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Title: Predator–vole interactions in northern Europe: the role of small mustelids revised

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

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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.

40

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

42   density dependence

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1. Introduction

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

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

Practically all terrestrial carnivores in northern Europe consume voles at least occasionally, and the following predators show a clear preference for voles: the small mustelids (9), the red fox (10), the pine marten (11) and several owl and raptor species (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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114 **Methods**

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116 <u>Vole population data</u>

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

6

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   <u>Mammalian predator data</u>

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 distance^2). The mammalian predator data were globally standardized to

175   mean = 0 to render the values of the different predator groups comparable.

176

177   <u>Avian predator data</u>

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

species, which prey on voles and which are relatively abundant in our study area: the

nomadic or migratory species *Asio flammeus, Asio otus, Aegolius funereus, Glaucidium*

passerinum, Falco tinnunculus, *Circus cyaneus*, and *Buteo lagopus;* and the resident

species *Strix uralensis, Strix aluco, Bubo bubo,* and *Buteo buteo*. Although it is known

that these species react slightly differently to vole abundances and differ in their

specialization in voles, their densities showed strong correlations (r > 0.8), which

justified the calculation of a total avian predator density index as $\log[\frac{n_{i,t}c_{i,t}+2n_{i,t}}{s_{i,t}}]$, where

$n_{i,t}$ refers to the number of nesting pairs in area i and year t, $c_{i,t}$ to the average number of

chicks per nest in area i and year t, and $s_{i,t}$ to the number of territories surveyed in area i

and year t. The avian predator density index was calculated for each vole-trapping site by

averaging over all raptor-monitoring areas within a 50 km distance. Prior to combining

the avian time series, they were de-trended, as some showed potentially artificial

increasing trends due to increased nest-box availability. The avian predator density was

calculated for each vole-trapping site by averaging over all raptor-monitoring areas

within a 50 km distance.

Influence of predators on vole population growth rates

To estimate the spatial and temporal variation in the impact of the different predator

groups on vole populations, we modelled vole population growth rates during winter

(Model 1) and summer (Model 2) as a function of vole and predator indices. Mammalian

predator indices were measured in winter, and avian predator indices in summer. We

assumed the linear models

206     $Y_{1,t} = S_t - A_{t-1} = a_1 + b_1 A_{t-1} + c_1 A_{t-2} + d_1 P_{1,t} + e_1 P_{2,t} + f_1 P_{3,t-1} + \varepsilon_{1,t}$ (Model 1)

207     $Y_{2,t} = A_t - S_t \;\;= a_2 + b_2 S_t + c_2 S_{t-1} + d_2 P_{1,t} + e_2 P_{2,t} + f_2 P_{3,t} + \varepsilon_{2,t}$ (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 + year^2) 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

$$\mathrm{Var}(Y_{1,t}) = b^2\mathrm{Var}(A_{t-1}) + c^2\mathrm{Var}(A_{t-2}) + d^2\mathrm{Var}(P_1) + e^2\mathrm{Var}(P_2) + f^2\mathrm{Var}(P_3)$$

$$+ 2bc\,\mathrm{Cov}(A_{t-1}, A_{t-2}) + 2bd\,\mathrm{Cov}(A_{t-1}, P_1) + 2be\,\mathrm{Cov}(A_{t-1}, P_2)$$

$$+ 2bf\,\mathrm{Cov}(A_{t-1}, P_3) + 2cd\,\mathrm{Cov}(A_{t-2}, P_1) + 2ce\,\mathrm{Cov}(A_{t-2}, P_2)$$

$$+ 2cf\,\mathrm{Cov}(A_{t-2}, P_3) + 2de\,\mathrm{Cov}(P_1, P_2) + 2df\,\mathrm{Cov}(P_1, P_3)$$

$$+ 2ef\,\mathrm{Cov}(P_2, P_3) + \sigma^2,$$

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

$$\mathrm{Var}_{P1} = (d^2\mathrm{Var}(P_1) + bd\,\mathrm{Cov}(A_{t-1}, P_1) + cd\,\mathrm{Cov}(A_{t-2}, P_1) + de\,\mathrm{Cov}(P_1, P_2)$$

$$+ df\,\mathrm{Cov}(P_1, P_3)) / \mathrm{Var}(Y_{1,t})$$

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   <u>Influence of vole population densities on predator abundance indices</u>

