452 lead to a collapse of the vole cycle (8). The observed strengthening of delayed density
453 dependence in vole populations coincided with strengthening small mustelid influence on
454 the summer population growth rates of voles. A strong impact of the small mustelids
455 during summers appears important to cyclic vole dynamics.

456

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463

464 **Data accessibility**

465 Data are archived in Dryad (doi:10.5061/dryad.h3bt7).

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603 *M. nivalis*, in Finland. *Oikos* 115:286-298.
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605

606 **Figure captions**

607

608 Figure 1. Data collection locations: vole trapping locations (map a), mammalian predator
609 snow-track-monitoring locations (map b), and avian predator monitoring areas (map c).
610 Letters in map a denote the three regions from which results were summarized (N=north,
611 SW=southwest, E=east).

612

613 Figure 2. Relative contributions of predators and non-predation-attributable density
614 dependence (“Delayed DD” and “Direct DD”) to the summer and winter population
615 growth rates of voles, estimated with Models 1 and 2 and averaged to northern, south-
616 western and eastern Finland, as in Figure 1.

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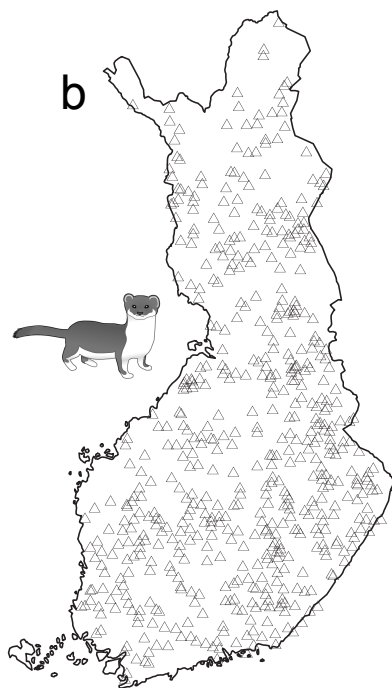
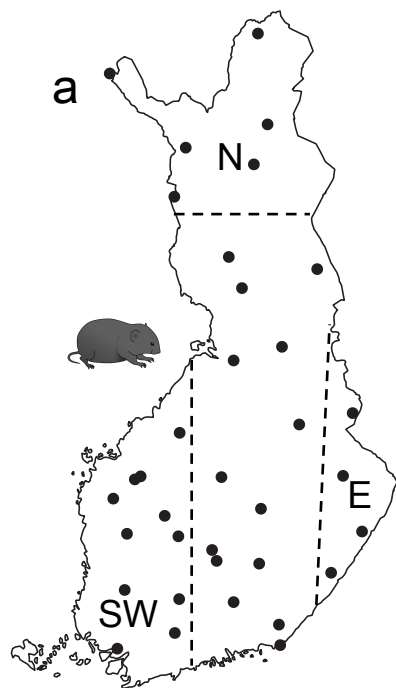
618 Figure 3. Relative contributions of vole densities at different time lags to predator
619 densities, estimated with Models 3a (mammalian predators) and 3b (avian predators) and
620 averaged to northern, south-western and eastern Finland, as in Figure 1. Mammalian
621 predator densities were monitored in winter, and therefore the time lags presented are ca.
622 5 months (vole density in autumn_{t-1}), ca. 10 months (vole density in spring_{t-1}), and ca. 17
623 months (vole density in autumn_{t-2}). Avian predator densities were monitored in summer,
624 and the time lags are ca. 2 months (vole density in spring_t), ca. 9 months (vole density in
625 autumn_{t-1}), and ca. 14 months (vole density in spring_{t-1}).

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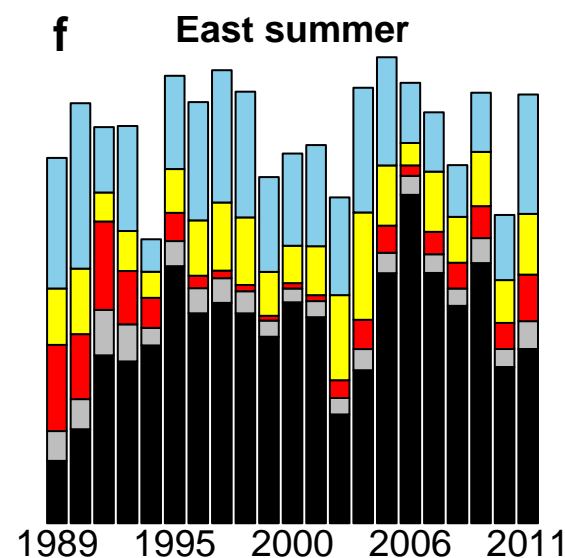
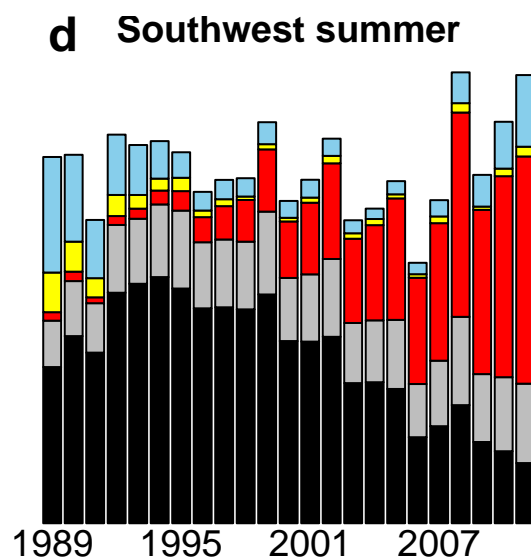
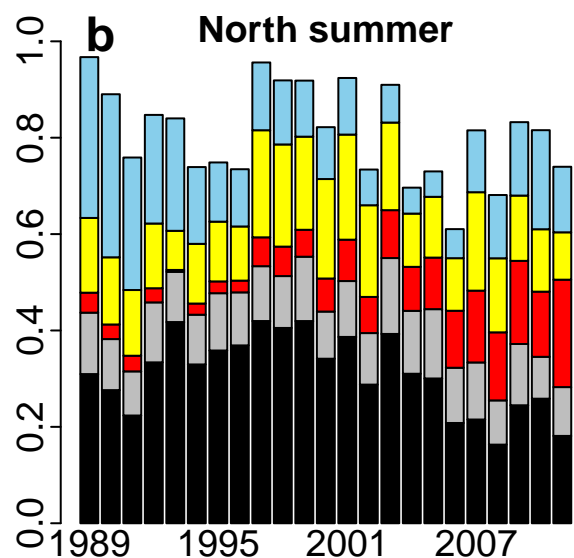
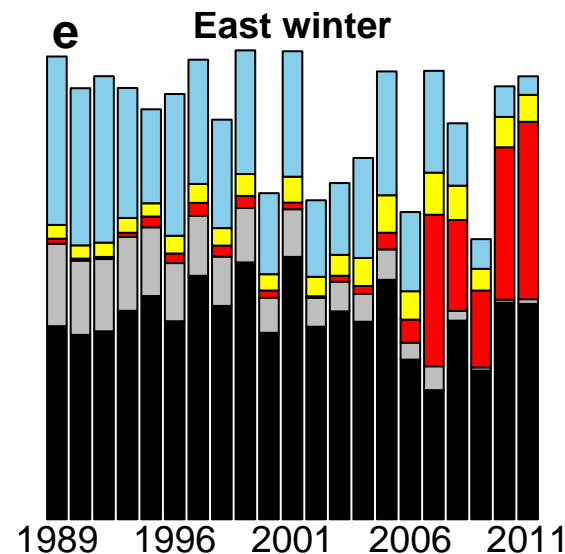
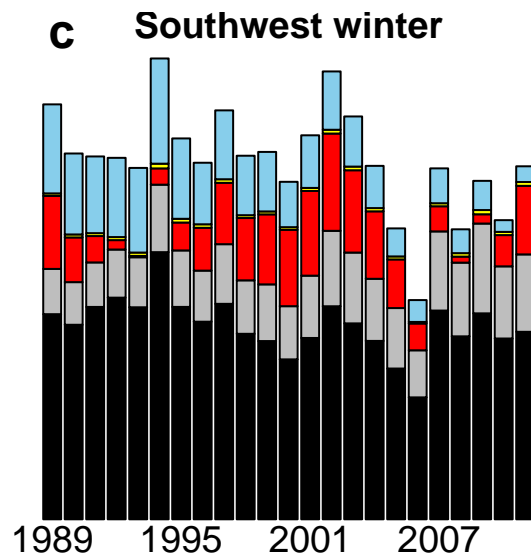
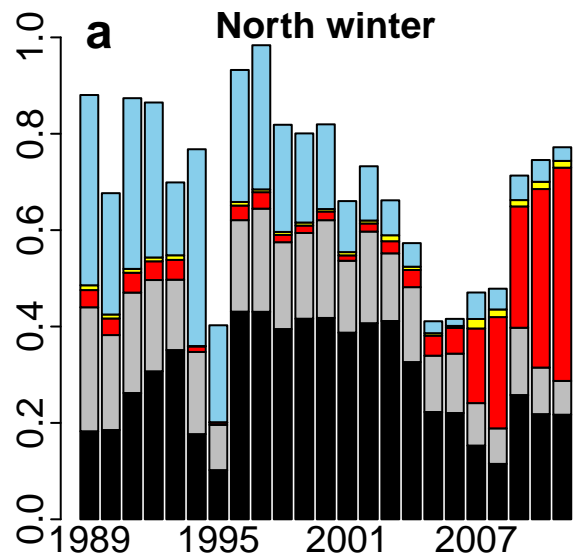
627 Figure 4. Results of simulations. Parameter estimates from Models 1-3 were used to
628 simulate vole (shown in figure) and predator (not shown) population dynamics under
629 different predation scenarios. The Full model scenario refers to a simulation with all

