1 **Determining patterns of variability in ecological communities: Time lag analysis**

2 **revisited**

3

4 Christian Kampichler[1,2] and Henk P. van der Jeugd[1]

5

6 Address:

7 [1] Vogeltrekstation – Dutch Centre for Avian Migration and Demography, NIOO-KNAW,

8 Postbus 50, 6700 AB Wageningen, The Netherlands

9 [2] Universidad Juárez Autónoma de Tabasco, División Académica de Ciencias Biológicas,

10 Carretera Villahermosa-Cárdenas Km. 0.5 s/n, C.P. 86150 Villahermosa, Tabasco, Mexico

11

12 Corresponding author:

13 Christian Kampichler, Vogeltrekstation – Dutch Centre for Avian Migration and

14 Demography, NIOO-KNAW, Postbus 50, 6700 AB Wageningen, The Netherlands;

15 email: christian.kampichler@web.de; tel +31 317 473-464; fax +31 317 473-675

16

17

18

19

20

21

Abstract

All ecological communities experience change over time. One method to quantify temporal variation in the patterns of relative abundance of communities is time lag analysis (TLA). It uses a distance-based approach to study temporal community dynamics by regressing community dissimilarity over increasing time lags (one-unit lags, two-unit lags, three-unit lags). Here, we suggest some modifications to the method and revaluate its potential for detecting patterns of community change. We apply Hellinger distance based TLA to artificial data simulating communities with different levels of directional and stochastic dynamics and analyse their effects on the slope and its statistical significance. We conclude that statistical significance of the TLA slope (obtained by a Monte Carlo permutation procedure) is a valid criterion to discriminate between (i) communities with directional change in species composition, regardless whether it is caused by directional abundance change of the species or by stochastic change according to a Markov process, and (ii) communities that are composed of species with population sizes oscillating around a constant mean or communities whose species abundances are governed by a white noise process. TLA slopes range between 0.02 and 0.25, depending on the proportions of species with different dynamics; higher proportions of species with constant means imply shallower slopes; and higher proportions of species with stochastic dynamics or directional change imply steeper slopes. These values are broadly in line with TLA slopes from real world data. Caution must be exercised when TLA is used for the comparison of community time series with different lengths since the slope depends on time series length and tends to decrease non-linearly with it.

48   **Key words**

49

50   community change; Markov process; species composition; stochasticity; temporal

51   dynamics

52

53   **Introduction**

54

55   All ecological communities are subjected to change over time (MacArthur and Wilson

56   1967[MacArthur and Wilson 1967]; White et al. 2006[White et al. 2006]; Magurran and

57   Henderson 2010[Magurran and Henderson 2010]). Long-term datasets of ecological

58   communities are the most important source of information on the temporal dynamics of

59   species composition and patterns of relative abundance (Magurran et al. 2010[Magurran et

60   al. 2010]). "Long-term", however, is relative (Rull and Vegas-Vilarúbia 2011[Rull and

61   Vegas-Vilarrúbia 2011]); while some studies analyse data collected over an exceptionally

62   long period of time—for example, the Park Grass Experiment at Rothamsted, England

63   (Silvertown et al. 2006[Silvertown et al. 2006])—the majority of datasets that are regarded

64   as "long-term" by ecologists are comparably short and do not allow for the application of

65   standard tools for time series analysis (Cowpertwait and Metcalfe 2009[Cowpertwait and

66   Metcalfe 2009]).

67

68   Time lag analysis (TLA) was introduced by Collins et al. (2000[Collins et al. 2000]) as a

69   method to quantify temporal variation in the patterns of relative abundance of

70   communities. It applies a distance-based approach and is used to study temporal

71   community dynamics by regressing community dissimilarity over increasing time lags

72   (one-unit lags, two-unit lags, three-unit lags,...). To prevent the smaller number of data

73   points of larger time lags from biasing the result, the time lags are square root transformed.

