Running head: Reindeer population dynamics

Title: The pursuit of populations collapses – long-term dynamics of semi-domestic reindeer in

Sweden.

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List of online supplements:

Supplement S1: Historic data (1945-1965).

Supplement S2: Density independent vs. the Ricker model – detailed information.

Supplement S3: AR(2) vs. AR(1) model – detailed information.

Supplement S4: ANOVA – detailed information.

Supplement S5: ANCOVA – detailed information.

Supplement S6: Spatial covariance.

Supplement S7: Descriptive statistics from the Swedish Saami Parliament.

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1 ABSTRACT

2 Spatiotemporal population fluctuations are an effect of several factors working in concert –

3 making it difficult to disentangle the impacts of single factors. Reindeer populations affect the

4 structure and functioning of Arctic and Sub-Arctic ecosystems. The management of these

5 populations and factors affecting them—e.g. habitat loss, fragmentation, climate change—have

6 been investigated in detail. Currently, there is a discussion on the viability of reindeer populations

7 and reindeer herding as a lifestyle, especially in Fennoscandia, where recent reports suggest an

8 industry in a state of crisis, including collapse or declining reindeer populations. We investigated

9 the population dynamics of Swedish semi-domestic reindeer from 1945 to 2012 at the reindeer

10 herding district-level (Sameby), with an aim to identify possible population collapses or declines.

11 We also explored if there were spatial trends and synchrony in population dynamics across

12 latitudinal-longitude gradients for two distinct periods: 1945-1965 and 1995-2012. Nonetheless,

13 we found no evidence of large-scale reindeer population declines and no visible synchrony across

14 adjacent populations. Our findings were unexpected as both reindeer populations and the

15 pastoral lifestyle are under threat due to increased habitat loss, predation, fragmentation and

16 climate change.

17 **INTRODUCTION**

18 Biological populations are regulated and limited (e.g. Turchin 1995, Sinclair and Pech 1996)

19 through a combination of density dependent (DD) factors, such as e.g. food limitation, and

20 density independent (DI) climatic factors (cf. Bonenfant *et al.* 2009 for a review of terrestrial large

21 herbivores). Both DD and DI affect populations through demographic processes acting at the

22 individual level; changes in population numbers/density may thus be viewed as a byproduct of

23 factors affecting individuals. For many long-lived animals, the effect of both DD and DI operate

24 through body mass or other state variables related to body condition (reviewed in Sæther 1997,

25 Gaillard *et al.* 2000, Lummaa and Clutton-Brock 2002). Body mass, for example, varies according

26 to habitat quality (Pettorelli *et al.* 2002, Reimers 1972), population density/abundance and climate

27 (Festa-Bianchet *et al.* 1998, Hewison *et al.* 2002, Clutton-Brock and Coulson 2002, Albon *et al.*

28 1983, Albon *et al.* 1987, Clutton-Brock *et al.* 1996, Rose *et al.* 1998). Of special importance for

29 understanding population dynamics is that the smallest individuals are less likely to reproduce

30 (e.g. Sæther *et al.* 1996, Sand 1996, Rönnegård *et al.* 2002), give birth later (Bårdsen *et al.* 2009,

31 Flydal and Reimers 2002), and their offspring are less viable as they are more prone to starvation

32 and predation than larger ones (Clutton-Brock *et al.* 1996, Tveraa *et al.* 2003).

33 For reindeer (*Rangifer tarandus*) in Norway, the relationship between winter weather

34 conditions and fitness is nonlinear (e.g. Bårdsen *et al.* 2014), which has consequences for the

35 observed population dynamics (Bårdsen *et al.* 2011). At one hand, a combination of a harsh

36 winter and low autumn body mass negatively affects both reproduction and survival (Tveraa *et al.*

37 2003, Skogland 1985, Aanes *et al.* 2002, Aanes *et al.* 2000). On the one hand, benign winters do

38 not positively affect survival and reproduction to a similar extent (Fauchald *et al.* 2004, Bårdsen *et*

39 *al.* 2008, Bårdsen *et al.* 2009). Such effects might give rise to strong interactions between DD and

40 DI factors–and in northern ecosystems it has been shown that harsh winters affect individuals

41 more at high than at low population density (Bårdsen *et al.* 2014). Consequently, there are good

42 reasons to expect that the causal mechanisms underlying patterns in population dynamics vary

43 both temporally (Coulson *et al.* 2001) and spatially (Tveraa *et al.* 2013, Lundqvist *et al.* 2009) as

44 well as across populations and species (Coulson *et al.* 2000).

