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4   Title:

5   Temporal Dynamics of Bird Community Composition: an Analysis of Base-line Conditions

6   from Long-term Data

7

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Abstract

Numerous anthropogenic activities threaten the biodiversity on earth. Because all ecological communities constantly experience temporal turnover due to natural processes, it is important to distinguish between change due to anthropogenic impact and the underlying natural rate of change. In this study, we used data sets on breeding bird communities that covered at least 20 consecutive years, from a variety of terrestrial ecosystems, to address two main questions: (1) How fast does the composition of bird communities change over time and can we identify a baseline of natural change that distinguishes primeval systems from systems experiencing varying degree of human impact? (2) How do patterns of temporal variation in composition vary among bird communities in ecosystems with different anthropogenic impact? Time lag analysis (TLA) showed a pattern of increasing rate of temporal compositional change from large-scale primeval systems to disturbed and protected systems to distinctly successional systems. TLA slopes of <0.04 were typical for breeding bird communities with natural turnover, while communities subjected to anthropogenic impact were characterised by TLA slopes of >0.04. Most of the temporal variability of breeding bird communities was explained by slow changes occurring over decades, regardless of the intensity of human impact. In most of the time series, medium and short-wave periodicity was not detected, with the exception of breeding bird communities subjected to periodic pulses (e.g. caterpillar outbreaks causing food resource peaks).

Keywords. Community dynamics; Long-term datasets; Periodicity; Primeval forests; Time lag analysis; Time series

Introduction

We live in a rapidly changing world. Numerous anthropogenic activities such as habitat destruction, habitat fragmentation, landscape change, overharvesting, spread of invasive species, pollution, soil erosion and global climate change threaten the biodiversity on earth (Pereira et al. 2010; Sodhi and Ehrlich 2010; Dawson et al. 2011). The detection of the influence of external factors on ecological communities is hampered, however, by the limited information on their natural background rates of change (Magurran et al. 2010). Because all ecological communities constantly experience temporal turnover, we need to know their natural rate of change to be able to identify and evaluate the change that is due to anthropogenic impact. Long-term datasets (LTDS) are indispensable resources for the determination of baselines against which on-going and future community change can be evaluated. Although there exist some well known LTDS with time series of up two almost 150 years (Magurran et al. 2010), the collection of LTDS has received only limited attention. This may possibly be attributed to a general monitoring "phobia" in ecology, noted as early as the 1980s by Franklin (1989). Also, Wiens (1989) commented that long-term studies are often not encouraged by contemporary views of scientific productivity or research funding policies. In the light of environmental problems such as climate change, this attitude is changing, and there is now wider acknowledgement for the need of high-quality, question-driven, statistically-designed monitoring (Collins 2001; Legg and Nagy 2010; Lindenmayer and Likens 2010). There are now many LTDS available on traditionally well-studied communities of short-lived organisms, e.g. phytoplankton and aquatic invertebrates (Korhonen et al. 2010). However, there are few LTDS on the community level of long-lived terrestrial animals, even for well-studied groups such as birds. This is because monitoring efforts have been focussed

83   on single species or small groups of species, under the assumption that they were adequate

84   indicators of some given environmental change (Lindenmayer and Likens 2010).

85

86   Thanks to the foresight of a few pioneering ornithologists, though, there are some LTDS of

87   breeding bird communities that extend several decades, for example, the work of Kendeigh

88   (1982) that commenced as early as in 1934 (Illinois, USA, 43 years), and of Enemar (1966),

89   who in 1953 started the monitoring of a passerine breeding bird community in the South of

90   Sweden (continued until today, Enemar et al. 1994; Svensson et al. 2010). Other LTDS

91   include the bird monitoring in the Hubbard Brook Experimental Forest in New Hampshire,

92   USA (initiated in 1969, Holmes and Sherry 2001; Holmes 2011), and the long-term study of

93   bird community dynamics in the primeval temperate forest of the Białowieża National Park in

94   Poland (since 1975, Wesołowski et al. 2010). Some LTDS have been published in less widely

95   available journals (e.g., Jansen and de Nie 1986, Dutch cultivated mixed forest, 1951 to 1981)

96   or even "hidden" in only locally available journals of ornithological societies (e.g., Sanders et

97   al. 2001, 20-year study in a Dutch recreational forest). Together, these LTDS cover a wide

98   variety from habitats from primeval to successional and heavily managed ecosystems, mainly

99   forests.

100

101   The apparent compositional stability of breeding bird communities has been repeatedly

102   reported. These observations stem from extensive primeval ecosystems of hundreds of square

103   kilometres (temperate primeval forest, Wesołowski et al. 2010; Scandinavian alpine

104   vegetation, Svensson 2006), but also from much smaller stands of protected forests (Beven

105   1976; Enemar et al. 1994). The idea that the study of primeval ecosystems may provide

106   benchmark data for the comparison with man-made systems is not new and the decision to

107 start the monitoring programme in the Białowieża National Park, for example, was

108 specifically based on that objective (Tomiałojć et al. 1984).

109

110 In this study, we used LTDS on bird communities from a variety of terrestrial ecosystems to

111 address two main questions: First, we asked: how fast do the compositions of bird

112 communities change over time and can we identify a baseline of natural change that

113 distinguishes primeval systems from systems experiencing more human impact? For these

114 analyses, we determined the rate of compositional change by means of time lag analysis

115 (TLA), a distance-based method for measuring community dissimilarity between years and

116 regressing it on increasing time-lags (Collins et al. 2000; Kampichler and van der Jeugd

117 2013). The advantage of this method is its computational simplicity and its output of a single

118 statistic—the regression slope, a measure indicating the rate of compositional change through

119 time—which can be easily compared among communities.

120

121 The second question was: how do patterns of temporal variation in composition vary among

122 bird communities in ecosystems with different anthropogenic impact? The many ecological

123 processes that take place over longer time periods, including slow processes, rare events,

124 episodic phenomena, processes with high annual variability, subtle processes and complex

125 phenomena (Franklin 1989), leave signals at different temporal frequencies. We accounted for

126 such non-linear dynamics using a method referred to as redundancy analysis with principal

127 coordinates of neighbour matrices (RDA-PCNM) (Borcard and Legendre 2002; Borcard et al.

128 2004). This method was originally designed for all-scale analysis of spatial patterns, but can

129 also successfully be applied in time series modelling to identify ecological patterns and

130 processes at different temporal scales and the taxa that contribute to these patterns (Angeler et

131 al. 2009; Angeler and Johnson 2012).