74   Collins et al. (2000[Collins et al. 2000]) mention three instances that can be distinguished

75   by TLA. (1) When the slope of the regression line of dissimilarity of lag is significant and

76   positive. In this case the community is undergoing directional change. (2) When the

77   regression line is significant and negative. This indicates a convergent dynamics of the

78   community, i.e., the community returns to an earlier state in the time series such as

79   following perturbation or other cyclical behaviour. (3) When there is stochastic variation

80   over time. This implies that the slope of the regression line is not significantly different

81   from zero. Collins et al. (2000[Collins et al. 2000]) further state that the slope of the

82   regression and the coefficient of determination, R^2, can be used as a measure of signal

83   versus noise. For example, a small but significant positive slope with a small R^2 would

84   indicate slow directional change with high stochastic variation between sample intervals,

85   whereas a steeper slope and a large R^2 would indicate a strong signal of directional change

86   and less stochastic variation. Since its publication, TLA has gained popularity, and it has

87   been applied to study the temporal dynamics of a variety of communities, for example,

88   desert rodents (Thibault et al. 2004[Thibault et al. 2004]), soil microarthropods

89   (Kampichler and Geissen 2005[Kampichler & Geissen 2005]), and tide pool fishes (Pfister

90   2006[Pfister 2006]).

91

92   The stochastic change as outlined above assumes that populations are governed by a white

93   noise process, which means that the abundance of a species at a given time is completely

94   independent of any previous state. Examples are communities in which species abundances

95   oscillate around time-invariant means according to a normal distribution, or communities

96 in which the abundance of each species corresponds to random values from a uniform

97 distribution at every time step (which in fact also leads to stationary population means

98 when the upper and lower limits of the uniform distribution are constant in time). In an

99 analysis of 544 natural populations of 123 species, Inchausti and Halley (2002[Inchausti

100 and Halley 2002]) showed, however, that in almost all cases population variability

101 increased with observed timespan, which is not consistent with the assumption of a white

102 noise population process. We therefore aimed to evaluate the behaviour of TLA with data

103 based on the most simple stochastic model next to a white noise process which assumes

104 that the abundance at any point in time is dependent only on its previous value (Williams et

105 al. 2002[Williams et al. 2002], p. 188). Processes whose future process behaviour is

106 influenced only by the present system state are known as Markov processes, and they are

107 widely used for the modelling of biological populations (Meyn and Tweedie 1993[Meyn

108 and Tweedie 1993], p. 5, Williams et al. 2002[Williams et al. 2002]). We argue that it is

109 highly improbable that a first-order Markov process, i.e. a state at time $t+1$ depends only

110 on the state at time t, will move a community back to a position in variable space where it

111 had been some time before. Thus, any stochastic change concerning the abundance of the

112 species that constitute the community inevitably will veer it away from the original state

113 and thus increase any distance measure. The terms "directional" and "stochastic" must be

114 used with caution since they suggest that directional community change implies the action

115 of an internal or external force that drives it from its original position in variable space.

116 According to our reasoning, stochastic variation that can be described by a first-order

117 Markov process also leads to "directional" change, for example, by ecological drift

118 (Hubbell 2001[Hubbell 2001]), which is analogous to genetic drift caused by random

119 mutation (Ricklefs 2003[Ricklefs 2003]).

120

In this paper, we apply TLA to artificial data simulating communities with different levels
of directional and stochastic dynamics and analyse their effects on the slope and its
statistical significance. According to our hypothesis, we expect to detect significant
community change when first-order Markov processes are involved. Finally, we draw
conclusions on the potential of TLA for the study of real-world community time series.

Materials and Methods

Simulation of community time series

We simulated community change with communities having a species richness of 20 and a
time-series length of 20 and 100 units. They were initialised according to a log-normal
model of abundance distribution with a mean of $\log(N)=3$ and a standard deviation of 2
and rounded to the closest integer. We assumed that all species within a community
behaved independently from the others. We used species with three types of dynamics:
species that fluctuate around a constant mean ("constant species"), species with stochastic
dynamics ("stochastic species"), and species with a monotonously increasing or decreasing
trend ("directional species").

Abundance values of the constant species time series were drawn from a normal
distribution with the initial abundance N_0 as the mean and the standard deviation s
calculated as $N_{t-1} * v$ where v is a scaling factor ranging from 0.001 to 0.5 thus fixing the
standard deviation in the range from 0.1% (species with small fluctuations) to 50%

6

144   (species with large fluctuations) of the mean of the preceding time step (Fig.1a). For the

145   stochastic species, we used the general model $N_t = f(N_{t-1}, \varepsilon_t)$ as a starting point where N is

146   the population density at time t, ε_t represents environmental stochasticity, and f is a

147   function that relates the density and environmental stochasticity to a population size at time

148    $t + 1$ (Lundberg et al. 2000[Lundberg et al. 2000]). We drew the abundance values N_t from

149   a normal distribution with mean N_{t-1} and standard deviation calculated as above as $N_{t-1} * v$