45   Declines have been reported for many *Rangifer* populations across the Circumpolar North,

46 declines coinciding with changed precipitation levels and raising temperatures (Vors and Boyce

47 2009). The temporal trends for both wild and domesticated *Rangifer* across Fennoscandia and

48 Russia are, however, highly variable as both declining and increasing trends are evident (Uboni *et*

49 *al.* 2016). Temporal trends in semi-domestic reindeer number for the Fennoscandian countries

50 seem rather synchronous during 1980-2000 (Pape and Löffler 2012:Fig. 1), which is even further

51 supported by the fact that population growth rates at the national-level shows positive

52 correlations (Uboni *et al.* 2016). In Sweden the number of reindeer has fluctuated, apparently at

53 the scale of decades, around ~225 000 individuals from 1880-2000 (Moen and Danell

54 2003:Fig.1), to vary between 240 801 to 261 491 animals from 2005 and onwards (Swedish Sami

55 Parliament[1]). Even though the number of reindeer in Norway also has fluctuated, it has generally

56 increased from around World War II and up to recently when reindeer populations have peaked

57 at historical high levels (Tømmervik and Riseth 2011). This trend, however, shows spatial

58 variability–Finnmark, the areas in Norway that currently contains 73% of the total Norwegian

59 population (Anonymous 2014:35), has showed a increase in numbers from 2000 and onwards

60 (e.g. Næss and Bårdsen 2013, Ulvevadet and Hausner 2011). In contrast, the number of reindeer

61 has been more stable in most other regions in Norway during the same time period (Anonymous

62 2014:20), and the dynamics of reindeer populations in Norway has been interpreted to be a result

63 of a combination of climate, vegetation quality and human harvest rates (Tveraa *et al.* 2007).

64 Similar to both Norway and Sweden, the Finnish population increased during the 1980's and then

65 dropped slightly during the 1990's (Kumpula 2001), but has been rather stable since 2000 (pers.

66 comm., the Reindeer Herders' Association in Finland, January 2016).

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[1] https://www.sametinget.se/statistik/renhjorden assessed 12.02.2016.

67   For Fennoscandia in general there is currently a debate on whether the reindeer

68   husbandry as a livelihood is threatened (Pape and Löffler 2012, e.g. Jernsletten and Klokov 2002).

69   For Sweden there has been a growing concern of the reindeer husbandry as being in a state of

70   crisis due to e.g. land use change and conflicts (e.g. Horstkotte 2013, Sandström 2015); increased

71   predation (e.g. Danell 2010, Åhman *et al.* 2014); and/or changing climatic conditions (Pape and

72   Löffler 2012, Löf 2013). In general, livelihood is for nomadic pastoralists intrinsically linked to

73   animal numbers and the pastoral economy is to a large degree predicated on the herd as a source

74   of animal products and money (Næss 2010). There is also a growing body of evidence indicating

75   that herd size is important for buffering climatic variation for pastoralists in general (Coughenour

76   *et al.* 1985, Fratkin and Roth 1990, McPeak 2005, Templer *et al.* 1993) as well as for reindeer

77   herders (Næss and Bårdsen 2010, Næss and Bårdsen 2013).

78   The overall aim of the present study is thus to assess if population dynamics of semi-

79   domestic reindeer have changed during the last 70 years, and more importantly if there are signs

80   of any population collapses (i.e. dramatic reductions in population size) or declines occurring

81   from 1945-1965 to present day at the population level. Moreover, we want to assess if any

82   potential changes in population dynamics are more or less pronounced along latitudinal and

83   longitudinal (mountains to coast) gradients. We use data on the number of animals from Swedish

84   populations (denoted as 'Sameby'; see Appendix S1) of semi-domestic reindeer covering two

85   distinct periods (~30 years apart): (1) 1945-1965; and (2) 1995-2012 in which the latter is official

86   statistics (spatiotemporal trends of abundance and growth rates shown in Fig. 1).