132

133 We hypothesised that breeding bird communities in large-scale primeval systems would

134 exhibit slow compositional change with a slope of close to (but significantly different from)

135 zero, while those in other systems (disturbed, managed, or small-scale; here, for the ease of

136 communication simply called disturbed) would show steeper slopes, indicating faster change

137 relative to the primeval systems. The rationale for this hypothesis is that the causes of

138 compositional change in primeval systems are due to a combination of neutral processes such

139 as demographic stochasticity (Hubbell 2001) and responses to slow changing environmental

140 variables that are extrinsic to the ecosystem (e.g., climatic conditions). Assuming that

141 disturbed sites are equally influenced by extrinsic factors as primeval systems, any observed

142 higher rates of community turnover there can be attributed to factors that influence

143 communities locally. These local factors may comprise management interventions or local

144 disturbance regimes or—in the case of small patches—landscape effects of the surrounding

145 matrix. Small and isolated ecosystems can be expected to show higher turnover rates due to

146 frequent stochastic extinction and recolonisation events. Regarding non-linear dynamics, we

147 expected temporal variation to be low-frequent (slow changes lasting over many years) in

148 primeval systems, tracking essentially broad-scale environmental variability. In disturbed

149 systems, these dynamics are expected to be high-frequent (rapid changes occurring within a

150 few years); that is, short term changes are due to management measures or forest succession

151 and a generally higher level of anthropogenic disturbance. By distinguishing the community

152 composition dynamics in primeval systems from other systems, we attempted to identify a

153 natural change baseline, based on linear and non-linear patterns, against which observed

154 community change can be integrally judged. Given (i) our interest in detecting general

155 patterns rather than in identifying the identity of the species responsible for the pattern on a

156 given site, and (ii) the heterogeneity of available LTDS stemming from various ecosystem

157 types and even from different continents and thus housing taxonomically different bird

158 assemblages, no emphasis was laid on species-specific analysis; such analyses are reserved

159 for in-depth studies of single LTDS.

160

161 **Methods**

162

163 *Data origin*

164

165 We searched national and international journals intending to identify all in-depth studies that

166 met our criteria, i.e., that reported breeding bird abundances from relatively small and well-

167 defined study plots that had been surveyed for a period of at least 20 consecutive years and

168 where sampling effort had been standardised and kept constant over time. We did not aim to

169 detect all grey data sources (such as files of local ornithological societies or articles published

170 in local newsletters), but added a few additional papers from Dutch regional and local journals

171 as well as an unpublished Dutch LTDS that were easily accessible to us. Large-scale surveys

172 such as the Breeding Bird Survey of North America (Sauer et al. 2008) were not included

173 since they are much wider scale and yield only indices to relative abundances for each species

174 rather than abundance estimates. In total, we found 15 studies reporting long-term breeding

175 bird data from 24 study plots. All but two studies in the far north of Sweden were performed

176 in the temperate zone of the northern hemisphere. The majority of studies (11) report LTDS

177 from forests (four in the USA, two each in Sweden and the Netherlands, one each in the UK,

178 Poland and Estonia), two from treeless islands (both in the UK), and one each from alpine

179   vegetation (Sweden) and coastal dunes (Netherlands). Their characteristics are summarized in

180   Table 1 (see Online Resource 1 for more detailed descriptions of the studied systems). For the

181   majority of LTDS bird abundance was determined by territory mapping. Exceptions are the

182   forests of the Gaisatj and Valle Mountains in Sweden (combination of territory mapping and

183   line transects, Enemar et al. 2004), the Mastbos forest (combination of territory mapping and

184   maximum score method, Jansen and de Nie 1986), and the forest at Gaudineer Knob (repeated

185   transect counts, Hall 1984). Bird abundance measures (number of territories in almost all

186   cases) were obtained directly from the published material (Robert Allerton Park and William

187   Trelease Wood, Kendeigh 1982; Bookham Common, Beven 1976; Farne Islands, Diamond

188   and May 1977; Gaudineer Knob, Hall 1984; Skokholm Island, Lack 1969), through contact

189   with the data holders (Hoekelum Manor, Sanders et al. 2001; Mastbos, Jansen and de Nie

190   1986; Meijendel) or were contributed by the authors of this paper. In the few cases where data

191   were missing in the time series, these were imputed by species-specific median values or were

192   interpolated by linear or quadratic models when such distinct abundance trends were apparent.

193

194   *Time lag analysis (TLA)*

195

196   In TLA, community dissimilarity is regressed on increasing time lags (one-year lags, two-year

197   lags, three-year lags, etc.) (Collins 2001). To prevent the smaller number of data points of

198   larger time lags from biasing the result, the time lags were square root transformed. The

199   regression slope is not significant when the relative abundances of the constituent species vary

200   around a constant value over time or when the species abundances vary randomly and without

201   temporal autocorrelation (Kampichler and van der Jeugd 2013). Significant positive slopes

202   indicate communities that veer away from their original state, either directionally driven by

203　internal or external factors or due to autocorrelated stochastic variability. Significant negative

204　slopes indicate convergent behaviour, e.g. the return of the community to an earlier state in

205　the time series. The absolute slope values characterise the rate of community change or

206　convergence.

207

208　For each LTDS, we transformed abundance data according to the Hellinger transformation

209　proposed by Legendre and Gallagher (2001),

210
$$N'_{ij} = \sqrt{\frac{N_{ij}}{\sum N_i}}$$

211　where N_{ij} is the population size of species i in year j, and ΣN_i is the sum of individuals across

212　all species in year j. Next, the Hellinger distances, i. e., the Euclidean distances of Hellinger

213　transformed data, for all possible pairs of years of a time series are calculated. The application

214　of Hellinger distance as dissimilarity measure distance in TLA has the following advantages:

215　first, it makes assemblages directly comparable independent of their species richness and

216　abundance of their constituent species, thus controlling for sampling variability between

217　studies; second, it can disentangle compositional change (in which we are interested here)

218　from numerical changes (Kampichler and van der Jeugd 2013). Since a time series of length n

219　yields $(n^2 - n)/2$ pairwise distance measures, the number of degrees of freedom is heavily

220　inflated and the data points are not independent, which impedes the use of the variance for

221　significance determination. We thus followed the suggestion of Thibault et al. (2004) and

222　determined the significance of the slope by a Monte Carlo permutation procedure. We

223　randomly shuffled the positions of the year columns in the species x year matrix 10,000 times

224　and calculated the error probability as the number of slopes larger than the observed slope

225　divided by 10,000. As a measure of year-to-year variability we used the mean of the $n - 1$

226 Hellinger distances measured at lag 1.

227

228 *Redundancy analysis with principal coordinates of neighbourhood matrices (RDA-PCNM)*

229

230 The RDA-PCNM (Borcard and Legendre 2002; Borcard et al. 2004) is a multivariate time

231 series modelling approach that decomposes the overall temporal structure of communities into

232 independent patterns shown by different groups of species that comprise a community

233 (Angeler et al. 2009, 2011). The method is based on Redundancy Analysis (RDA), where

234 time is modelled with a Principal Coordinate of Neighborhood Matrices (PCNM) approach.

235 In a first step, the analysis converts a time vector comprised of n years in a series of PCNM

236 variables akin to a Fourier transform; that is, a number of different sine waves with different

237 temporal frequencies is obtained through conversion of a single variable (i.e., the time vector).