630 parameters included in the model, as thus represents the model prediction for current
631 population dynamics. In the different predation scenarios, the densities of the different
632 predator groups were set to the minimum observed value. Panels a-c show the simulated
633 vole time series in density dependence space. Multiannual cycles exist under the parabola
634 with cycle length increasing from left to right, and irregular dynamics above the parabola.
635 Panels d-f show the s-indices (averages \pm sd) and panels g-i show the seasonality in vole
636 population growth rates, calculated as the difference between average summer and
637 average winter population growth rates.

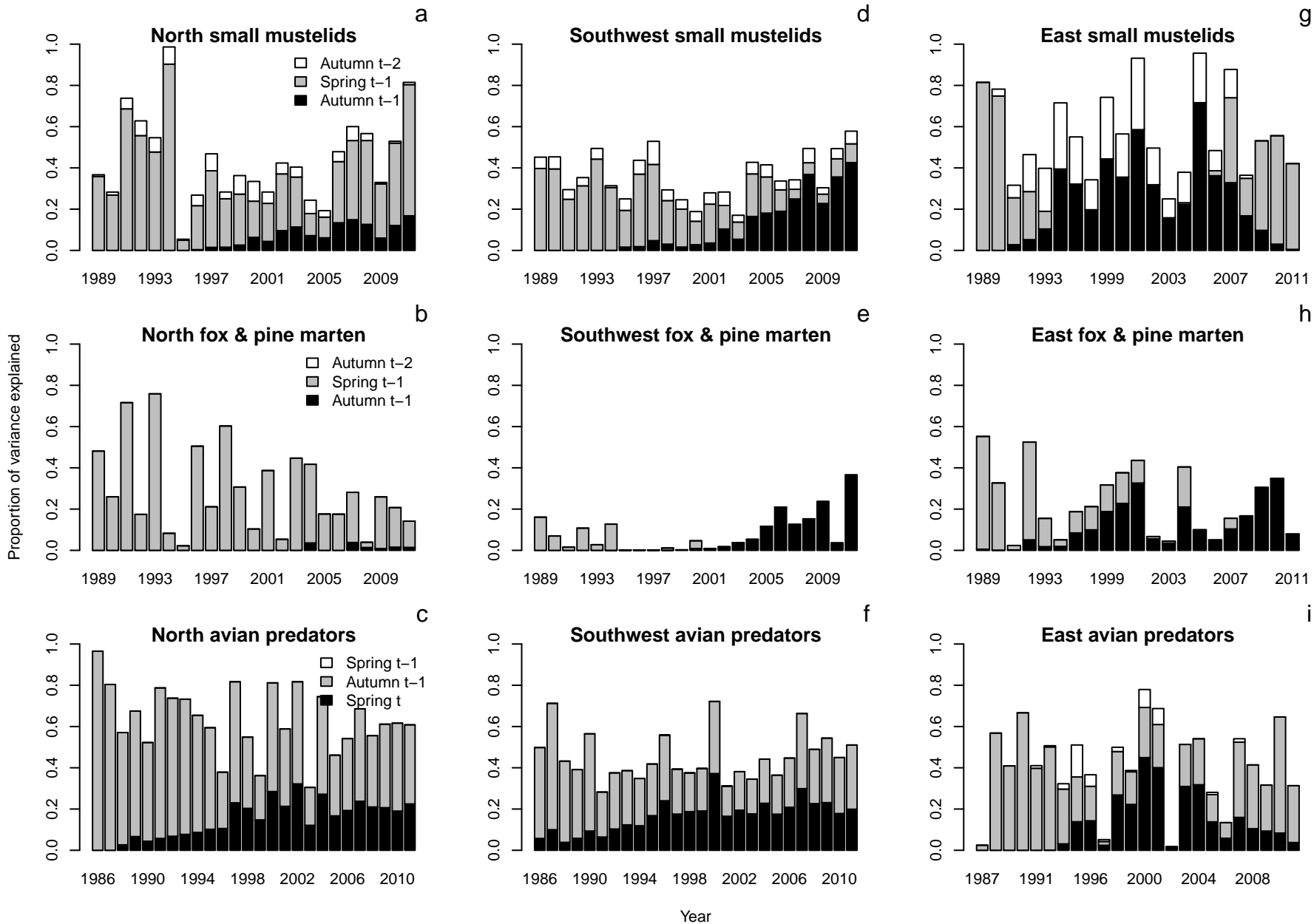
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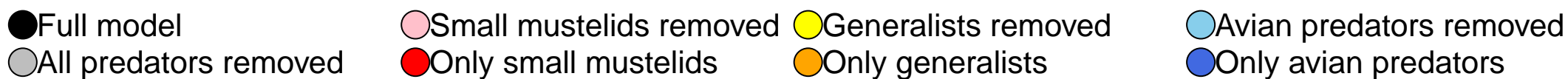
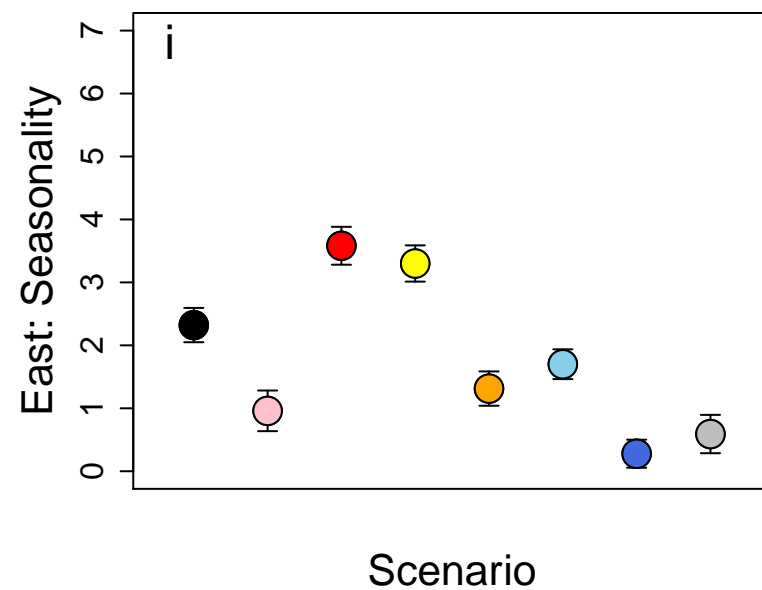
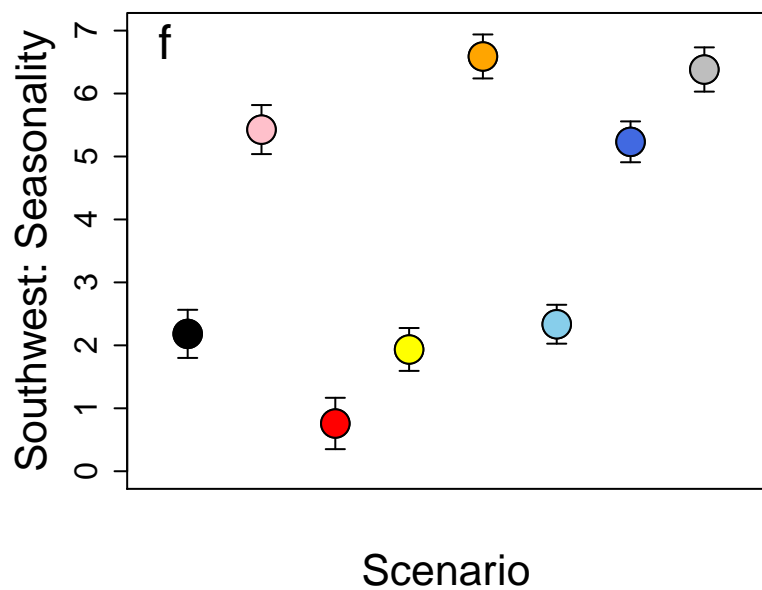
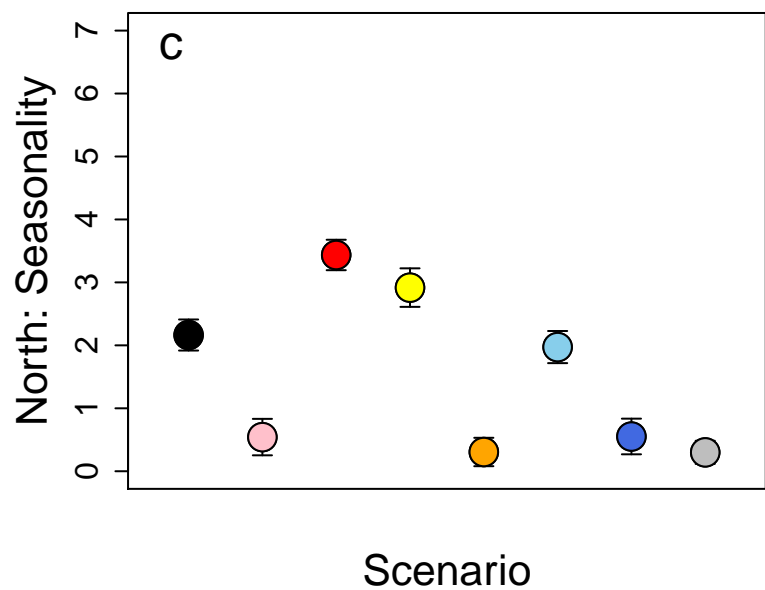
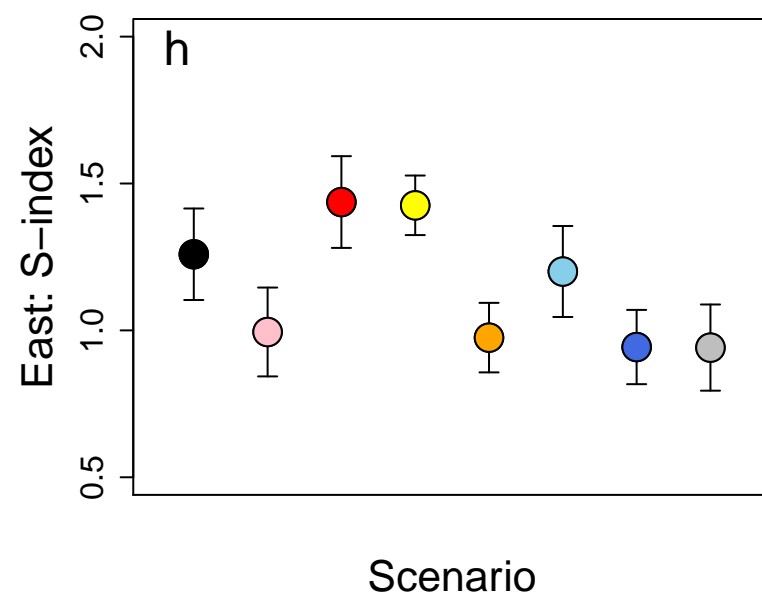
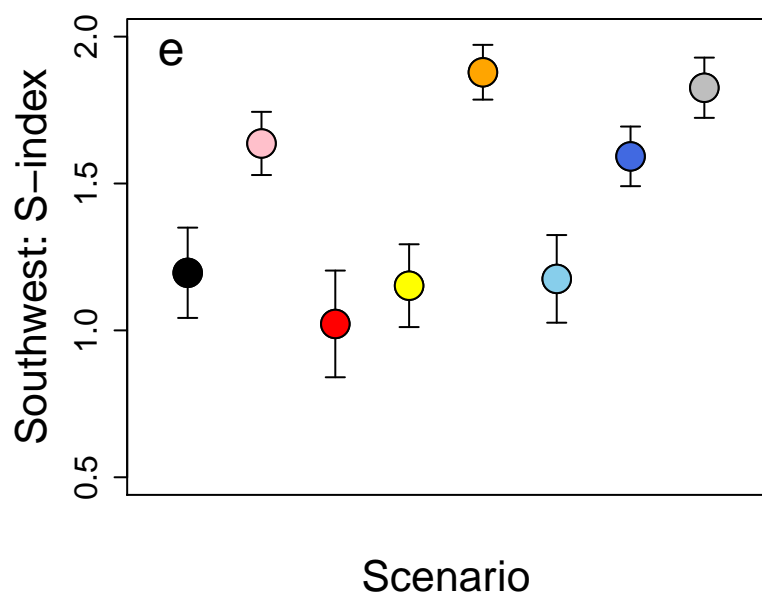
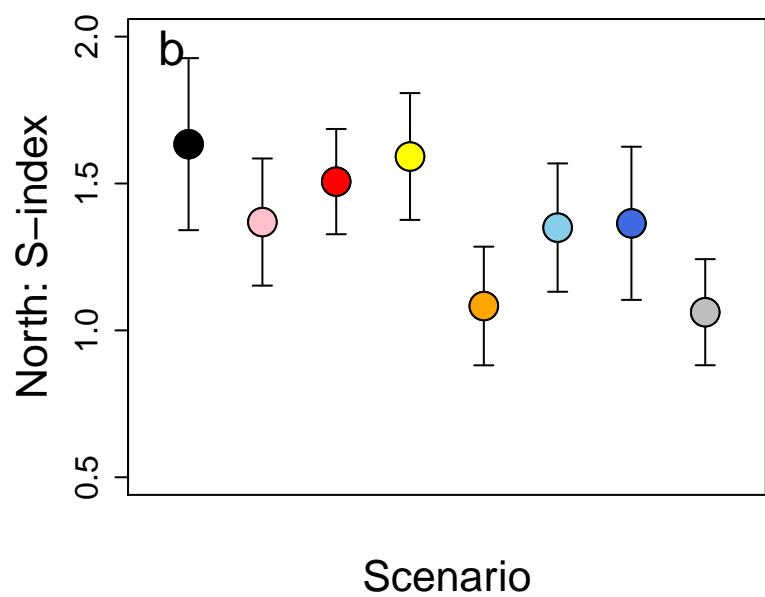
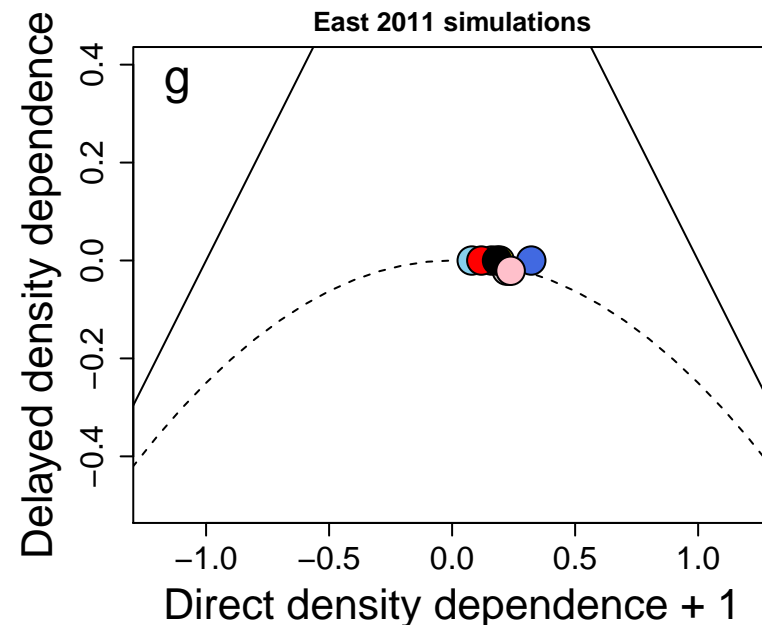
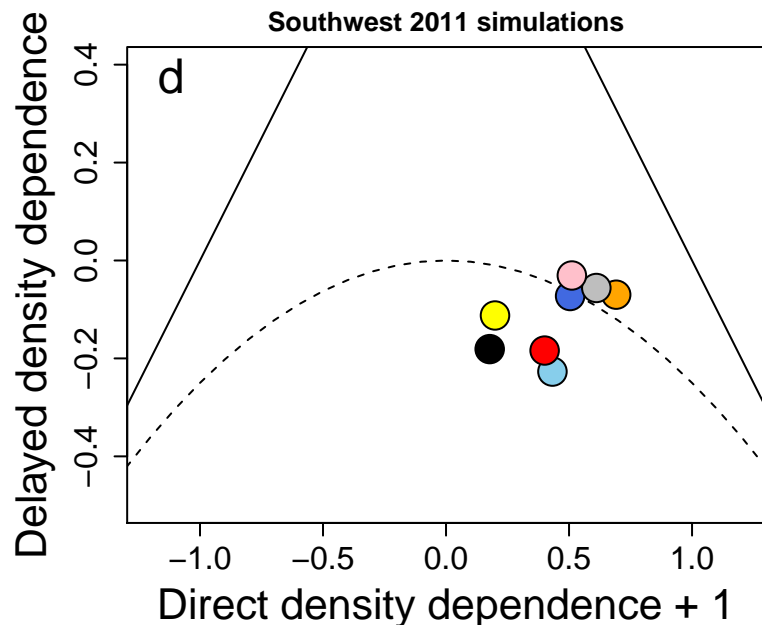
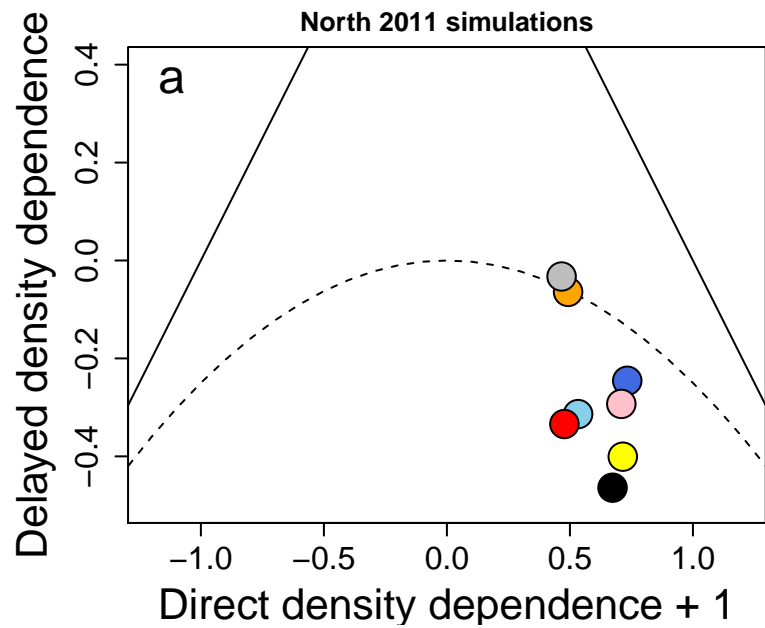