87

88   **METHODS**

89   **STUDY AREA: THE SWEDISH REINDEER HUSBANDRY**

90   Reindeer herding in Sweden is organized in 51 so-called Samebys (Sami villages), which is a legal

91   and geographical unit consisting of members herding together (Fig 1c). Within each Sameby the

92   herders utilize a given area together, and thus represent the unit for defining a population. The

93   shapes of these areas are mostly spanning from northwest in the mountains to southeast towards

94   the coast, with some exceptions being smaller areas within the mountains and some close to the

95   coast. A detailed description of Reindeer herding and management in Sweden is found in

96   Jernsletten (1999) with recent updates at the Sami Parliament webpage (see legends in Fig. 1 for

97   details). Reindeer are migratory in most of the areas (Sandström 2015), using mountain habitats

98   in the west during summer and coniferous forests land in the east during wintertime. Some

99   Samebys are stationary and use forestland during the whole year. Human density is generally low,

100   and the climate is cold with deep snow in winter, although there are variations in environmental

101   conditions among regions (Lundqvist *et al.* 2007).

102

103   **STUDY PROTOCOL**

104   The dataset, which is limited to semi-domestic reindeer herding, contained the following

105   variables:

106   Population-- A factor variable with the name of each population ('Sameby') as levels.

107   Period-- A factor variable with two periods: past (1945-1965) and present (1995-2012).

108   Area-- A continuous variable denoting the current area-size utilized by each population (km^2).

109   We extracted these values using a Geographical Information System (GIS) software using

110   the polygons representing each Sameby acquired from the National Geodata

111   (www.geodata.se/en/).

112   Population abundance (N_t).-- A continuous variable denoting the number of animals after

113   harvest for each population for each year (t; see Supplement S1 for details).

114   Population density ($D_t = N_t\ km^{-2}$).-- A continuous variable denoting the population density at

115   time t for each population.

116   Population growth rate [$\lambda_t = \log_e(N_{t+1}/N_t)$].-- A continuous variable denoting net population

117   growth from one year (t) to the next ($t+1$). This variable is interpreted as follows: (1) $\lambda_t = 0$

118   means no change in population abundance from t to $t+1$ (i.e. $N_{t+1} = N_t$); (2) $\lambda_t < 0$ means

119   population increase as $N_{t+1} < N_t$; and (3) similarly $\lambda_t > 0$ means population decrease.

120   Latitude [decimal degrees North].-- A continuous variable denoting geographic coordinate for

121   the centroid of each Sameby polygon (population) along a north-south gradient.

122   Longitude [decimal degrees East].-- Same as longitude except that it provided the geographic

123   coordinate along an east-west gradient.

124

125   Additionally, we extracted the following variables, for each of the two period, by fitting the

126   Ricker population model (Morris and Doak 2002) and time series analyses to the λ_t (see

127   MODELLING POPULATION DYNAMICS section below):

128   Intrinsic growth (r).-- The theoretic population growth when density is zero (from the Ricker

129   model).

130   Carrying capacity (K).-- The density that corresponds to expected zero population growth

131   (estimated from the Ricker model: Morris and Doak 2002).

132   Sigma (σ_R).-- Even though this variable represents the model's unexplained variance, i.e. the

133   residual Standard Error (SE), it can be used as a rough proxy on how much populations are

134   perturbed by climate and other stochastically variable factors (from the Ricker model).

135    $1-\beta_1$.-- The first-order autoregressive (AR) coefficient in which negative values imply direct

136   negative density dependence (from the time series analyses).

137   β_2.-- The second-order AR coefficient where negative values imply lagged negative density

138   dependence (from the time series analyses).