238 The number of PCNM variables depends on the length of the time vector and equals 2n/3.

239 Their wavelengths range from n+1 to 3 years. Through a forward selection procedure, these

240 PCNMs are related to the community data sets by means of RDA. The RDA retains

241 significant PCNM variables, and these are linearly combined in ways to extract temporal

242 patterns from the species x time matrices of each community; that is, the RDA identifies

243 species with similar temporal patterns in the species x time matrix and uses their temporal

244 pattern to calculate a modelled species group trend for these species based on linearly

245 combined PCNMs. The significance of the temporal patterns of all modelled species groups

246 revealed by the RDA is tested by means of permutation tests. The temporal patterns and

247 frequency structure that can be discerned have upper bounds set by the limit of the temporal

248 extent of the data series, and lower bounds set by the frequency of sample collection.

249

250   The RDA relates each modelled species group trend with a significant canonical axis. It

251   generates linear combination (lc) score plots, which visually present the modelled temporal

252   patterns of species groups that are associated with each canonical axis. Based on the number

253   of significant canonical axes, the number of modelled species groups with different temporal

254   patterns can be deduced. The ecological relevance of these temporal patterns can be

255   quantified, using adjusted R^2 values of the canonical axes. The overall temporal structure of

256   the whole community can then be deduced from the number of significant canonical axes in

257   the RDA models. Since RDA-PCNM is designed to identify periodical or non-linear

258   dynamics, potential linear trends are eliminated from the data prior to analysis. Online

259   Resource 2 presents a flow chart summarizing the steps of time series modelling with RDA-

260   PCNM and a calculated example with sample plots.

261

262   We used the R function quick PCNM by D. Borcard (URL

263   http://biol09.biol.umontreal.ca/ULaval08/quickPCNM-77.R) which invokes the R packages

264   ape (Paradis et al. 2004), ade4 (Dray and Dufour 2007) and vegan (Oksanen et al. 2010) as

265   well as functions of the R package packfor (Dray 2009). All analyses (TLA, RDA-PCNM)

266   were made with R (R Development Core Team 2011).

267

268   **Results**

269

270   *Rate of compositional change*

271

272   As expected, all breeding bird assemblages showed a highly significant directional change of

273 community composition ($p < 0.0001$) over time (Table 2). The slope of TLA, and thus the rate

274 of community change, varied widely between the studies. The breeding birds in the primeval

275 subalpine birch forests on the Gaisatj and Valle Mountains displayed the slowest change; the

276 fastest change was observed in the successional forest of Robert Allerton Park (Table 2, Fig.

277 1a and b; see Online Resource 3 for diagrams for all sites).

278

279 Year-to-year variability of bird communities, measured as the mean Hellinger distance at lag

280 1, also varied considerably and ranged from 0.159 on Skokholm Island to 0.445 at Gaudineer

281 Knob (Table 2, Fig 1c and d).

282

283 The rate of compositional change and year-to-year variability were not significantly correlated

284 ($r_P = 0.288$, $p = 0.28$) and breeding bird communities with slow change did not necessarily

285 display low year-to-year variability. For example, slowly-changing Kraipe (plot K1) ranked

286 second in terms of ascending rate of compositional change but showed considerable year-to-

287 year variability and ranked 17th in terms of ascending year-to-year variability, while the rather

288 fast-changing Skokholm Island community (ranked 19th in terms of ascending TLA slope) had

289 the lowest year-to-year variability (Fig. 2). Fast compositional change and large year-to-year

290 variability coincided only for the two successional forests at Gaudineer Knob and in Robert

291 Allerton Park, which had the highest values for TLA slope and Hellinger distance at lag 1

292 among all study sites.

293

294 *Temporal patterns*

295

296 The adjusted R² of the RDA varied between 0.0791 on Hanikatsi Island and 0.6500 on

297 Skokholm Island (Table 2), indicating a range of model fit from low to quite good. In some of

298 the LTDS no temporal patterns were detectable at all and no RDA models could be fitted

299 (Kraipe plot K1, Białowieża National Park plot CM, Mastbos and Gaudineer Knob). The

300 proportion of variance explained by the first two canonical axes ranged from 0.4565 for

301 Birdsong Valley to 1.0 for Hoekelum Manor (Table 2), averaging at 0.6245.

302

303 The linear combination score plots of temporal dynamics of bird communities that were

304 associated with the first canonical axis in the RDA models across study sites are shown in

305 Figure 3. The first canonical axis captures the most important trend in the data, in terms of

306 variance explained. The lc scores represent a synthetic measure of temporal dynamics, based

307 on the patterns of groups of individual species that show similar temporal dynamics,

308 identified by the RDA. In our analysis, most bird communities fluctuated at frequencies of

309 roughly 10 - 30 year intervals (see Fig. 3a-e for a community from a large-scale primeval

310 system and four examples of communities from other systems; see Online Resource 4 for the

311 lc score plots of all study sites). This result indicates that processes at long time scales are the

312 main cause of variability in breeding bird communities, regardless of the intensity of human

313 impact (Table 2). An exception is the breeding bird community from the Gaisatj and Valle

314 mountains (Fig. 3f), which shows a periodicity of roughly 5 years. Considering temporal

315 patterns associated with the remaining canonical axes in the RDA models across communities

316 and sites, we found that the shortest periodicity in compositional change varied between three

317 and 12 years (Table 2; see Online Resource 5 for the significant principal coordinates of all

318 study sites). These results show that the RDA-PCNM approach makes fluctuation frequencies

319 of bird communities at independent temporal scales tractable.

320

321 *Comparison among bird communities*

322

323 In order to identify general patterns in the data we aimed to classify the bird communities into

324 different categories based on the degree of human impact in each study site and to compare

325 the outcome of TLA and RDA-PCNM in a statistical analysis. Apart from primeval

326 ecosystems, none of the different ecosystem types represented in the available LTDS (large

327 protected forest, small and isolated forest, successional forest and regrowth, managed and

328 recreational forest, protected dunes, treeless islands), however, was sufficiently replicated to

329 allow the definition of a human impact category of its own and to allow a proper statistical

330 analysis. We thus decided to form only one more or less homogeneous category, namely the

331 bird communities from large-scale primeval ecosystems, and contrast them to the remaining

332 bird communities from all other systems by a type 3 sum of squares ANOVA. As an

333 alternative we applied a regression analysis, using all site characteristics (see Table 1) as

334 explanatory variables for the results of TLA and RDA-PCNM. None of these analyses,

335 however, yielded any significant difference between primeval and other ecosystems or any

336 significant regression model (results not shown; see Online Resource 6 for a closer

337 description of the used methods).

338

339 **Discussion**

340

341 *Rate of compositional change*

342

343 As expected, all bird communities in our sample displayed compositional change over time.

344 When ordered according to ascending TLA slope, the top ranks were mostly occupied by bird

345 communities from pristine systems (Gaisatj and Valle, Białowieża, Kraipe) (Fig. 2) indicating

346 the tendency that they experienced the slowest compositional change among the different

347 systems represented in this study. Also within-study comparisons support the assumption that

348 undisturbed systems show slower compositional change. For example, in the Białowieża

349 National Park, the TLA slope varies between 0.025 and 0.034 for most of the sites with

350 exception of plots NE and NW, which show considerably faster rate of compositional change

351 (slopes: 0.040 and 0.053, respectively) (Table 2, Fig. 2). These two plots have experienced

352 distinct natural disturbance in the past decades, including large gaps created by tornadoes in

353 1987 and 2002, and a bark beetle outbreak in 2002–2003. The latter killed numerous spruces,

354 reducing the number of living canopy spruces by almost 50% (Wesołowski et al. 2010).