Proportion of variance explained



Year





Appendices

Supplementary Figure Legends

Supplementary Figure S1. Average densities of vole (spring and autumn) and predator (one annual density) populations in northern (above the 66th latitude), south-western (<64th latitude and < 25th longitude), and eastern Finland (> 27th longitude).

Supplementary Figure S2. Model-predicted vs. observed values. The data were randomly divided (50 times) into a training set (50%), to which the models were fitted and which was used to predict the values in the remaining 50%. (a) Winter population growth rates of voles. (b) Summer population growth rates of voles. (c) Small mustelid index. (d) Generalist predator index. (e) Avian predator index.

Supplementary Figure S3. Sections of simulated time series and the autocorrelation plots calculated based on the simulated time series. The simulations were based on parameter values from Models 1-3 for northern Finland.

Supplementary Figure S4. Sections of simulated time series and the autocorrelation plots calculated based on the simulated time series. The simulations were based on parameter values from Models 1-3 for southwestern Finland.

Supplementary Figure S5. Sections of simulated time series and the autocorrelation plots calculated based on the simulated time series. The simulations were based on parameter values from Models 1-3 for eastern Finland.

Supplementary Figure S6. Relative abundances of species within the small mustelid (top row) and the generalist predator (bottom row) groups in the different regions (black lines), and autumn vole densities (red lines).

Supplementary Tables

Supplementary Table 1. Best model (in AIC-based model selection) for the winter population growth rate of voles (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. A = autumn vole density; P_1 = small mustelid density (winter); P_2 = generalist mammalian predator density (winter); P_3 = avian predator density (summer).