139   Sigma^2 (σ_{TS}^2).-- Unexplained variance (from the time series analyses).

140

141   Statistical analyses and plotting were carried out in R (R Core Team 2013), all tests were two-

142   tailed and the null-hypothesis was rejected at an a-level of 0.05.

143

MODELLING POPULATION DYNAMICS

144

Density independence vs. the Ricker model

145

146 We fitted the Ricker model, which is a model that predicts λ_t as function of population density

147 (ind. km^{-2}), to the time series data for each population for the past and present period separately

148 in order to estimate the two parameters of interest (e.g. Morris and Doak 2002). In this analysis

149 we used $\log_e(\lambda_t)$ as the response and D_t as the only predictor using the 'nls' function in the library

150 'nlme' (Pinheiro *et al.* 2012), an approach similar to that applied by Hanssen et al. (2013, see also

151 Pinheiro and Bates 2000, Zuur et al. 2009). Similarly, we fitted a density independent model,

152 where we only estimated the intercept [i.e. the average $\log_e(\lambda_t)$; Morris and Doak 2002], and

153 assessed if this model provided better fits to the data as compared to the density dependent

154 Ricker model (Supplement S2). As the Ricker model had good support in the data for 89% of the

155 populations in the past and in all populations in the present, we used parameters from the Ricker

156 model for all populations in further analyses of population dynamics.

157

Autoregressive time series analyses

158

159 Time series analyses of population growth rates (λ_t) were modelled using second-order

160 autoregressive models [AR(2), fitting an ARIMA($p = 2$, $d = 0$, $q = 0$) model using the arima

161 function]. The linear predictor of the models included direct (t) and delayed (t-1) density

162 dependence. We, thus, estimated the first- and second-order AR coefficient (1-β_1 and β_2,

163 respectively). This approach is similar to Tveraa et al. (2007) except that we did not include any

164 effect of climate as a covariate in our analyses, which is due to our lack of good measures of

165 climate for the past. Similar to the approach above we assessed if the a first-order autoregressive

166 model [AR(1)] provided a better fit to the data as compared to the AR(2) model (Supplement S3),

167 but as the AR(2) model had good support in the data for all populations and periods, we used

168 estimates from this model in further analyses.

169

STATISCAL ANALYSES: ESTIMATED PARAMETERS

Past vs. present dynamics

We performed Analysis of Variances (ANOVAs) in order to check if the average value for each

parameter estimate from the above models, i.e. r, K, σ_R, 1-β_1, β_2 and σ_{TS}, differed between the two

periods (Supplement S4). Subsequently, we applied multiple linear regression models to estimate

the extent in which the same parameter estimates differed between the two periods. In these

linear regressions, recent estimates, i.e. estimates using data from 1995-2012, was predicted based

on their initial values (1945-1965)[2]. For the intrinsic growth rate this baseline model was, for

example, defined as follows: $r_{1995\text{-}2012} = a + \beta r_{1945\text{-}1965} + \varepsilon$, where a, β and ε represents the estimated

intercept, slope, later on referred to as the models' key parameters, and the models' normally

distributed error (residual SD), respectively. Additionally, we included longitude and latitude as

potential covariates as well as we assessed if the addition of *a priori* expected interactions

improved the fit of the models (details provided in Supplement S5).

We chose to perform these analyses in such a manner for several reasons. First, as our

primary objective was to assess if population dynamics differed between the two periods, we

wanted to assess the magnitude of these slope estimates, which represents an 'estimation

problem', as these effect sizes are reported irrespectively of whether they were statistically

significant or not. Consequently, our predictions were tested statistically by estimating β: the

effect of the initial values for the parameters (all continuous predictors were centred: i.e.

subtracting their average values) as we wanted to assess if populations associated with large initial

values still, on average, were associated with larger values. Second, while the main purpose of this

part was to estimate the magnitude of the key parameter, the second part represents a 'model

selection problem' as we wanted to know if the effect size of other potential terms (Supplement

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[2] It was, for example, reasonable to *a priori* expect a large K in the past to be associated with a large K in the present
for the same population.