355

356 The bird communities from successional systems (Gaudineer Knob, Robert Allerton Park)

357 showed the fastest change (Fig. 2). Protected forests which cannot be regarded as pristine but

358 which have been left undisturbed for a long time (Birdsong Valley, Bookham Common,

359 Hubbard Brook, William Trelease Woods) were located between the extremes (primeval vs.

360 successional). Of course, natural succession occurs also in undisturbed systems. Those

361 protected systems where distinct successional changes (maturation of trees, disappearance of

362 certain species due to diseases or pests etc.) have been reported (William Trelease Woods,

363 Hubbard Brook) (Kendeigh 1982; Holmes and Sherry 2001) showed the fastest rate of change

364 following the purely successional systems.

365

366 Plotting TLA slopes against Hellinger distances allows for an evaluation of the position of

367 each LTDS in a plane spanned by speed of change and interannual variability. Four quadrants

368 can be defined: "slow change – low variability", "slow change – high variability", "fast

369 change – high variability" and "fast change – low variability" (clockwise beginning at bottom

370 left) (Fig. 2). Along the TLA slope axis, the results more or less correspond to the expectated

371 increasing rate of compositional change: primeval systems > protected systems > successional

372 systems. Interestingly, disturbed forests (Hoekelum, Mastbos) show comparably slow

373 compositional change of bird communities over time with rates close to those of primeval

374 systems and an interannual variability even lower than the primeval Białowieża plots not

375 suffering from natural disturbance (plots L, K. MS, W) (Table 2, Fig. 2). Continuous forest

376 management (Mastbos) obviously imposes stability on the bird community, since it inhibits

377 natural forest succession by harvesting mature trees and planting young ones. While at the

378 plot scale there may be temporal variation as a result of forest management measures (clear-

379 cutting, understory removal etc.), the forest as a whole may display more constancy being

380 composed of a stable mosaic of stands with trees of different age. Also the use of forests as

381 recreation areas seems to affect breeding bird composition less than might be expected. While

382 the researchers abandoned Hoekelum Manor after 20 years of bird monitoring because of the

383 increasing density of strollers, joggers and dog-owners letting their pets running free (Sanders

384 et al. 2001), its breeding bird community showed a high degree of stability with a surprisingly

385 low rate of compositional change. Remarkably, the Hellinger distances at lag 1 of the

386 managed and disturbed forests of Mastbos and Hoekelum Manor indicate lowest year-to-year

387 variability among all studies (only equaled by the treeless islands) and underscore the high

388 stability of their breeding bird communities as already indicated by their low TLA slopes.

389 Consequently, they were located in the "slow change – low variability" corner together with

390 the primeval forests of the Białowieża National Park and the Gaisatj and Valle mountains

391 (Fig. 2). In contrast the successional forests Robert Allerton Park and Gaudineer Knob were

392 located in the "fast change – much variability" quadrant. This finding is contrary to those of

393   several studies that report the effects of anthropogenic management and disturbance on forest

394   bird communities (Hobson and Schieck 1999; Canterbury et al. 2000; Drapeau et al. 2000).

395   None of these latter studies, however, were based on long uninterrupted community time

396   series. Hansen et al. (1995) reported a non-linear response of species' abundances to tree

397   density across a wide range of natural and managed stand structures and ages. Probably

398   Mastbos and Hoekelum Manor maintain a tree density above the threshold at which bird

399   abundance changes dramatically. Both stands have been forested for two centuries and longer

400   (see details of land-use history in Online Resource 1) and no fundamental land-use change

401   occurred in this period (with the exception of a change of the dominant tree species) which

402   might have created quite stable conditions for the breeding bird community apart from

403   forestry measures at the stand scale.

404

405   Another interesting case is Hanikatsi Island, a protected forest that showed slow

406   compositional change but high year-to-year variability—almost as high as the successional

407   forests in Robert Allerton Park and on Gaudineer Knob. This can be explained by a distinct

408   in-and-out-effect (Diamond and May 1977) of species that repeatedly become extinct and

409   then immigrate, while at the same time the regional species pool from which the Hanikatsi

410   community may draw is restricted due to the effect of its isolated location on an island.

411

412   The position of the bird communities on treeless islands in the speed of change – year-to-year

413   variability plot (Fig. 2) is hard to explain. Both Skokholm Island and the Farne Islands

414   showed very low inter-annual variability, but Skokholm Island underwent a faster

415   compositional change, probably related to the marked increase in population size of a few

416   abundant species (Lack 1969).

417

418   In conclusion, the TLA slopes (b) show a gradient from primeval ($b < 0.04$) over managed or

419   disturbed ($0.04 < b < 0.06$) (Mastbos and Hoekelum) and protected ($0.06 < b < 0.1$) (Birdsong

420   Valley, Bookham Common, Western Trelease Woods, Hubbard Brook and Meijendel) to

421   successional ($b > 0.1$) (Robert Allerton Park and Gaudineer Knob) systems; year-to-year

422   variability was highest in successional forests and lowest in managed and disturbed forests.

423   While these conclusions seem to be ecologically plausible, they are of a hypothetical nature

424   since none of these differences were statistically significant. We must not prematurely

425   conclude, however, that there is no difference between large-scale primeval systems and other

426   systems as long as there are no data available that allow for higher statistical power (Steel et

427   al. 2013). It is evident that more LTDS—particularly from forests subjected to forestry—

428   would be desirable to confirm our conclusions.

429

430   *Temporal patterns*

431

432   In almost all of the time series analysed, one of the long-wave principal coordinates (PCMN 2

433   in most cases) was the one with the highest importance (Table 2), indicating that most of the

434   temporal variability was explained by slow changes lasting over many years. In many time-

435   series, medium and short-wave principal coordinates did not appear in the model at all or had

436   only little importance, showing that there was little short-term variation. Thus, the results are

437   particularly interesting as they deviated from our expectations. It is increasingly recognised

438   that anthropogenic stress increases the short-term temporal variability of ecological

439   communities (e.g., Angeler and Moreno 2007; Hillebrand et al. 2010), and that this increased

440   temporal variance in ecological systems can even be used as an early warning signal of

441   impending catastrophic regime shifts in ecosystems (Carpenter and Brock 2006). Based on

442   these previous findings—although from communities rather different from avian ones in

443   temporal as well as spatial scales—, we expected that anthropogenic impact should increase

444   the temporal variability in stressed communities relative to assemblages in pristine sites, and

445   that this should be manifested in the increased importance of principal coordinates with

446   medium to high-frequent wavelengths in the RDA models. The lack of such patterns, and the

447   finding that long-wave principal coordinates similarly influence bird community dynamics