150   with v ranging from 0.001 to 0.5 (Fig.1b). Thus the trajectories of the stochastic species

151   through time form first-order Markov chains since the transition probabilities from N_{t-1} to

152   N_t depend only on N_{t-1}, not on how N_{t-1} was reached (e.g., by an increase or a decrease

153   from N_{t-2} to N_{t-1}) like in a correlated random walk (Meyn and Tweedie 1993[Meyn and

154   Tweedie 1993]; Williams et al. 2002[Williams et al. 2002]). Stochastic species were

155   allowed to go extinct and to re-enter the community. We applied a procedure similar to the

156   random walk on a half-line (Meyn and Tweedie 1993) and permitted the species trajectory

157   to include negative abundances during data generation. Prior to TLA these data were set to

158   zero, i.e. the species were "absent" from the community at the corresponding points in

159   time. Time series of the directional species were constructed in the same manner as for

160   stochastic species, but for each species the changes were forced to be always either

161   positive or negative (Fig.1c). Due to their directional character, species that went extinct in

162   the time series could not re-enter the community. The minimum change between time steps

163   was set to one. Finally, all of the time series values were rounded to the closest integer. For

164   the sake of clarity in this paper we replace the term stochasticity, which is introduced into

165   the time series by v, with *temporal variability* and thus avoid confusing it with the terms

166   referring to the three different types of dynamics (constant, stochastic, directional).

167

168 We constructed communities that were exclusively composed of constant species

169 (const100), stochastic species (stoch100) and directional species (dir100), as well as

170 communities that were composed of 25 and 75%, 50 and 50% and 75 and 25% species of

171 two given types. For example, community const50stoch50 was composed of 50% constant

172 and 50% stochastic species. Among the directional species in a given community, one half

173 was assigned an increasing trend, and the other half a decreasing one. For all species in a

174 given community s had the identical value. Thus, we constructed communities with a range

175 from very low to very high temporal variability. No attempt was made to simulate

176 communities with a converging dynamic, that is, communities that return to a state of one

177 of the early sample dates, which should yield a significant negative slope according to

178 Collins et al. (2000).

179

180 Data transformation

181

182 In using Euclidean distance based on the absolute abundances (ED_{abs}) as a distance

183 measure, any changes in species abundances in the same direction that do not change

184 relative abundance patterns—e.g., all species increase their population size by 10%—will

185 lead to increasing dissimilarity over time and yield significant TLA slopes. It is, thus,

186 difficult to disentangle the abundance component and the compositional component. We

187 assume that in most cases it is desirable to model changes in abundance and changes in

188 composition separately, and in these cases distance measures other than ED_{abs} should be

189 used. Furthermore, the comparison of temporal trends of communities with different

190 numbers of individuals is hampered since higher numerical abundance leads to larger ED_{abs}

191 between years and, thus, to steeper TLA slopes. Last but not least, ED_{abs} can cause the

192 well-known species-abundance paradox: two sites having no species in common may be

193 more similar than two sites sharing species but with different abundances (Legendre and

194 Legendre 1998[Legendre and Legendre 1998]). Based on a preliminary evaluation of

195 different data transformations to circumvent the undesired properties of ED_{abs} (Online

196 Resource 1) we applied the Hellinger transformation $N'_{ij} = \sqrt{(N_{ij}/\sum N_{ij})}$ where N_{ij} is the

197 population size of species i in year j, and ΣN_{ij} is the sum of individuals across all species in

198 year j (Legendre and Gallagher 2001[Legendre and Gallagher 2001]). TLA based on

199 Hellinger distance (HD), i.e., Euclidean distance of Hellinger transformed data, has the

200 properties of (i) not being sensitive to changes in absolute abundance while patterns of

201 relative abundance stay constant, (ii) making assemblages directly comparable independent

202 of their species richness, and (iii) being sensitive also to rare species (Online Resource 1).

203 Hellinger distance is not mandatory for TLA; depending on the research question other

204 distance measures might be preferred for example when abundance effects are to be

205 included or when more emphasis is to be given to dominant species (Online Resource 1).