193   S5) were large enough to justify their inclusion in the models used for drawing inference (e.g.

194   Anderson *et al.* 2000).

195   As a final test of whether any population collapses have taken place at the Sameby-level,

196   we assessed if we could relate population-specific median population growth rates and density

197   from the present to similar values in the past. A lack of such a relationship or a positive one gives

198   no support of an average decline, and hence an absence of an overall collapse. A negative

199   relationship indicates a decline, and a steep negative relationship will imply a collapse.

200

201   **Spatial autocorrelations**

202   We estimated univariate spatial spline correlograms of both the estimated parameters from the

203   Ricker and the autoregressive models (past and present separately) to test if neighbouring

204   populations to a larger degree behaved similar as distant populations (Supplement S6). Moreover,

205   we extended this using spatial cross-correlation to assess if population growth rates in a given

206   year (λ_t) and population density (D_t) co-vary with the growth in other populations, and if such

207   cross-correlations varied as a function of distance between the populations (using the latitude and

208   longitude of each population as input). This was done using spline correlogram (review:

209   Bjørnstad *et al.* 1999) with the default input for the spline.correlog-function in the ncf library

210   both for the univariate data [estimates from the Ricker and AR(2) models] and the multivariate

211   data on population growth rates (Bjørnstad 2013).

212

213   **RESULTS**

214   **PAST VS. PRESENT DYNAMICS**

215   In the ANOVAs, neither intrinsic growth rate (r) nor the carrying capacity (K) was significantly

216   different across the periods (Supplement S4). Nonetheless, both the first- and second-order

217   autoregressive coefficients were, on average, more negative in the past compared to the present

218   (Fig. 2). Both the Ricker- and the AR(2)-models explained a larger proportion of the growth rates

219   in the present compared to the past (Supplement S4). This might be an effect that the most

220   recent data are expected to be less biased and more precise than the data from the past.

221   In the multiple regressions of the Ricker estimates, neither todays' intrinsic growth ($r_{1995\text{-}2012}$)

222   nor the unexplained variance ($\sigma_{R1995\text{-}2012}$) was dependent on their past values, while todays'

223   carrying capacity ($K_{1995\text{-}2012}$) was positively related to past values ($K_{1945\text{-}1965}$: Table 1, Fig. 3).

224   Moreover, $r_{1995\text{-}2012}$ increased and decreased along the west-east and the south-north gradient,

225   respectively (Table 1a), whereas for $K_{1995\text{-}2012}$ the relationships with longitude and latitude showed

226   opposite trends (Table 1b, Fig. 3). Neither longitude nor latitude was included in the selected

227   model of $\sigma_{R1995\text{-}2012}$ (Supplement S5; Table 1c). As the predictors were centred, significantly positive

228   intercepts, which we documented for $\sigma_{R1995\text{-}2012}$ and $r_{1995\text{-}2012}$ (Table 1a,c), mean that these responses

229   were positive when the predictor(s) were kept at their averages (Fig. 3).

230   In the multiple regressions of the AR(2) estimates, we documented a decreased direct

231   density dependence, i.e. more positive values for 1-β_1, in the north compared to the south (Fig.

232   4), whereas there was no effect of initial values (Table 2a). The only effect included in the

233   analyses of delayed density dependence, β_2, was its initial value, and no significant effect of the

234   key parameter (Table 2b). The precision of the autoregressive models ($\sigma_{TS}^2{}_{1995\text{-}2012}$), however,

235   showed a positive relationship with latitude and a negative relationship with longitude keeping all

236   other predictors at their average values (Table 2c). This means that the model explained a larger

237   proportion of the variance in the response in the south, i.e. the models were more precise, than in

238   the north, and the precision increased along the east-west gradient. The negative latitude-

239   longitude interaction (Table 2c), however, implies that negative effect of latitude became

240   increasingly more negative further north and/or that the positive effect of longitude became

241   weaker further west.