448   across our habitat categories, suggests that environmental factors that are extrinsic to the

449   system have a proportionally stronger influence than factors associated with local-scale

450   anthropogenic stress. Although speculative, we attribute this finding to the dispersal capacity

451   of birds, especially migratory species. Their capacity to carry out long-distance migration may

452   enhance source-sink dynamics allowing for the colonization of sites that would otherwise be

453   unsuitable to sustain populations in the long-term (Wesołowski and Tomiałojć 1997;

454   Wesołowski et al. 2009). Long-term metacommunity dynamics could help mitigate local-

455   scale human impact on bird communities, provided that regional species pools and/or habitat

456   characteristics are not deteriorated. Another more simple explanation could be that through

457   learning and phenotypic adjustment birds may tolerate a rather high degree of human impact

458   so that their communities are robust assemblages provided that the human stressors do not

459   become too strong. This kind of mechanism could be tested if systems with varying degrees

460   of human pressure could be compared in this respect, but this is not possible with the

461   available LTDS data. Moreover, we can state for some of the study areas, for example, the

462   Białowieża forest, that the majority of birds are not site tenacious (e.g. Piotrowska and

463   Wesołowski 1989, Wesołowski et al 2009, Wesołowski and Rowiński 2012), so every spring

464   the community consists of a new set of "naïve" breeding birds, which have no former

465   knowledge of the local conditions.

466

467   Regarding the importance of local vs. regional scale dynamics it is interesting to note that the

468   bird community inhabiting the primeval subalpine birch forest in the Gaisatj and Valle

469   mountains tracked the cyclic appearance of masses of caterpillars of the Autumnal Moth

470   *Epirrita autumnata*, which provides a superabundant food resource at approximately ten-year

471   intervals (Enemar et al. 2004). These mass appearances clearly transcend ecological dynamics

472   at the plot scale to influence community dynamics over broader spatial extents, enabling us to

473   detect these changes by means of the RDA-PCNM. The dominant periodicity as identified by

474   RDA-PCNM occurred at a wavelength of 0.30 of the study period representing a periodicity

475   of 11 years. Also the principal coordinates with the third largest weight had a wavelength of

476   10 years, which is in agreement with the periodicity of the moth caterpillar outbreaks and

477   emphasises their impact on the periodical compositional variability of the breeding bird

478   community. Interestingly, in the original publication of these data, Enemar et al. (2004) stated

479   that "*Fringilla montifringilla* increased in density during the first two years of each caterpillar

480   outbreak, whereas the other species responded only weakly". This substantiates the potential

481   of RDA-PCNM for detecting periodic community dynamics that might remain unidentified

482   with other methods. Also in the Białowieża forest, caterpillars outbreaks are regularly

483   observed. There, however, they do not lead to detectable effects on breeding bird numbers

484   (e.g. Wesołowski and Tomiałojc 1997; Wesołowski et al. 2009, 2010), and no indications of

485   periodic community dynamics tracking these outbreaks were found by RDA-PCNM.

486

487   Although we did not aim to analyse which species or species-groups contribute to the

488   temporal patterns of the different breeding bird communities—an exercise beyond the scope

489   of this paper—it is worth noting that some species occur remarkably often among those

490   correlated with the significant PCNM, as can be seen in the biplots delivered by RDA-PCNM

491   (see Online Resource 7 for biplots for all LTDS). For example, winter wren *Troglodytes*

492   *troglodytes* (Białowieża forest, Birdsong Valley, Bookham Common, Hanikatsi Island,

493   Hoekelum Manor, Meijendel dunes), chiffchaff *Phylloscopus collybita* (Białowieża forest,

494   Birdsong Valley, Hanikatsi Island, Meijendel dunes) and willow warbler *Phylloscopus*

495   *trochilus* (Białowieża forest plot L, Gaisatj and Valle Mountains, Hanikatsi Island, Meijendel

496   dunes) appear in various of the European LTDS among the most influential bird species.

497   Interestingly, in open systems—such as the Meijendel dunes—these species mostly appear in

498   up-coming shrubs, while in closed forests they prefer disturbed places with sufficient

499   understory (Haffer 1985a, b; Tiainen 1985), thus characterising local successional dynamics.

500   Not surprising, the winter wren is among the species most closely related to low-frequent

501   PCNM in those plots of Białowieża forest with natural disturbance in the form of storm

502   damage (plots NE and NW) while in the stable plots it seems to have less influence on

503   temporal community patterns. In-depth studies of the single sites where the LTDS were

504   collected certainly will elucidate the relationships between single species population

505   dynamics and more global community patterns.

506

507   *A natural baseline?*

508

509   We acknowledge that the correlative nature of our approach can be very useful for examining

510   patterns, while it falls short of elucidating mechanisms. However, the generation of patterns

511   alone can be insightful and inform ecological theory and management. For example,

512   contrasting rates of compositional change across habitats with different anthropogenic

513 influence serves to identify an "ecologically meaningful", empirical baseline close to the

514 natural composition change in terrestrial breeding bird communities. The "real" baseline that

515 corresponds to natural turnover not being impacted by any form of anthropogenic impact is

516 illusive, because past or already occurring continental or global scale consequences of human

517 activities (acid rain, airborne nutrients, climate change), cannot be fully accounted for. It has

518 to be underlined, however, that various of the time series analysed here have been either

519 collected, or initiated, well before any climate change effects had became discernible.

520 Moreover, though some warming was observed, until now its effects were modest. For

521 example, changes observed in the Białowieża Forest remained within the range of natural

522 variation recorded before the onset of warming, and up to now no climate forced directional

523 changes in composition of tree or birds communities have been recorded (Wesołowski and

524 Cholewa 2009, Wesołowski et al. 2010). Thus the predicted large scale turnover of fauna due

525 to climate change (Pereira et al. 2010; Sodhi and Ehrlich 2010; Dawson et al. 2011) has not

526 occurred yet.

527

528 Patterns of periodic dynamics do not vary much among systems with different levels of

529 human influence. Regardless of the duration of the LTDS, the low frequency dynamics

530 always seem to be the most important ones and are overridden by high frequency dynamics

531 only under peculiar circumstances, for example, periodic food outbreaks, which may be due

532 to metacommunity dynamics that are specific to birds (i.e., their high dispersal capacity). It

533 will be interesting to determine the generality of this finding in time series analyses in other

534 groups of organisms.

535

536 *Conclusions*

537

538   Despite the determination of baselines of temporal compositional change being important for

539   assessing and managing ecological systems in face of environmental change, the paucity of

540   available data sets, particularly for longer-lived organisms such as terrestrial vertebrates,

541   currently limits strong inference. Our use of LTDS in this paper demonstrates the potential

542   value of so-called passive monitoring (as opposed to question-driven monitoring), which can

543   provide valuable data even when not all of the possible analyses can be anticipated at the

544   outset. Due to the moderate number of available independent LTDS for temperate bird

545   communities our study was hampered by the heterogeneity in the systems other that large-

546   scale primeval ones, which prevented the definition of more specific categories of human

547   impact and their statistical comparison. As a result, our attempts of comparison between bird

548   communities from large-scale primeval systems and other systems did not yield any

549   statistically significant differences, neither did our approach to regress community change,

550   interannual variability and temporal community patterns on the characteristics of the sites

551   where the LTDS were collected. Nevertheless, specific patterns in the data call for more

552   information and closer analysis (e.g. the comparison between primeval and successional forest

553   systems). Although our results must be viewed with caution, we believe that our approach

554   serves as an instructive example on how baselines of compositional change can be compared

555   and evaluated.