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    $$Y_{3,t} = a_3 + b_3 A_{t-1} + c_3 S_{t-1} + d_3 A_{t-2} + \varepsilon_{3,t}, \text{ (Model 3a: Mammalian predators)}$$

251    $$Y_{3,t} = a_3 + b_3 S_t + c_3 A_{t-1} + d_3 S_{t-1} + \varepsilon_{3,t} \text{ (Model 3b: Avian predators)}$$

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

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

259

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

261

262   <u>Roles of the different predators in the boreal vole cycle: simulation</u>

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 <u>Model validation</u>

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 <u>Spatiotemporal variation in predator-vole interactions</u>

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   <u>Is predation necessary for cyclic vole population dynamics?</u>

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   <u>Changes within the predator community</u>

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 abudance 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 km^2) 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

17

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 strenghten, 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

457   **Acknowledgements**

463

464   **Data accessibility**

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

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

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.

617

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

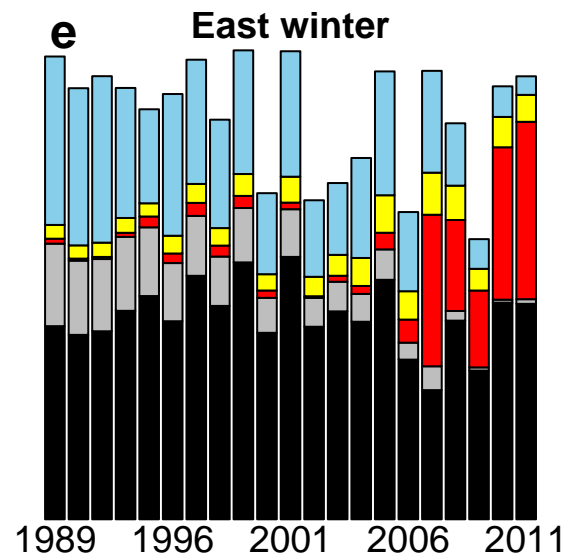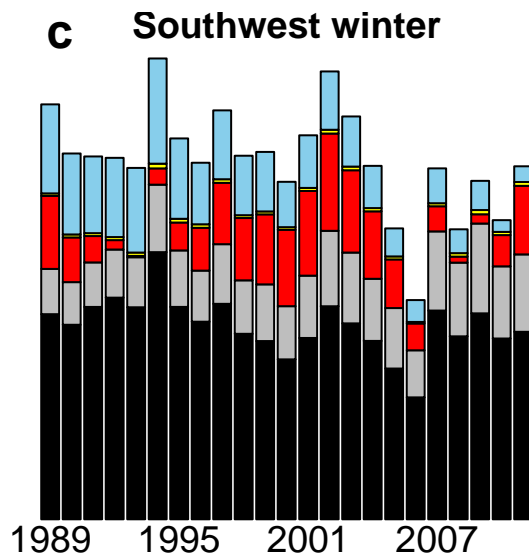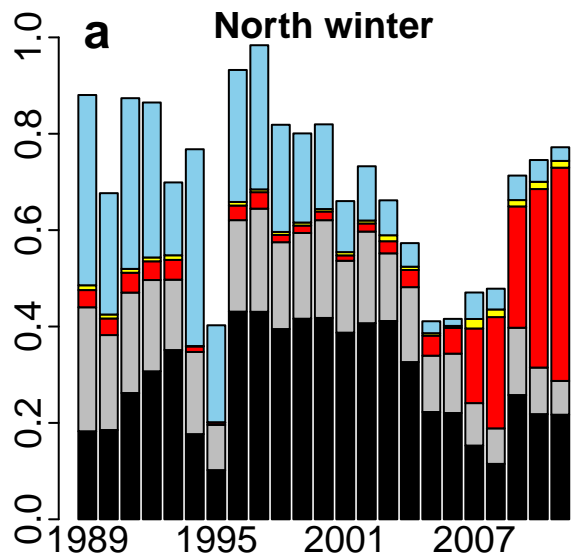625   autumn$_{t-1}$), and ca. 14 months (vole density in spring$_{t-1}$).