242   There was no evidence of a general decline in population-specific median λ_t, both within

243   and across periods (Fig. 5A), and this was also apparent judging from the Pearson's product-

244   moment correlation: -0.060 [95% Confidence Intervals (CI) = -0.381, 0.274; degrees of freedom

245   (df) = 34]. Moreover, fitting linear models with only the intercept revealed that the average of

246   these median λ_t were not significantly different from zero within each period: -0.003 (95% CI = -

247   0.009, 0.003; df = 35) in the past; and 8.6×10^{-4} (95% CI = -0.007, 0.009; df = 39) in the present.

248   Looking into the individual populations even further does not reveal any population collapses

249   neither from the past to the present. Four populations experienced a consistent decline in the

250   past (but are still present today), whereas the rest experienced no consistent changes in their

251   growth rates as the range between 25-75$^{\text{th}}$ quantiles contained zero (i.e. neither positive nor

252   negative growth) except one that experienced a consistent increase (Fig. 5A). At present,

253   however, none experienced negative growth, but one experienced a consistent increase (Fig. 5A,

254   see also Fig. 1). Similar analyses revealed that average density was similar across the periods: 0.948

255   animal km^{-2} (95% CI = 0.728, 1.168; df = 35) in the past; and 1.007 (95% CI = 0.841, 1.173; df =

256   39) in the present. The relationship between median density across periods was, however,

257   positive (Fig. 5B) judging from the correlations: 0.772 (95% CI = 0.594, 0.878; df = 34).

258

259   **SPATIAL AUTOCORRELATIONS**

260   The analyses using spatial spline correlograms revealed no evidence of any spatial autocorrelation

261   for the estimates neither from the Ricker models nor the AR(2) models–a finding that was similar

262   for both periods (Supplement S6). The similar multivariate analyses revealed no evidence of any

263   spatial autocorrelations for neither population growth rates nor density neither in the past nor in

264   the present (Fig. 6).

265

266   **DISCUSSION**

267   This study shows no evidence of general collapses in Swedish populations of semi-domestic

268   reindeer or declines in the number of reindeer, even though several authors have concluded

269   otherwise for specific study populations (e.g. Danell 2010, Åhman *et al.* 2014), especially at the

270   southern edge of their distribution (Jernsletten and Klokov 2002:5). In fact, we documented few

271   indications of changed dynamics comparing 1995-2012 with 1945-1965, and the result from this

272   study indicates that the reindeer husbandry is in better conditions at present compared to post

273   World War II. First, we observed that populations were more regulated in the past than they are

274   now as the coefficients of both 1) direct ($1-\beta_1$) and 2) delayed (β_2) density dependence was more

275   negative in the past, and 3) today's carrying capacity (K) was positively related to past values.

276   Second, even though average density was similar across periods, there was a positive relationship

277   between past and present population-level density. This relationship was, however, not 1:1, which

278   indicates that low-density populations in the past grew larger than high-density populations from

279   1945-1965 to 1995-2012. Third, the unexplained variance in the models was reduced today

280   compared to just after the war, which might be a consequence of improved data quality over

281   time. Several of the parameters, such as the intrinsic growth (r), K and $1-\beta_1$, varied across latitude

282   and/or longitude gradients, indicating that population dynamics differed in space. Fourth, spatial

283   synchrony between nearby populations was not important at the level of aggregation defining our

284   study. Finally, at the national-level, an increase in the number of reindeer, harvested animals and

285   number of owners from 2000 to present (Supplement S7) indicates a lack of a recent general

286   collapse in the Swedish Reindeer Husbandry.

287

288   **LACK OF POPULATION COLLAPSES**

289   In line with the literature (e.g. Danell 2010, Åhman *et al.* 2014), we expected to find population

290   collapses, or at least declines, when comparing the present to the past. While not evident from

291   our analyses, we cannot rule out the possibility that single herd collapses have occurred.

292   Moreover, since we do not have data at the level of the individual herds (see e.g. Næss and

293   Bårdsen 2010, Næss and Bårdsen 2013), we base our inferences on aggregated data from several

294   herds within our defined populations. This implies that individual herds, i.e. sub-populations

295   within each area, may have experienced declines or collapses (see Åhman *et al.* 2014) not

296 observed in this study due to the coarse scale of resolution. Nevertheless, the number of

297 enterprises (i.e. sub-populations) in Sweden has increased since 1997 (Supplement S7).