556

557   **Acknowledgements**

558

566

567 **References**

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Fig. 1 Time lag analysis (TLA) results of the breeding bird communities from different ecosystem types—a) Gaisatj and Valle Mountains (primeval subalpine birch forest), b) Robert Allerton Park (successional forest on abandoned fields), c) Gaudineer Knob (second-growth spruce forest) and d) Skokholm Island (small treeless island)—showing the Hellinger distances between all pairs of years at different time lags and the fitted regression line

Fig. 2 Position of the study sites (large filled circles: large-scale primeval systems; large open circles: other systems) in the variable space of rate of community change (characterised by the TLA slope) and interannual variability (characterised by the Hellinger distance at lag 1). At the seven sites in Białowieża National Park (Wesołowski 2011) and the three sites in the dunes of Meijendel, the numbers of birds tended to be highly synchronous across years. These plots are thus not regarded as independent. In the figure their means of community change and interannual variability are shown with values of their single plots represented as small filled (Białowieża) and as small open circles (Meijendel).

Fig. 3 Linearly combined scores of principal coordinates of neighbourhood matrices on the first redundancy axis for four sites from different ecosystem types characterised by long periodicity: a) Białowieża National Park (plot K) (primeval forest), b) Meijendel (middle zone) (protected dune ecosystem), c) Hoekelum Manor (managed forest), d) Skokholm Island (small treeless island); and for two sites characterised by shorter periodicity: e) Robert Allerton Park (successional forest on abandoned fields), and f) Gaisatj and Valle mountains (primeval subalpine birch forest)