Parameter	Estimate	Std. Error	t-value	p-value
Intercept	-0.51	0.12	-4.30	<0.0001
A_{t-1}	-0.78	0.09	-8.28	<0.0001
A_{t-2}	-0.33	0.05	-6.10	<0.0001
$P_{1,t}$	-0.09	0.07	-1.15	0.25
$P_{2,t}$	0.08	0.08	1.10	0.27
$P_{3,t-1}$	-0.86	0.24	-3.62	<0.001
Year	-0.36	0.20	-1.84	0.07
Year ²	-0.15	0.27	-0.57	0.57
Latitude	-0.46	0.20	-2.33	0.02
Longitude	0.28	0.26	1.05	0.29
Year: A_{t-1}	0.42	0.13	3.25	<0.01
Year ² : A_{t-1}	0.44	0.28	1.59	0.11
Year: A_{t-2}	0.18	0.10	1.87	0.06
Year: $P_{1,t}$	-0.31	0.12	-2.61	0.01
Year ² : $P_{1,t}$	0.01	0.21	0.04	0.97
Year: $P_{3,t}$	0.85	0.48	1.78	0.08
Latitude: A_{t-1}	-0.02	0.14	-0.14	0.89
Latitude: $P_{1,t}$	0.21	0.13	1.63	0.10
Latitude: $P_{3,t-1}$	0.44	0.31	1.43	0.15
Year:Latitude	0.30	0.31	0.95	0.34
Year ² :Latitude	-0.66	0.45	-1.47	0.14
Longitude: A_{t-1}	-0.47	0.25	-1.88	0.06
Longitude: A_{t-2}	0.00	0.09	-0.05	0.96
Longitude: $P_{1,t}$	0.24	0.15	1.65	0.10
Longitude: $P_{2,t}$	0.19	0.11	1.63	0.10
Longitude: $P_{3,t-1}$	-0.13	0.45	-0.30	0.77
Year:Longitude	-0.72	0.40	-1.81	0.07
Year ² :Longitude	-0.94	0.68	-1.39	0.16
Latitude:Longitude	0.72	0.49	1.48	0.14
A_{t-1} :Year:Latitude	0.12	0.19	0.62	0.54
A_{t-1} :Year ² :Latitude	0.97	0.42	2.29	0.02
$P_{1,t}$:Year:Latitude	-0.28	0.19	-1.50	0.13
$P_{1,t}$:Year ² :Latitude	-0.77	0.36	-2.14	0.03
$P_{3,t-1}$:Year:Latitude	-0.35	0.58	-0.61	0.54
A_{t-1} :Year:Longitude	0.67	0.34	1.96	0.05
A_{t-1} :Year ² :Longitude	1.11	0.75	1.49	0.14
A_{t-2} :Year:Longitude	0.30	0.17	1.76	0.08
$P_{1,t}$:Year:Longitude	-0.42	0.26	-1.60	0.11
$P_{1,t}$:Year ² :Longitude	-1.14	0.33	-3.42	<0.001
$P_{3,t-1}$:Year:Longitude	-0.67	0.90	-0.74	0.46
A_{t-1} :Longitude:Latitude	-0.62	0.46	-1.35	0.18
$P_{1,t}$:Latitude:Longitude	-0.18	0.23	-0.77	0.44
$P_{3,t-1}$:Latitude:Longitude	0.85	0.66	1.29	0.20
Year:Latitude:Longitude	-0.76	0.67	-1.14	0.25
Year ² :Latitude:Longitude	-1.67	1.28	-1.31	0.19
A_{t-1} :Year:Latitude:Longitude	0.85	0.63	1.34	0.18
A_{t-1} :Year ² :Latitude:Longitude	2.08	1.38	1.51	0.13
$P_{1,t}$:Year:Latitude:Longitude	-0.66	0.44	-1.49	0.14
$P_{3,t-1}$:Year:Latitude:Longitude	-2.40	1.28	-1.87	0.06

Supplementary Table 2. Best model (in AIC-based model selection) for the summer population growth rate of voles (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. S_t = spring vole density; P_1 = small mustelid density (winter); P_2 = generalist mammalian predator density (winter); P_3 = avian predator density (summer).

Parameter	Estimate	Std. error	t-value	p-value
Intercept	0.58	0.11	5.36	<0.0001
S_t	-0.47	0.08	-5.92	<0.0001
S_{t-1}	-0.26	0.04	-6.59	<0.0001
$P_{1,t}$	-0.08	0.05	-1.82	0.07
$P_{2,t}$	-0.23	0.10	-2.18	0.03
$P_{3,t}$	0.01	0.30	0.02	0.99
Year	-0.10	0.19	-0.54	0.59
Year ²	0.02	0.31	0.06	0.95
Latitude	0.33	0.21	1.63	0.10
Longitude	0.20	0.22	0.93	0.35
Year: S_t	-0.02	0.08	-0.24	0.81
Year ² : S_t	-0.02	0.22	-0.09	0.93
Year: $P_{1,t}$	-0.13	0.08	-1.74	0.08
Year: $P_{2,t}$	-0.20	0.12	-1.67	0.10
Year ² : $P_{2,t}$	0.35	0.24	1.46	0.14
Year: $P_{3,t}$	0.18	0.51	0.36	0.72
Year ² : $P_{3,t}$	0.18	0.90	0.20	0.85
Latitude: S_t	0.48	0.14	3.50	<0.001
Latitude: $P_{1,t}$	0.24	0.08	3.00	<0.005
Latitude: $P_{2,t}$	-0.36	0.13	-2.80	0.01
Latitude: $P_{3,t}$	-0.46	0.40	-1.16	0.25
Year:Latitude	0.04	0.32	0.11	0.91
Year ² :Latitude	-0.48	0.54	-0.90	0.37
Longitude: S_t	0.53	0.20	2.59	0.01
Longitude: S_{t-1}	0.13	0.07	1.90	0.06
Longitude: $P_{1,t}$	0.30	0.10	2.95	<0.01
Longitude: $P_{2,t}$	-0.61	0.17	-3.54	<0.001
Longitude: $P_{3,t}$	0.90	0.59	1.53	0.13
Year:Longitude	-0.46	0.31	-1.46	0.15
Year ² :Longitude	0.38	0.56	0.67	0.50
Latitude:Longitude	0.63	0.42	1.50	0.14
S_t : Year ² :Latitude	-0.86	0.37	-2.35	0.02
$P_{3,t}$:Year:Latitude	-0.55	0.62	-0.89	0.37
$P_{3,t}$:Year ² :Latitude	2.99	1.15	2.60	0.01
S_{t-1} : Year:Longitude	-0.28	0.14	-1.95	0.05
S_{t-1} : Year ² :Longitude	-1.12	0.51	-2.21	0.03
$P_{1,t}$: Year:Longitude	0.57	0.12	4.61	<0.0001
$P_{3,t}$:Year:Longitude	-0.66	0.86	-0.77	0.44
$P_{3,t}$:Year ² :Longitude	1.47	1.61	0.91	0.36
S_t :Latitude:Longitude	1.28	0.39	3.27	<0.01
$P_{1,t}$: Latitude:Longitude	0.34	0.19	1.83	0.07
$P_{2,t}$: Latitude:Longitude	-1.18	0.30	-3.98	<0.0001
$P_{3,t}$: Latitude:Longitude	0.47	0.87	0.54	0.59
Year:Latitude:Longitude	-0.62	0.55	-1.14	0.26
Year ² :Latitude:Longitude	-0.19	1.03	-0.19	0.85
S_t :Year ² :Latitude:Longitude	-2.76	0.90	-3.06	<0.01
$P_{3,t}$: Year:Latitude:Longitude	-1.62	1.17	-1.38	0.17
$P_{3,t}$:Year ² :Latitude:Longitude	3.90	2.48	1.58	0.12

Supplementary Table 3. Best model (in AIC-based model selection) for the winter density index of the small mustelids (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. A = autumn vole density; S = spring vole density.