206

207 Time lag analysis

208

209 Community change was replicated 1000 times for each combination of composition (const

210 100, stoch100, dir100, const25stoch75, const50stoch50, const75stoch25, const25dir75,

211 const50dir50, const75dir25, stoch75dir25, stoch50dir50, stoch75dir25), temporal

212 variability ($v = 0.001, 0.0025, 0.005, 0.0075, 0.01, 0.025, 0.05, 0.075, 0.1, 0.2, 0.3, 0.4,$

213 0.5) and time series length (20 and 100), yielding a total of $12*13*2 = 312\ 000$ simulation

214 runs. For each simulated community we fitted the linear model $HD = a + b*\text{sqrt}(lag)$. For a

215 time series of length n there are $(n^2 - n)/2$ possible distance values. The time series of

216   length 20 and 100 thus produce 190 (19 values for lag 1, 18 values for lag 2, …, 1 value

217   for lag 19) and 4950 distance values, respectively. The inflated number of degrees of

218   freedom and the lack of independence between the data points are problematic for the

219   determination of the statistical significance of the slope. Following Thibault et al.

220   (2004[Thibault et al. 2004]) we applied a Monte Carlo permutation procedure and (i)

221   permuted the order of the year columns in the data matrix, (2) calculated the slope b for

222   each permutation, and (3) compared the resulting distribution of slopes with the slope for

223   the original data matrix by dividing the number of random slopes greater than the original

224   TLA slope by the number of permutations. Doing this for all 312 000 simulated

225   communities, however, would have increased the number of calculations to an unfeasible

226   amount. We therefore limited significance testing to a 100-fold randomisation of 100

227   simulated communities for each combination of community composition, temporal

228   variability and time series length, which still added up to 3 120 000 permutation runs.

229   Slopes were regarded significant when the error probability P was equal to or < 0.05. The

230   highest level of significance attainable with the applied Monte Carlo permutation

231   procedure was $P < 0.01$, when all random slopes were lower than the original TLA slope.

232   All simulations were performed with the R language and environment for statistical

233   computing (R Development Core Team 2010[R Development Core Team 2010]).

234

235   **Results**

236

237   Community const100 did not show significant slopes (Figs. 2 and 3) whereas the slopes of

238   stoch100 (Figs. 2 and 4) and directional100 (Figs. 3 and 4) were highly significant

239   ($P < 0.01$) at any given level of temporal variability. Even if a small proportion of species

240 in the communities containing constant species was stochastic or directional, p decreased

241 rapidly and the slopes attained high significance ($P < 0.01$) in almost all cases (Figs. 2 and

242 3). For the mixture of constant and stochastic species with a temporal variability of

243 $v \leq 0.05$ these slopes were very low ($b < 0.02$) but still highly significant ($P < 0.01$) (Fig.

244 2a-d). The only exception was community constant75stoch25 (composed of many constant

245 species and few stochastic species) whose p varied between 0.25 and 0.45 (Fig. 2c). All

246 communities composed of stochastic and directional species had highly significant

247 ($P < 0.01$) slopes (Fig. 4).

248

249 Slopes became steeper with increasing temporal variability; at the highest levels of

250 variability, however, slopes tended to decrease. This pattern was more pronounced for the

251 longer (Fig. 2b, 3b, 4b) than for the shorter time series (Fig. 2a, 3a, 4a). Slopes were

252 clearly dependent on time series length and were generally higher in the shorter time

253 series, particularly in the communities with higher temporal variability (Figs. 2a-b, 3a-b

254 and 4a-b).

255

256 **Discussion**

257

258 The results confirm our hypothesis that stochastic change other than a white noise process

259 would lead to significant slopes when regressing community dissimilarity over increasing

260 time lags. Collins et al. (2000) also presented simulated stochastic data and concluded that

261 the resulting slope would be non-significant (Collins et al. 2000, Fig. 4). Their trajectories

262 through time, however, were constructed in a different way, randomly choosing the

263 abundance for each species at each point in time. For natural populations this rarely seems

264 to be the case as has been shown by Inchausti and Halley (2002[Inchausti and Halley

265 2002]). The Markov chains of abundance of "stochastic species" used in our study

266 represent a more realistic realisation of the time series of animal populations that have

267 neither a stable mean ("constant species") nor tend to approach an attractor of high or low

268 abundance ("directional species") but are governed only by random fluctuations (Williams

269 et al. 2002[Williams et al. 2002]). Consequentially the significance level of the slope does

270 not allow the discrimination between communities with directional and stochastic change.

271 Both processes—directional change of constituent species and stochastic change according

272 to a Markov process—lead to directional changes in species composition and these are

273 identified as such by TLA even when the changes between sampling dates are very small.