298

299 **CONFOUNDING AND LIMITATIONS**

300 As in any observational study, our analyses have limitations because we lack data on, and hence

301 do not control for, a number of factors known to affect population dynamics. Confounding

302 might lead to spurious relationships between predictor(s) and the response as well as to biased

303 estimates (see e.g.: Næss *et al.* 2011, Næss *et al.* 2012 for a discussion pertaining to the reindeer

304 husbandry). To reduce potential confounding we performed confirmatory analyses, which were

305 based on our *a priori* expectations, forming the basis for (Anderson *et al.* 2001 discuss the

306 difference between exploratory vs. confirmatory analysis): 1) the models of population

307 dynamics—commonly used and specifically designed to assess important processes affecting

308 population growth (AR models: e.g. Tveraa et al. 2007; Ricker models: e.g. Hanssen et al. 2013

309 and Ballesteros et al. 2013); and 2) the analyses performed on the estimated parameters extracted

310 from these models. In the analyses of the estimates, we also defined a set of candidate models,

311 representing multiple hypotheses, from which we selected the most parsimonious model and

312 used this model for inference (see e.g. Burnham and Anderson 2002, Anderson 2008).

313

314 **Harvest**

315 Harvest is the most important factor controlled by humans, as harvest is a tool for adjusting herd

316 size as well as animal size and body condition and the distribution of animals across age- and sex-

317 classes (e.g. Lenvik *et al.* 1988) and the inclusion of harvest would strengthen our analyses.

318 Nevertheless, harvest, slaughter carcass mass as well as the age- and sex-distribution is available

319 only for the recent period (e.g. Hobbs *et al.* 2012) and in order to make the parameter estimates

320 from the two periods directly comparable we chose not to include them in our analyses. Harvest,

321 if unaccounted for, always leads to negative bias in population size/density, but given that a

322   constant proportional harvest occurs, population growth rates will be unbiased as a similar

323   proportion of animals will be removed at both N_t and N_{t+1}. Harvest may regulate population

324   numbers, and may thus affect the extent in which populations are sensitive to climatic

325   perturbation (Tveraa *et al.* 2007) as populations may respond stronger if exposed to harsh

326   conditions at high than at low population density. There are situations where growth might be

327   biased, for instance if (as previously documented): 1) herders with large herds harvest

328   proportionally more (Hausner *et al.* 2012, Næss *et al.* 2012) or selects different types of animals to

329   slaughter (e.g. Næss *et al.* 2012); 2) herders make slaughter decisions based on their neighbours

330   behaviour (Næss *et al.* 2012); 3) herders in different areas employ different harvest strategies

331   (Næss and Bårdsen 2015); and/or 3) proportional harvest varies a lot across years (Hausner *et al.*

332   2011). Nevertheless, population collapse would most likely be reflected in slaughter strategies,

333   since an obvious strategy for countering an impending collapse would be for herders to restrict

334   slaughter. In contrast, the total number of harvested calves and meat production per female (for

335   the calf-segment only) increased from 1997 to ca. 2010 while the number of harvested calves per

336   female did not show a similar temporal trend (Supplement S7). In spite of this, harvest is

337   probably the most important unaccounted factor affecting our results.

338

339   **Climate change**

340   Many of the predicted climate changes are expected to happen sooner and to be more

341   pronounced in the northern hemisphere (e.g. Benestad 2007, Tebaldi *et al.* 2006); an area that

342   overlaps with the geographical distribution of *Rangifer*. Rising temperatures and changing

343   precipitation patterns have already been suggested to lead to population declines for *Rangifer*

344   (Vors and Boyce 2009). In the European Arctic and Sub-Arctic, increased occurrences of rain-

345   on-snow and freeze-thaw events have had negative impacts on reindeer demography and

346   population growth (Hansen *et al.* 2011, Solberg *et al.* 2001), and these are the candidates for

347   causing more frequent population collapses (see also Pape and Löffler 2012). For semi-domestic