Parameter	Estimate	Std. error	t-value	p-value
Intercept	0.01	0.11	0.08	0.94
A_{t-1}	0.19	0.10	1.88	0.06
S_{t-1}	0.10	0.10	1.07	0.28
A_{t-2}	0.22	0.08	2.82	<0.01
Year	-0.59	0.10	-5.76	<0.0001
Year ²	0.50	0.28	1.76	0.08
Latitude	0.50	0.12	4.34	<0.0001
Longitude	-0.59	0.20	-2.90	<0.01
Year ² :Longitude	1.61	0.45	3.56	<0.001
Latitude:Longitude	0.24	0.24	1.02	0.31
A_{t-1} :Year	0.35	0.10	3.38	<0.001
A_{t-1} :Year ²	-0.43	0.24	-1.74	0.08
A_{t-1} :Latitude	-0.13	0.10	-1.23	0.22
A_{t-1} :Longitude	0.31	0.19	1.63	0.10
S_{t-1} :Year	-0.17	0.10	-1.72	0.09
S_{t-1} :Year ²	0.58	0.24	2.39	0.02
S_{t-1} :Latitude	0.22	0.10	2.22	0.03
S_{t-1} :Longitude	-0.32	0.15	-2.19	0.03
A_{t-2} :Year ²	-0.31	0.20	-1.54	0.12
A_{t-2} :Longitude	0.30	0.13	2.24	0.03
A_{t-1} :Year ² :Longitude	-0.97	0.35	-2.74	0.01
A_{t-1} :Latitude:Longitude	-0.42	0.25	-1.67	0.10
S_{t-1} :Year ² :Longitude	0.95	0.34	2.78	0.01
A_{t-2} :Year ² :Longitude	-0.66	0.35	-1.89	0.06

Supplementary Table 4. Best model (in AIC-based model selection) for the winter density index of the generalist mammalian predators (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. A = autumn vole density; S = spring vole density.

Parameter	Estimate	Std. error	t-value	p-value
Intercept	0.06	0.09	0.64	0.52
A_{t-1}	-0.05	0.05	-0.90	0.37
S_{t-1}	0.09	0.04	2.09	0.04
Year	-0.31	0.12	-2.50	0.01
Year ²	-0.30	0.24	-1.25	0.21
Latitude	-0.22	0.14	-1.59	0.11
Longitude	0.26	0.18	1.41	0.16
Year ² :Latitude	0.28	0.33	0.87	0.38
Year ² :Longitude	-1.28	0.47	-2.74	0.01
Latitude:Longitude	1.00	0.29	3.48	<0.001
A_{t-1} :Year	0.17	0.06	2.78	0.01
A_{t-1} :Latitude	-0.14	0.07	-1.90	0.06
A_{t-1} :Longitude	0.12	0.05	2.29	0.02
S_{t-1} :Year	-0.12	0.05	-2.24	0.03
S_{t-1} :Latitude	0.16	0.07	2.23	0.03
S_{t-1} :Longitude	0.03	0.08	0.36	0.72
Year ² :Latitude:Longitude	-1.41	0.76	-1.86	0.06
S_{t-1} :Latitude:Longitude	-0.03	0.15	-0.22	0.82

Supplementary Table 5. Best model (in AIC-based model selection) for the summer density index of the avian predators (year t). Latitude, longitude, and year were scaled to vary between -1 and 1. A = autumn vole density; S = spring vole density.

Parameter	Estimate	Std. error	t-value	p-value
Intercept	-0.18	0.03	-6.36	<0.0001
S_t	0.05	0.02	2.54	0.01
A_{t-1}	0.06	0.03	2.31	0.02
S_{t-1}	-0.02	0.02	-0.90	0.37
Year	0.00	0.02	0.21	0.84
Year ²	-0.02	0.07	-0.28	0.78
Latitude	-0.49	0.05	-10.73	0.00
Longitude	0.01	0.07	0.07	0.94
Year ² :Latitude	0.24	0.11	2.11	0.04
Year ² :Longitude	0.13	0.16	0.83	0.41
Latitude:Longitude	0.38	0.13	2.95	<0.0001
S_i :Year	0.04	0.02	2.31	0.02
S_i :Year ²	-0.01	0.05	-0.29	0.77
S_i :Latitude	-0.03	0.03	-0.86	0.39
S_i :Longitude	-0.02	0.05	-0.38	0.71
A_{t-1} :Year ²	0.11	0.07	1.66	0.10
A_{t-1} :Latitude	0.01	0.04	0.20	0.84
A_{t-1} :Longitude	-0.01	0.07	-0.18	0.85
S_{t-1} :Year ²	-0.08	0.05	-1.53	0.13
S_{t-1} :Latitude	-0.04	0.04	-0.88	0.38
S_{t-1} :Longitude	-0.02	0.06	-0.27	0.79
Year ² :Latitude:Longitude	0.18	0.29	0.61	0.54
S_i :Year ² :Latitude	0.07	0.08	0.84	0.40
S_i :Year ² :Longitude	0.04	0.12	0.31	0.75
S_i :Latitude:Longitude	-0.01	0.10	-0.11	0.91
A_{t-1} :Year ² :Latitude	-0.02	0.11	-0.20	0.84
A_{t-1} :Year ² :Longitude	-0.14	0.15	-0.93	0.35
A_{t-1} :Latitude:Longitude	0.05	0.12	0.45	0.65
S_{t-1} :Year ² :Latitude	0.02	0.10	0.18	0.86
S_{t-1} :Year ² :Longitude	0.12	0.12	1.01	0.31
S_{t-1} :Latitude:Longitude	-0.13	0.11	-1.16	0.25
S_i :Year ² :Latitude:Longitude	0.23	0.22	1.03	0.30
A_{t-1} :Year ² :Latitude:Longitude	-0.27	0.26	-1.05	0.30
S_{t-1} :Year ² :Latitude:Longitude	0.27	0.22	1.20	0.23

North

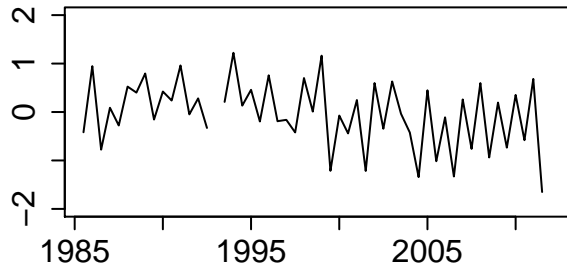
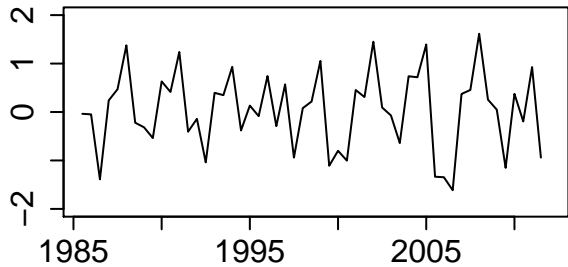
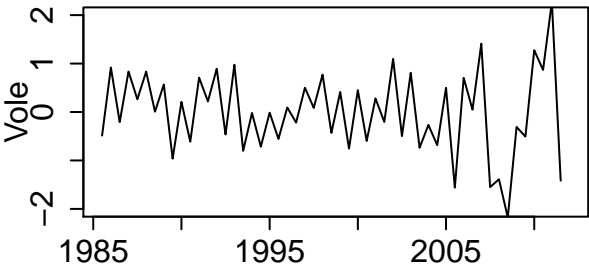
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East