274 Applied to real community data, TLA will yield significant slopes for communities

275 characterised by directional and stochastic dynamics, and will discriminate them from the

276 communities that are almost entirely composed of species with constant population sizes

277 (Figs. 2 and 3) and communities whose species abundances are governed by a white noise

278 process, such as in the simulations of stochastic dynamics by Collins et al. (2000).

279

280 Since significance will be achieved in almost any case, the slope itself remains as the most

281 important measure to judge the dynamic of a community undergoing changes in species

282 composition. When temporal variability is low, the slope rarely exceeds values of 0.05; in

283 the communities composed of constant and stochastic species it even remains below 0.02.

284 The maximum values attained for higher temporal variability fall between 0.15 and 0.25

285 (Fig. 2a, 3a, 4a); only community stoch75dir25 yielded a slope even larger than 0.25 (Fig.

286 4a). The range of slopes observed in the simulations correspond quite well to the empirical

287 Hellinger-distance based TLA slopes of bird communities (Kampichler et al., in

preparation). Bird communities from pristine ecosystems have been described as being remarkably stable (primeval temperate forests: [Enemar et al. 2004]Enemar et al. (2004);[Wesolowski et al. 2010] Wesołowski et al. (2010); Scandinavian alpine vegetation: [Svensson 2006]Svensson (2006)). Their slopes range from 0.02 to 0.04 which would be consistent with the assumption that these communities are mainly composed of a mixture of constant species and stochastic or directional species with low temporal variability. Slopes from successional forests (deciduous forest on abandoned fields: [Kendeigh 1982]Kendeigh (1982); spruce regrowth after clearcutting: Hall (1984)) with a considerable number of directional bird species (early species that later become locally extinct, species that enter the community later and continually increase their abundance) show slopes steeper than 0.1. A closer interpretation of the slopes seems to be hampered by the lack of a monotonous relationship between temporal variability and slope, as shown by the undulating curves in Figs. 3b and 4b. This is, however, due to the fact that in this simulation the directional species continue to increase or decrease their abundance throughout the entire time series which might be the case in short time series but cannot be assumed to be very realistic for long real-world time series. At high levels of temporal variability the decreasing directional species very rapidly become extinct while the remaining species continue increasing; relative abundance patterns change only slightly for the rest of the time series and thus lead to a lower TLA slope.

A more serious complication is that longer time series yield lower slopes than shorter ones, particularly when temporal variability is high (Fig. 2b, 3b, 4b), although the generation process of the time series of the constituent species is identical. To explore this hitherto unreported behaviour of TLA we simulated another 6000 communities—2000 each for the

13

312   compositions const50stoch50, const50dir50 and stoch50dir50—for time series lengths

313   (TSL) increasing from 10 to 200 in steps of 10 (ten replicates for each TSL, temporal

314   variability set at $v = 0.1$) and regressed their slopes on TSL. TLA slopes vary considerably

315   with the TSL; their relationship is quite complicated and cannot be approximated by a

316   linear model but only with a segmented regression approach (Muggeo 2003), fitting

317   separate line segments to different TSL intervals (Fig. 5a, 5c, 5e). Standardising TSL and

318   thus regressing Hellinger distance on sqrt(lag)/max(sqrt(lag)) eliminates much of the

319   nonlinearity of the relationship between slope and TSL (no segmented regression could be

320   fitted). On the one hand, this would permit the direct comparison of community data with

321   different TSL; on the other hand, comparability with conventional TLA studies becomes

322   lost due to the changed slope (compare the slopes on the y-axes of Fig. 5a, c and e with

323   Fig. 5b, d and f). Consequentially, caution has to be exercised when TLA is used for the

324   comparison of communities where time series length differs.

325

326   There are a number of alternatives to distance-based time lag analysis, such as redundancy

327   analysis based on principal coordinates of neighbourhood matrices (Borcard et al. 2004) or

328   asymmetric eigenvector maps (Blanchet et al. 2011). These methods were developed for

329   the analysis of spatial patterns but can easily be adopted for time series analysis (Angeler

330   et al. 2009). These direct canonical ordination approaches conserve the taxonomic identity

331   of species during the calculation of distance metrics and allow identification of the species'

332   contributions to the patterns of temporal change. Thus it has been argued that they are

333   superior to distance based methods (Angeler et al. 2009). We suspect that distance and

334   ordination methods do not exclude each other but mutually complement the other. The

335   merits of TLA compared to these powerful methods are its computational ease, its easy

336 comprehensibility for an audience not experienced in interpreting ordination results, and

337 the possibility of characterising and comparing the temporal dynamics of large numbers of

338 communities with a single measure (the slope along with its significance level) without

339 being drowned in masses of detailed information. We thus feel that further methodological

340 improvements of TLA are desirable and necessary.