626

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
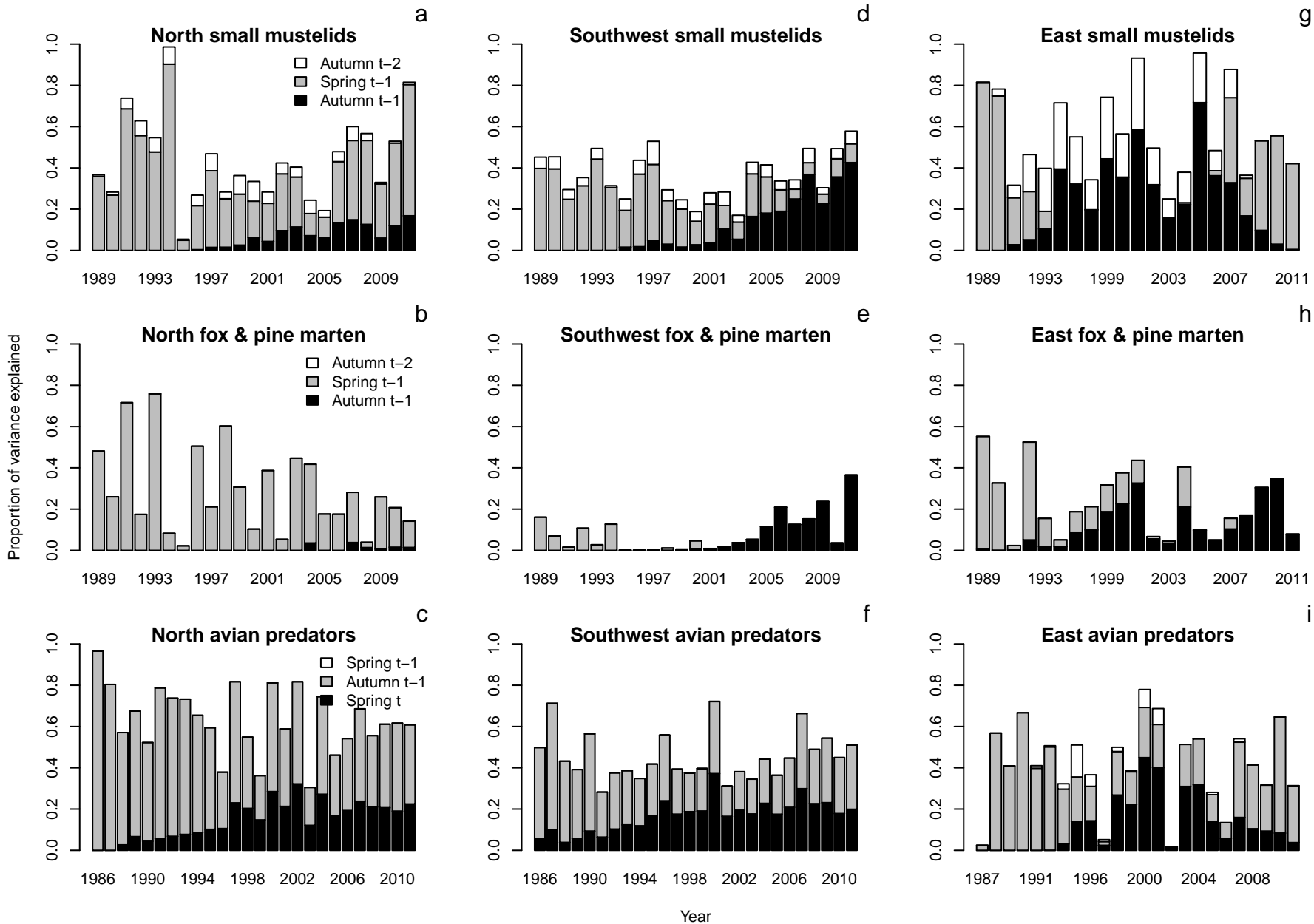
630   parameters included in the model, as thus represents the model prediction for current