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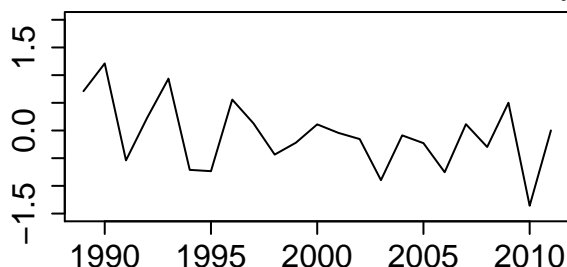
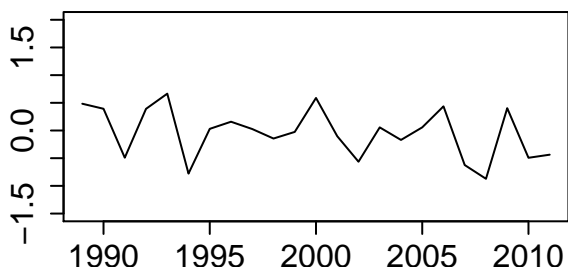
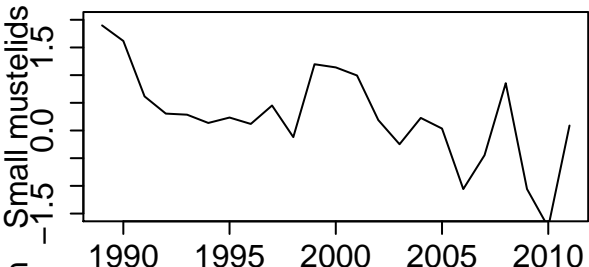
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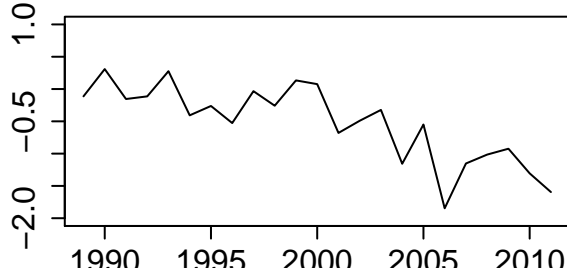
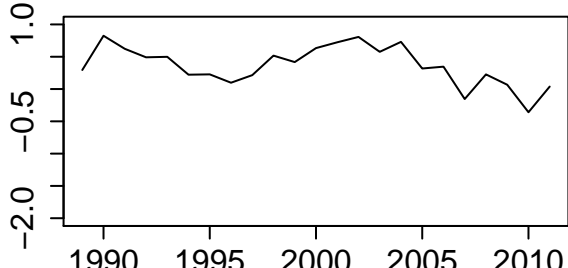
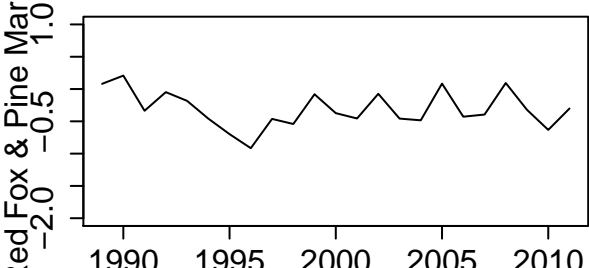
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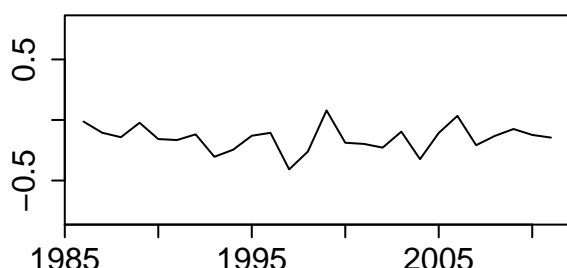
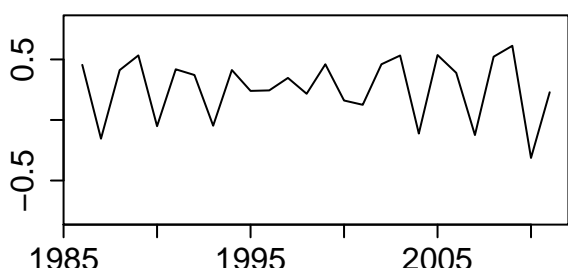
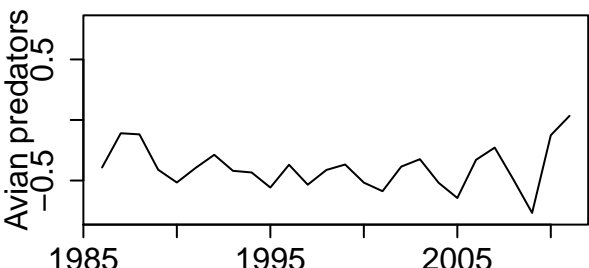
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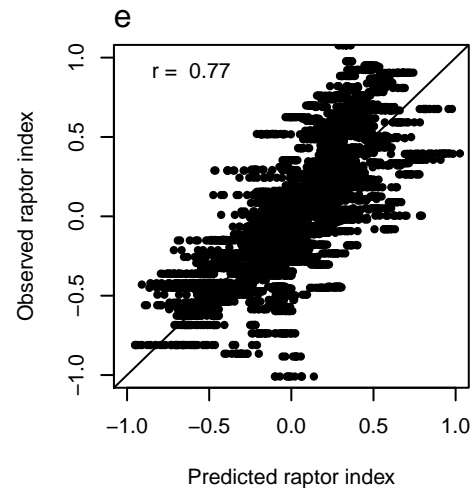
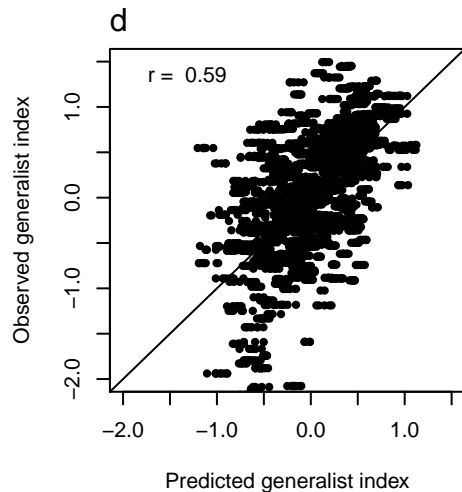
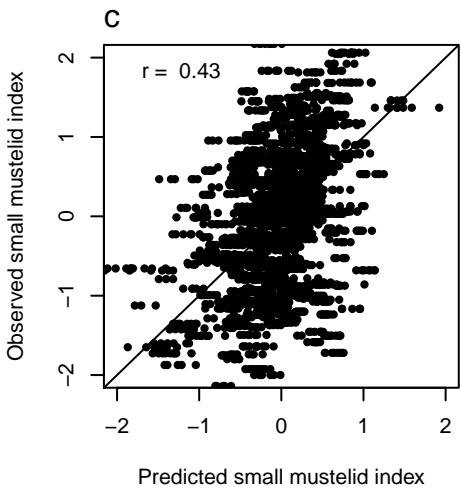
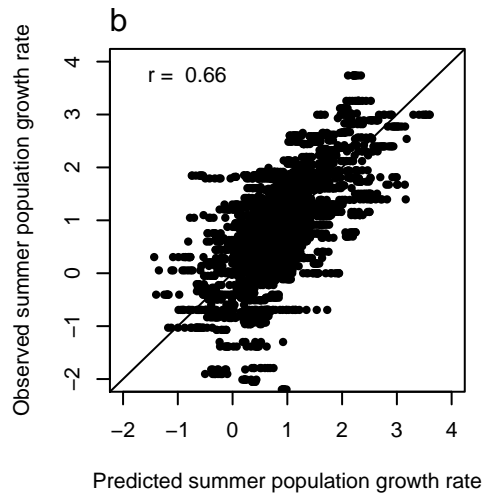
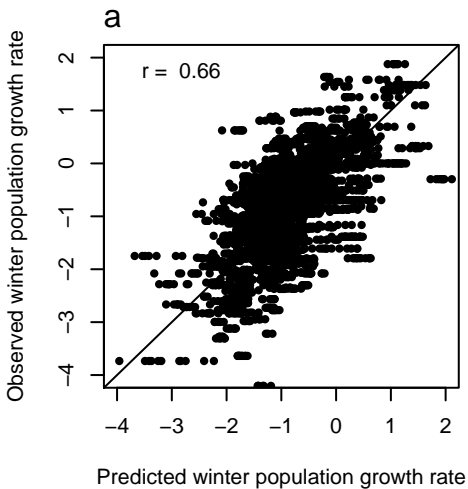