341

342 **Acknowledgements**

343

345

346 **References**

347

348 Angeler DG, Viedma O, Moreno JM (2009) Statistical performance and information

349 content of time lag analysis and redundancy analysis in time series modelling. Ecology

350 90:3245-3257 doi: 10.1890/07-0391.1

351

352 Blanchet FG, Legendre P, Maranger R, Monti D, Pepin P (2011) Modelling the effect of

353 directional spatial ecological processes at different scales. Oecologia 166:357-368

354

355 Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial

356 structure of ecological data at multiple scales. Ecology 85:1826-1832.

357

358 Collins SL, Micheli F, Hartt L (2000) A method to determine rates and patterns of

359 variability in ecological communities. Oikos 91:285–293 doi: 10.1034/j.1600-

360   0706.2000.910209.x

361

362   Cowpertwait PSP, Metcalfe AV (2009) Introductory Time Series with R. Springer,

363   Heidelberg doi: 10.1007/978-0-387-88698-5

364

365   Enemar A, Sjöstrand B, Andersson G, von Proschwitz T (2004) The 37-year dynamics of a

366   subalpine passerine bird community, with special emphasis on the influence of

367   environmental temperature and *Epirrita autumnata* cycles. Ornis Svecica 14:63–106

368

369   Hall GA (1984) A long-term bird population study in an Appalachian spruce forest. Wilson

370   Bulletin 96:228-240

371

372   Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton

373   University Press, Princeton

374

375   Inchausti P, Halley J (2002) The long-term temporal variability and spectral colour of

376   animal populations. Evol Ecol Res 4:1033–1048

377

378   Kampichler C, Geissen V (2005) Temporal predictability of soil microarthropod

379   communities in temperate forests. Pedobiologia 49:41–50 doi:

380   10.1016/j.pedobi.2004.07.011

381

382   Kendeigh SC (1982) Bird Populations in East Central Illinois: Fluctuations, Variations, and

383   Development over a Half-Century. Illinois Biological Monographs 52, University of

384   Illinois Press, Champaign.

385

386   Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination

387   of species data. Oecologia 129:271-280 doi: 10.1007/s004420100716

388

389   Legendre P, Legendre L (1998) Numerical Ecology, 2nd edn. Elsevier, Amsterdam

390

391   Lundberg P, Ranta E, Ripa J, Kaitala V (2000) Population variability in space and time.

392   Trends Ecol Evol 15:460-464 doi: 10.1016/S0169-5347(00)01981-9

393

394   Magurran AE, Baillie SR, Buckland ST, Dick JMcP, Elston DA, Scott EM, Smith RI,

395   Somerfield PJ, Watt AD (2010) Long-term datasets in biodiversity research and

396   monitoring: assessing change in ecological communities through time. Trends Ecol Evol

397   25:574-582 doi: 10.1016/j.tree.2010.06.016

398

399   Magurran AE, Henderson PA (2010) Temporal turnover and the maintenance of diversity in

400   ecological assemblages. Phil Trans R Soc B 365:3611–3620 doi: 10.1098/rstb.2010.0285

401

402   McArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton

403   University Press, Princeton

404

405   Meyn SP, Tweedie RL (1993) Markov Chains and Stochastic Stability. Springer, London

406

407   Muggeo VMR (2003) Estimating regression models with unknown break-points. Stat Med

408   22:3055–3071

409

410   Muggeo VMR (2008) segmented: an R package to fit regression models with broken-line

411   relationships. R News 8 (1):20-25 URL http://cran.r-project.org/doc/Rnews/

412

413   Pfister CA (2006) Concordance between short–term experiments and long–term censuses

414   in tide pool fishes. Ecology 87: 2905–2914 doi: 10.1890/0012-

415   9658(2006)87[2905:CBSEAL]2.0.CO;2

416

417   R Development Core Team (2010) R: A language and environment for statistical

418   computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-

419   project.org

420

421   Ricklefs RE (2003) A comment on Hubbell's zero-sum ecological drift model. Oikos

422   100:185-192 doi: 10.1034/j.1600-0706.2003.12018.x

423

424   Rull V, Vegas-Vilarrúbia T (2011) What is long-term in ecology? Trends Ecol Evol 26:3-4

425   doi: 10.1016/j.tree.2010.10.002

426

427   Silvertown J, Poulton P, Johnston E, Edwards G, Heard M, Biss PM (2006) The Park Grass

428   Experiment 1856-2006: its contribution to ecology. J Ecol 94:801–814 doi: 10.1111/j.1365-

429   2745.2006.01145.x

430

431   Svensson S (2006) Species composition and population fluctuations of alpine bird

432 communities during 38 years in the Scandinavian mountain range. Ornis Svecica 16:183–