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 ± sd) and panels g-i show the seasonality in vole

636   population growth rates, calculated as the difference between average summer and

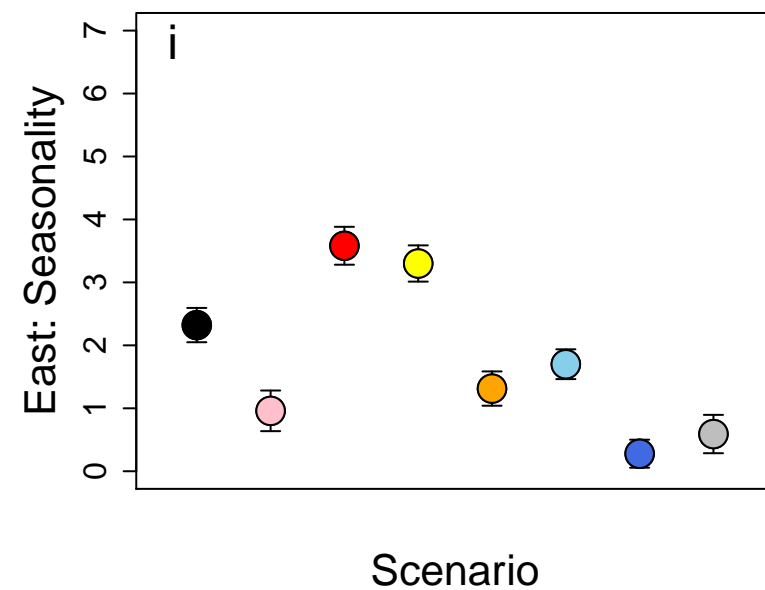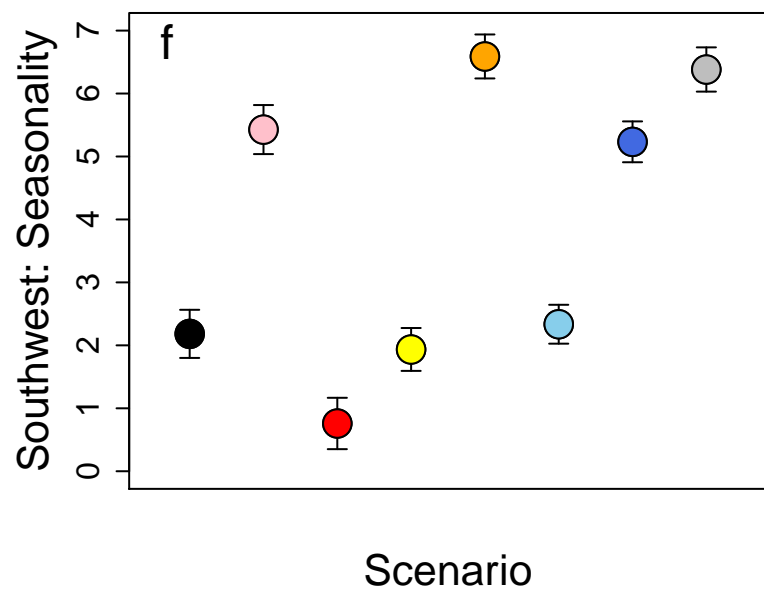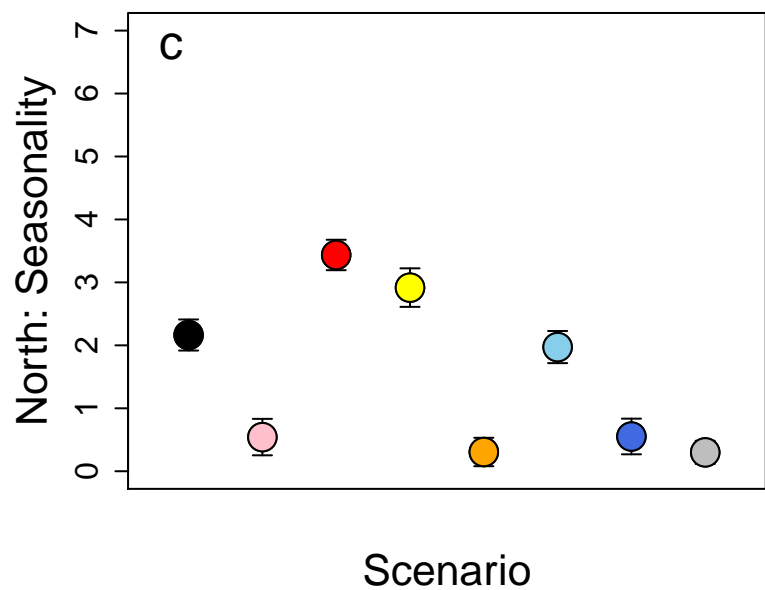637   average winter population growth rates.