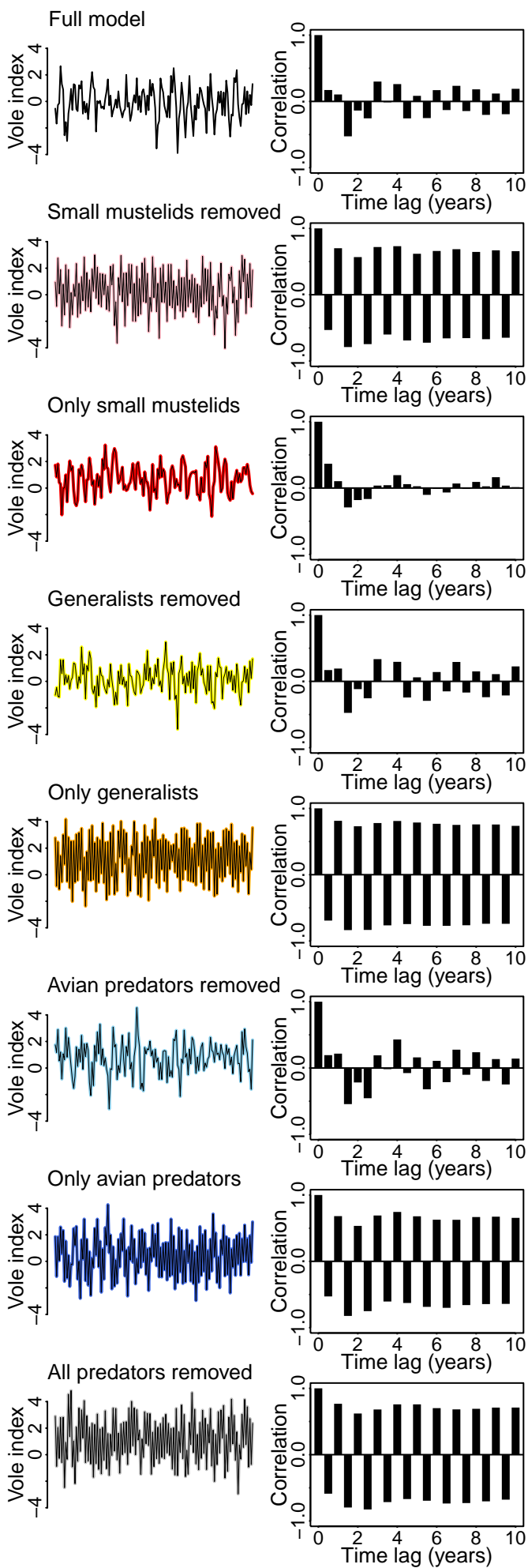
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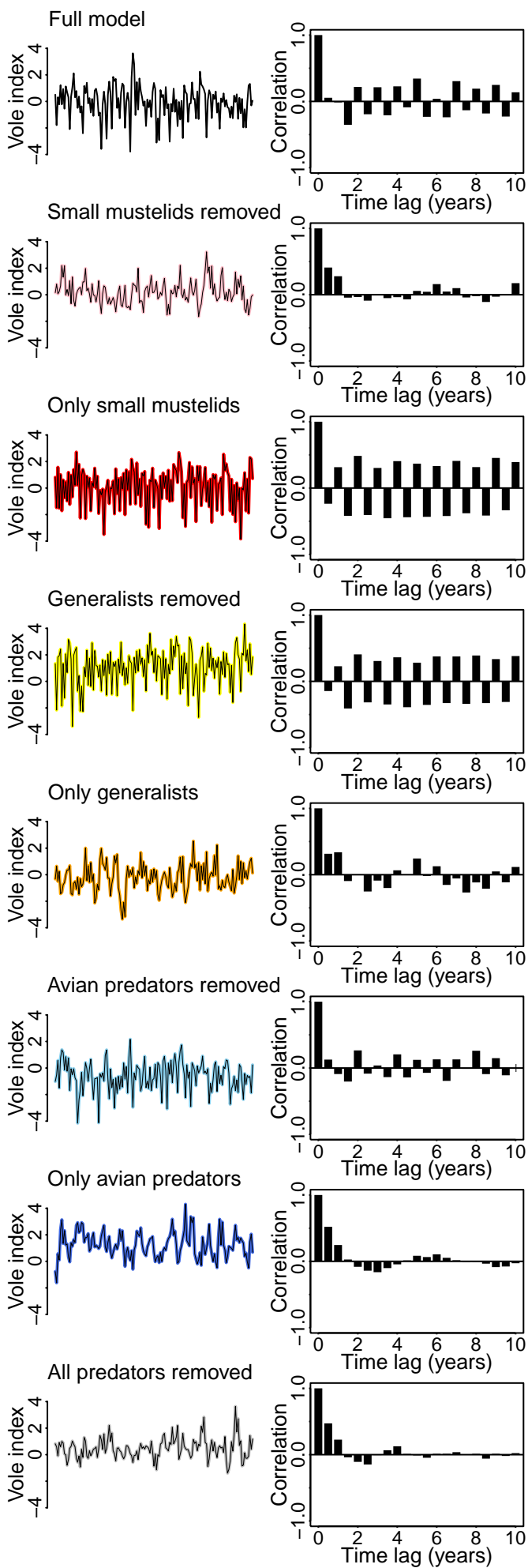
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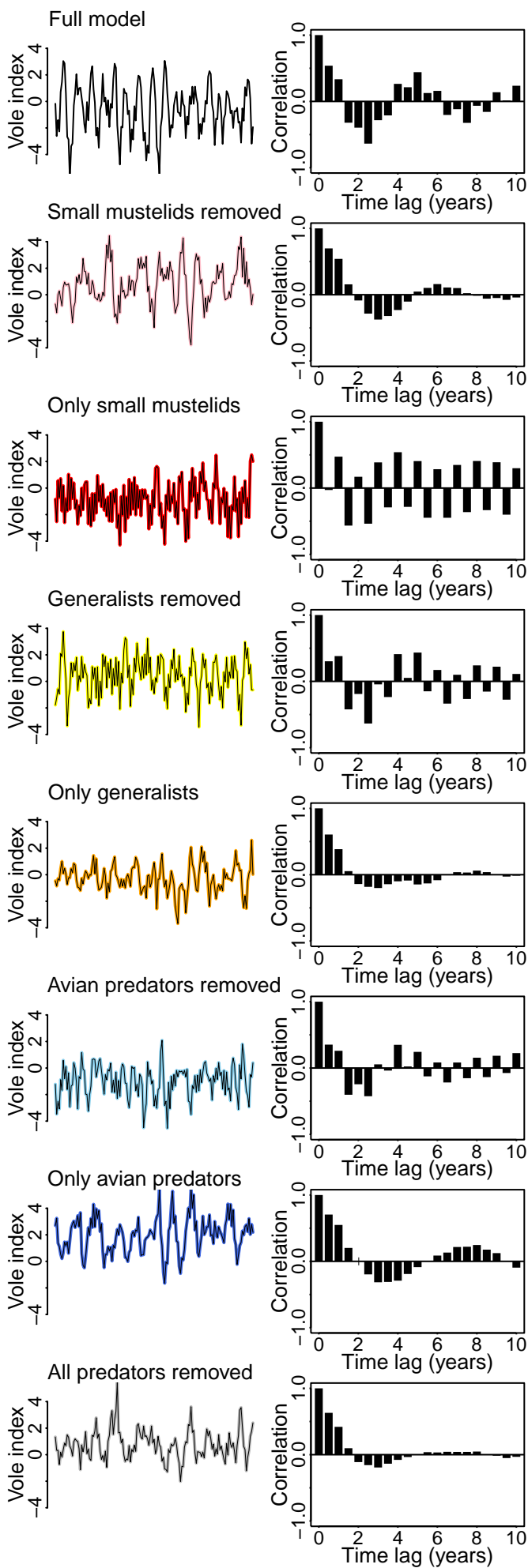




Supplemental figure S3



Supplemental figure S4



Supplemental figure S5