433 210

434

435 Thibault KM, White EP, Ernest SKM (2004) Temporal dynamics in the structure and

436 composition of a desert rodent community. Ecology 85: 2649–2655. doi: 10.1890/04-0321

437

438 Wesołowski T, Mitrus C, Czeszczewik D, Rowiński P (2010) Breeding bird dynamics in a

439 primeval temperate forest over thirty-five years: variation and stability in the changing

440 world. Acta Ornithologica 45:209–232 doi: 10.3161/000164510X551354

441

442 White EP, Adler PB, Lauenroth WK, Gill RA, Greenberg D, Kaufman DM, Rassweiler A,

443 Rusak JA, Smith MD, Steinbeck JR, Waide RB, Yao J (2006) A comparison of the

444 species/time relationship across ecosystems and taxonomic groups. Oikos 112:185-195

445 doi: 10.1111/j.0030-1299.2006.14223.x

446

447 Williams BK, Nichols J, Conroy M (2002) Analysis and Management of Animal

448 Populations. Academic Press, San Diego

449   Figure captions

450

451   **Fig. 1.** Sample time series of constant (A), stochastic (B) and directional (C) species with

452   varying temporal variability, characterised by the scaling factor v. For ease of comparison

453   all sample time series share the same initial value $N_0 = 50$. The scaling factor v used for

454   constructing the time series ranges from 0.001 to 0.5 (see text for details). Note the

455   different scaling of y-axes.

456

457   **Fig. 2.** Time lag analysis of simulated communities composed of constant and stochastic

458   species in time series of a, c) length 20 and b, d) length 100 with different temporal

459   variability, determined by the scaling factor v used in the generation of the species time

460   series (see text for description). Reported are a, b) the slopes of the regression lines of

461   Hellinger distance on square root of time lag and c, d) the error probability, P, as

462   determined by a Monte Carlo permutation procedure.

463

464   **Fig. 3.** Time lag analysis of simulated communities composed of constant and directional

465   species in time series of a, c) length 20 and b, d) length 100 with different temporal

466   variability, determined by the scaling factor v used in the generation of the species time

467   series (see text for description). Reported are a, b) the slopes of the regression lines of

468   Hellinger distance on the square root of time lag and c, d) the error probability, P, as

469   determined by a Monte Carlo permutation procedure.

470

471   **Fig. 4.** Time lag analysis of simulated communities composed of stochastic and directional

472   species in time series of a, c) length 20 and b, d) length 100 with different temporal

473   variability, determined by the scaling factor v used in the generation of the species time

474   series (see text for description). Reported are a, b) the slopes of the regression lines of

475   Hellinger distance on the square root of time lag and c, d) the error probability, P, as

476   determined by a Monte Carlo permutation procedure.

477

478   **Fig. 5.** Relationship between TLA slope for different time series lengths for communities

479   composed of equal proportions of a, b) constant and stochastic species , c, d) directional

480   and stochastic species, and e, f) constant and directional species (E, F). The scaling factor v

481   used for determining temporal variability in the generation of the time series was set at 0.1

482   (see text for description). Panels on the left (a, c, e) are based on conventional TLA, panels

483   on the right (b, d, f) are based on TLA with Hellinger distance regressed on

484   sqrt(lag)/max(sqrt(lag)) instead on sqrt(lag). Break-points and slopes in panels a), c) and e)

485   were determined by segmented regression (Muggeo 2003[Muggeo 2003]) using the

486   package `segmented` (Muggeo 2008[Muggeo 2008]) for the R language and environment

487   for statistical computing (R Development Core Team 2010[R Development Core Team

488   2010]). Regression lines in panels b), d) and f) are not significant ($P > 0.05$), significant at

489    $P < 0.01$ and significant at $P < 0.001$, respectively.