Figure 1
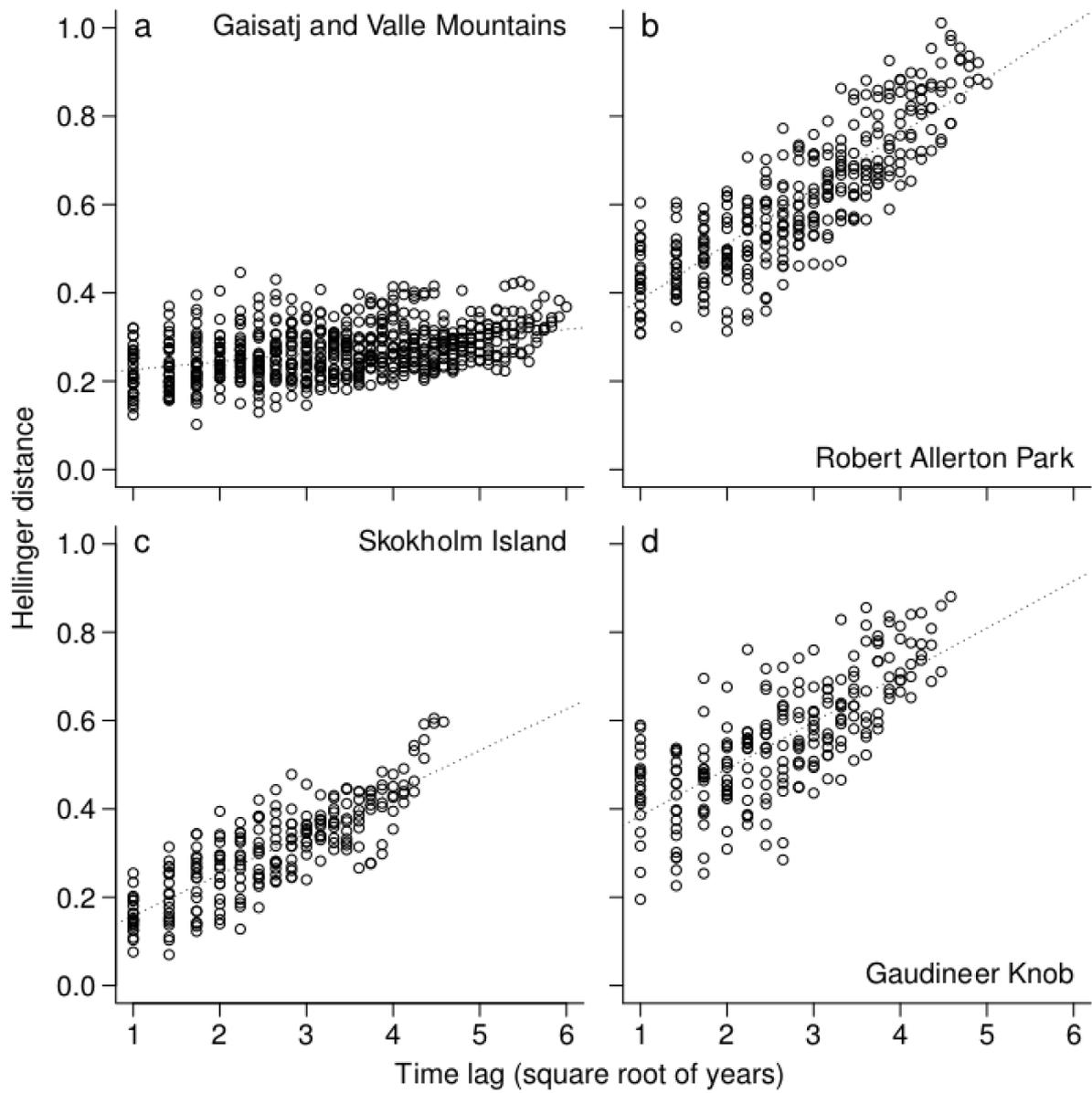
Figure 2
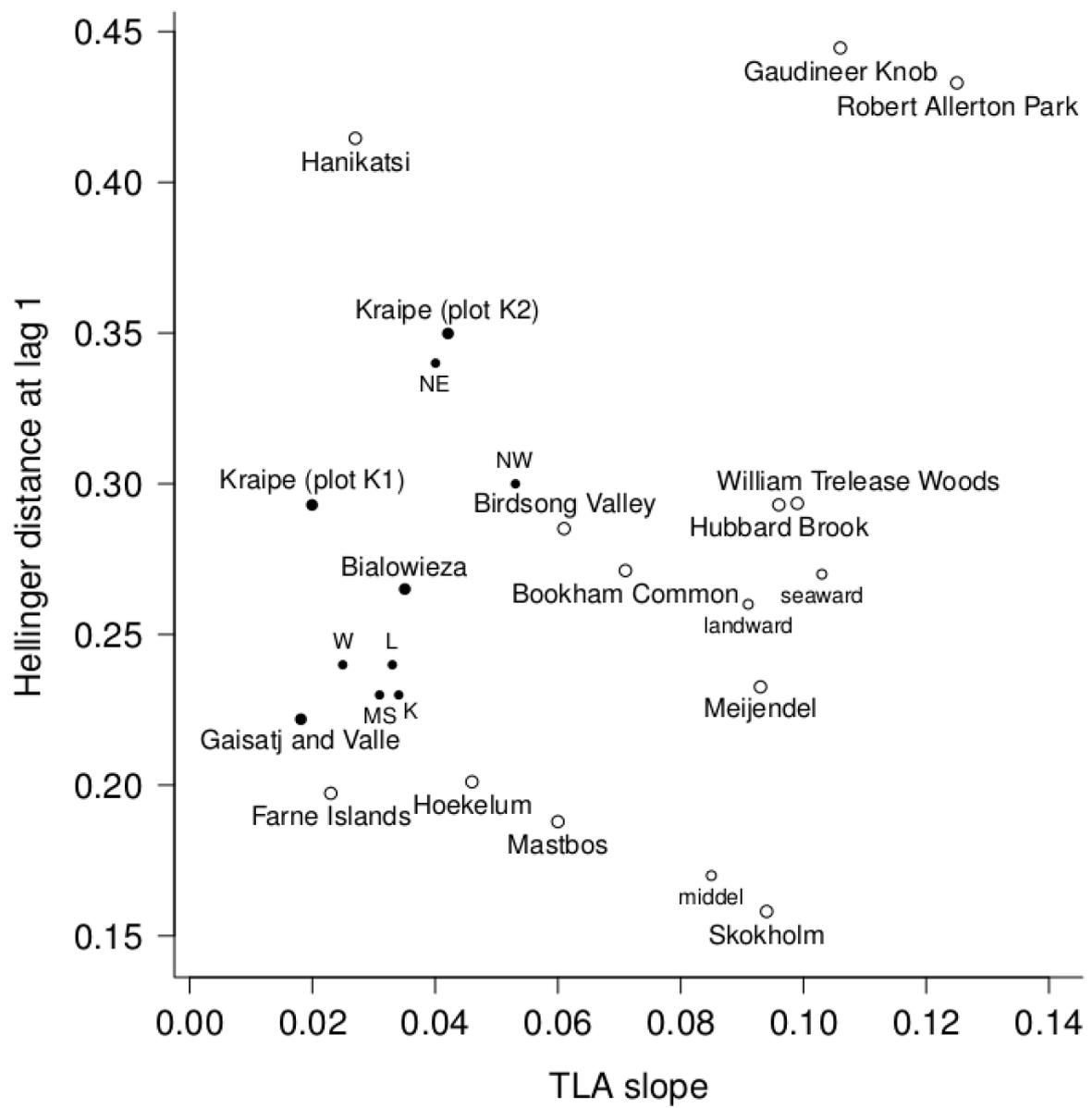
Figure 3
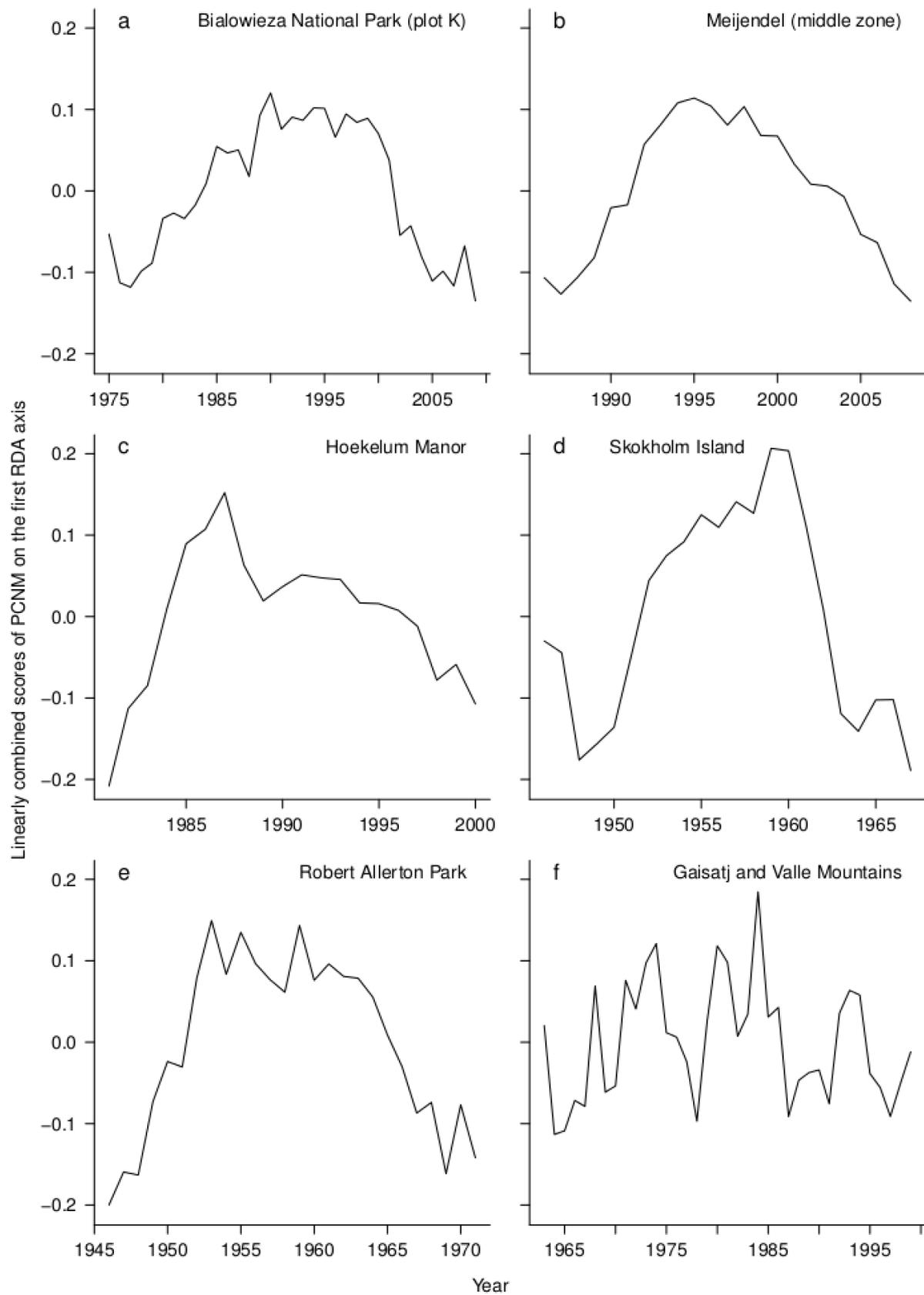
Online Resource 1 Detailed description of studied systems

Online Resource 2 Short guide through Redundancy Analysis (RDA) with Principal Coordinates of Neighbourhood Matrices (PCNM)

Online Resource 3 Time lag analysis results of all breeding bird communities included to the analysis, showing the Hellinger distances between all pairs of years at different time lags and the fitted regression line. See Table 2 in the main document for statistical parameters of the regression.