638

a

N

SW

E

b

c

a North winter
b North summer
c Southwest winter
d Southwest summer
e East winter
f East summer

Proportion of variance explained

Year

- ■ Direct DD
- ■ Delayed DD
- ■ Small mustelids
- ■ Generalists
- ■ Avian predators

a North small mustelids
d Southwest small mustelids
g East small mustelids
b North fox & pine marten
e Southwest fox & pine marten
h East fox & pine marten
c North avian predators
f Southwest avian predators
i East avian predators

Autumn t−2
Spring t−1
Autumn t−1

Spring t−1
Autumn t−1
Spring t

Proportion of variance explained

Year

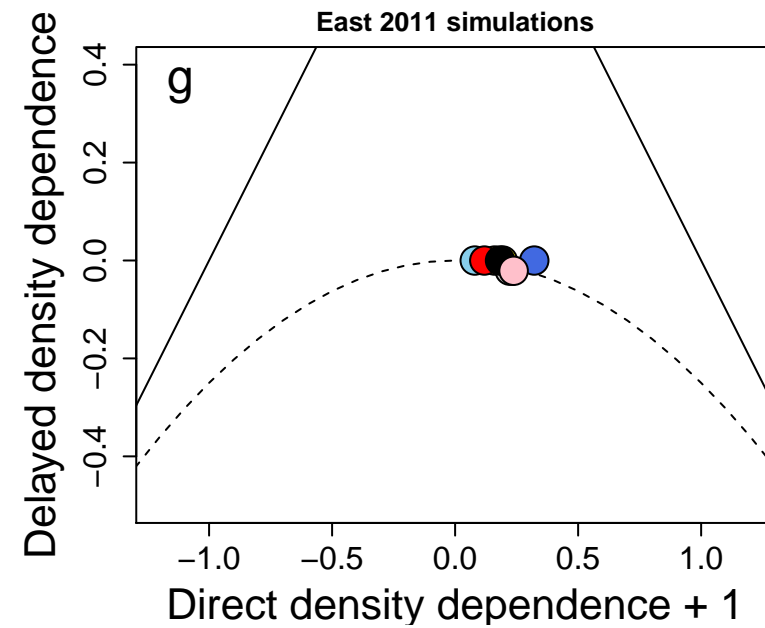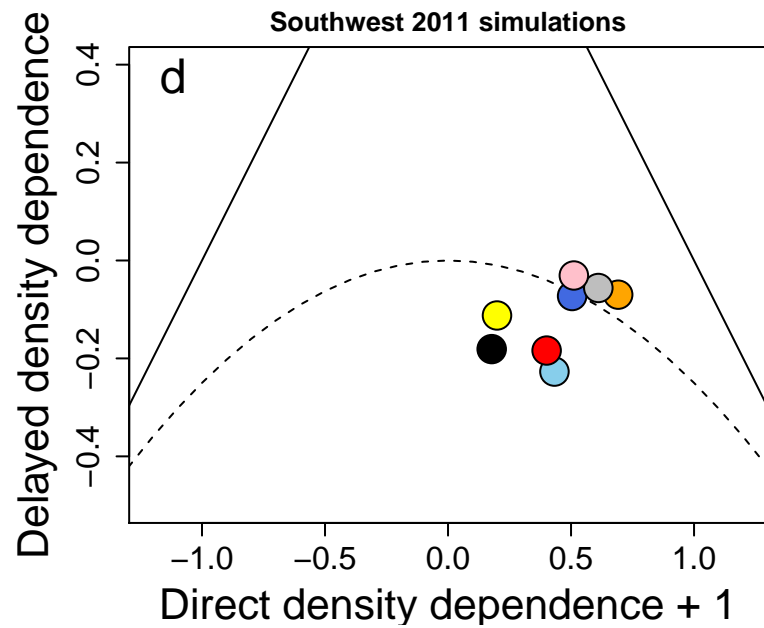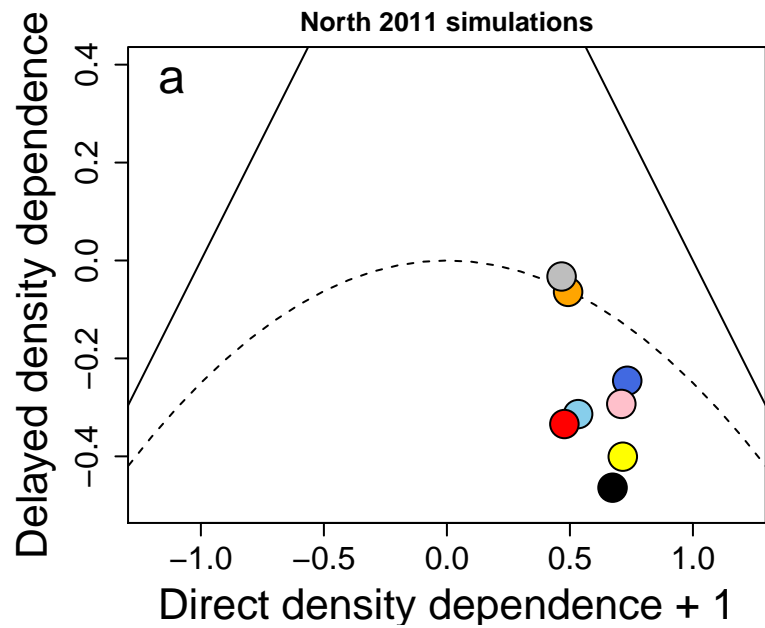|			
● Full model	● Small mustelids removed	● Generalists removed	● Avian predators removed
● All predators removed	● Only small mustelids	● Only generalists	● Only avian predators

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 growht 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 =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_t:Year	0.04	0.02	2.31	0.02
S_t:$Year^2$	-0.01	0.05	-0.29	0.77
S_t:Latitude	-0.03	0.03	-0.86	0.39
S_t: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_t:$Year^2$:Latitude	0.07	0.08	0.84	0.40
S_t:$Year^2$:Longitude	0.04	0.12	0.31	0.75
S_t: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_t:$Year^2$: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

Supplemental figure S3

Full model

Small mustelids removed

Only small mustelids

Generalists removed

Only generalists

Avian predators removed

Only avian predators

All predators removed

Supplemental figure S4

Full model

Small mustelids removed

Only small mustelids

Generalists removed

Only generalists

Avian predators removed

Only avian predators

All predators removed

Supplemental figure S5