Online Resource 4 Results of redundancy analyses with principal coordinates of neighborhood matrices (lc score plots) of all breeding bird communities included to the analysis. See Table 2 in the main document for statistical parameters of the analysis.

Online Resource 5 Significant principal coordinates of neighborhood matrices (PCNM) for all breeding bird communities included to the analysis. The PCNM are characterised by their wave-lengths expressed in years.

Online Resource 6 Methods applied for the comparison of TLA and RDA-PCNM results among bird communities

Online Resource 7 RDA-PCNM biplots of all breeding bird communities included to the analysis. No RDA models could be fitted to Kraipe plot K1, Białowieża National Park plot CM, Mastbos and Gaudineer Knob. See Online Resource 2 for an explanation of how to read an RDA-PCNM biplot.

Table 1. Studies of breeding bird communities with time series of at least 20 years used in the analyses. Studies are alphabetically ordered by site names. System size = contiguous habitat in km^2 in which study plots were embedded.

Name and location[a]	Habitat	Bird community	Species number	Time series	Plot size [ha]	System size	References
Białowieża National Park, Poland (plots CM, K, L, MS, NE, NW and W)	primeval mixed forest	all	51 (CM) 75 (K) 56 (L) 50 (MS) 54 (NE) 50 (NW) 63 (W)	1975–2009 (all except L) 1980-2009 (L)	24 (CM) 33 (K) 25 (L, NE, NW) 30 (MS) 25.5 (W)	>1400	Tomiałojć et al. 1984; Tomiałojć and Wesołowski 1994, 1996; Wesołowski et al. 2002, 2006, 2010
Birdsong Valley, Sweden	protected isolated deciduous forest	passerines	41	1953–2009	13	0.13	Enemar 1966; Enemar et al. 1994; Svensson et al. 2010
Bookham Common, UK	protected mature oak-wood	all	44	1949–1975	16	1.12	Beven 1976
Farne Islands, UK	group of rocky islands	land birds	16	1946–1974	32	0.32	Diamond and May 1977
Gaisatj and Valle, Vindel mountain nature reserve, Sweden	primeval subalpine birch forest	passerines	46	1963–1999	900	>1000	Enemar et al. 2004
Gaudineer Knob, W Virginia, USA	second-growth spruce forest	passerines	20	1962–1983	6.08	3719	Hall 1984
Hanikatsi Island, Estonia	protected isolated forest patch on an island	all	33	1974–2004	10	0.1	Leito et al. 2006
Hoekelum Manor, Netherlands	recreational forest	all	50	1981–2000	69	1000	Sanders et al. 2001
Hubbard Brook, New Hampshire, USA	protected northern hardwood forest	all	36	1969–2010	10	>3000	Holmes and Sturges 1975; Holmes et al. 1986; Holmes 1990; Holmes and Sherry 2001; Holmes 2011

Kraipe, Vindel mountain nature reserve, Sweden (plots K1 and K2)	primeval alpine vegetation	all	26 (K1) 19 (K2)	1964–2001 (K1) 1964-1999 (K2)	100 (K1) 114 (K2)	300	Svensson et al. 1984; Svensson 2006
Mastbos, Netherlands	cultivated mixed forest	passerines	18	1955–1981	50	5.7	Jansen and de Nie 1986
Meijendel, Netherlands (seaward, middle and landward zone)	protected coastal dunes	all (except colonial breeders)[b]	60 (seaward) 98 (middle) 89 (landward)	1986–2008	12.2 (seaward) 166.7 (middle) 68.4 (landward)	30	van Ommering and van der Salm 1990[c]
Robert Allerton Park, Illinois, USA	successional forest on abandoned fields	all	51	1946–1971	24.3	1.8	Kendeigh 1982
Skokholm Island, UK	treeless island	land birds	18	1946–1967	96	0.96	Lack 1969
William Trelease Woods, Illinois, USA	protected isolated deciduous forest	all	59	1934–1976	24	0.24	Kendeigh 1982

[a] including plot names when more than one plot was monitored

[b] Colonial breeders such as cormorants and gulls move their breeding sites from one place to the other within a few years, for example, from within a study plot to outside or vice versa. Since colony movement might misleadingly appear to indicate huge abundance changes and, thus, bias the results, we skipped colonial breeders from the analysis.

[c] This paper describes the study area and reports earlier investigations on its breeding bird community. The time series from 1986 through 2008 used in our analysis has not been published before.

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Table 2. Model outputs of time lag analysis (TLA) and redundancy analysis (RDA) with principal coordinates of neighbourhood matrices (PCNM) for breeding bird community time series of at least 20 years. The PCNM with the largest weight in the RDA model is expressed as proportion of the time series length, the shortest PCNM in the RDA model is expressed in years. ND, not determined since no RDA model could be fitted.

Name	TLA slope	Mean Hellinger distance at lag 1	Adjusted R^2 of RDA model	Explained variance of RDA axes 1 and 2	PCNM with largest weight in RDA model	Shortest PCNM in RDA model
Białowieża National Park (plot CM)	0.029	0.28	ND	ND	ND	ND
Białowieża National Park (plot K)	0.034	0.23	0.30	0.52	0.74	7
Białowieża National Park (plot L)	0.033	0.24	0.22	0.52	0.70	3.5
Białowieża National Park (plot MS)	0.031	0.23	0.34	0.47	0.74	3.3
Białowieża National Park (plot NE)	0.040	0.34	0.20	0.50	0.74	6
Białowieża National Park (plot NW)	0.053	0.30	0.24	0.57	0.74	8
Białowieża National Park (plot W)	0.025	0.24	0.27	0.59	0.74	8
Birdsong Valley	0.061	0.29	0.51	0.46	0.70	4
Bookham Common	0.071	0.27	0.24	0.63	0.74	8
Farne Islands	0.023	0.20	0.44	0.58	0.69	6
Gaisatj and Valle mountains	0.018	0.22	0.14	0.67	0.30	10
Gaudineer Knob	0.106	0.45	ND	ND	ND	ND
Hanikatsi Island	0.027	0.42	0.08	0.79	0.71	9
Hoekelum Manor	0.046	0.20	0.11	1.00	0.75	8
Hubbard Brook	0.096	0.29	0.42	0.59	0.74	3.5
Kraipe (plot K1)	0.020	0.30	ND	ND	ND	ND
Kraipe (plot K2)	0.042	0.35	0.22	0.82	0.75	12
Mastbos	0.060	0.19	ND	ND	ND	ND
Meijendel (landward zone)	0.091	0.26	0.34	0.52	0.70	5

Meijendel (middle zone)	0.085	0.17	0.42	0.58	0.70	5
Meijendel (seaward zone)	0.103	0.27	0.41	0.68	0.70	3.5
Robert Allerton Park	0.125	0.43	0.17	0.71	0.54	9
Skokholm Island	0.094	0.16	0.65	0.75	0.77	3.8
William Trelease Woods	0.099	0.29	0.52	0.56	0.70	4

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