348   reindeer in Europe, pasture quality (e.g. earlier spring and higher plant biomass: Bårdsen and

349   Tveraa 2012, Tveraa *et al.* 2013) and longer growing season, combined with climate change are

350   predicted to affect the husbandry negatively in Sweden and Norway, neutral in Finland and

351   positively in Russia (Rees *et al.* 2008). The results from this study indicates that: 1) climate change,

352   from 1945-2012, has had little or no negative effect on the Swedish reindeer husbandry; 2)

353   negative and positive effects of changes in climatic conditions cancel each other out; and/or 3)

354   existence of functioning migratory systems allowing animals to access between areas all year

355   round and therefore remain in a better body condition (Moen and Keskitalo 2010).

356

357   **Habitat fragmentation and pasture losses**

358   The reindeer husbandry in Fennoscandia faces challenges as much of their pastures are located

359   close to populated areas and are in conflict with other industries (Jernsletten and Klokov 2002:5).

360   From the 20th century and onwards the reindeer husbandry has been struggling with competing

361   claims over pasture areas concomitant with increasing development of hydroelectric power,

362   mining, wind farms, forestry (Horstkotte 2013), the construction of buildings, roads and railways

363   (Lindquist 2009). In general, these changes resulted in the loss of important pastures utilized for

364   herding (Jernsletten and Klokov 2002), e.g. migration routes between summer and winter, good

365   calving grounds or winter pastures with favorable conditions (Horstkotte 2013). The extent in

366   which these activities have long-term effects on wildlife and livestock is currently uncertain

367   (Benítez-López *et al.* 2010), but Skarin and Åhman (2014:1041) argue that "[o]ne of the major

368   threats for contemporary Saami reindeer husbandry is habitat loss due to direct or indirect impact

369   from competing land use" (see also review by Pape and Löffler 2012).

370   Horstkotte (2013) argues, for example, that the intensification of silviculture has reduced

371   the carrying capacity of winter pastures by reducing the abundance of terrestrial and arboreal

372   lichen. This is important as winters represents a bottleneck for reindeer survival (e.g. Tveraa *et al.*

373   2003, Adams *et al.* 1995), winter conditions affect reproduction (e.g. Bårdsen *et al.* 2010), and it

374   also affects population growth (e.g. Ballesteros *et al.* 2013, Tveraa *et al.* 2007) and viability (e.g.

375   Bårdsen *et al.* 2011). Forest with abundant lichen cover has decreased by 71% in the last 60 years,

376   a change co-occurring with losses of old and open pine (*Pinus sylvestris*) forest while dense and

377   young forest stands have increased (Sandström 2015:paper V, see also Kivinen et al. 2010). It has

378   thus been argued that forestry in Sweden has changed the composition and configuration of the

379   forest landscape mosaic making it less suitable for sustainable reindeer husbandry (Kivinen *et al.*

380   2012).

381   Human disturbances are also known for affecting the behaviour of reindeer (i.e.

382   movements and habitat selection: e.g. Colman *et al.* 2013, Flydal *et al.* 2009, Skarin and Åhman

383   2014) and currently there is a debate if disturbances, such as the establishments of wind mills and

384   power lines, primarily affects reindeer in the construction phase (Colman *et al.* 2013) or if they

385   have more permanent effects due to increased habitat loss and fragmentation (and whether wild

386   and domestic reindeer are affected to similar extents: Skarin and Åhman 2014). In sum, while loss

387   of suitable habitat for reindeer and increased fragmentation has undoubtedly occurred over the

388   course of our study (on the winter ranges in particular: Sandström 2015)—and both these

389   processes probably started before 1945—we did not find any changes in population dynamics of

390   Swedish reindeer populations.

391

392   **Predation**

393   The number of predators in Scandinavia has increased considerably since post World War II

394   (Swenson *et al.* 1994, Wabakken *et al.* 2001, Chapron *et al.* 2014, Jernsletten and Klokov 2002).

395   Moreover, the increase in the number of lynx (*Lynx lynx*) and wolverine (*Gulo gulo*), as they are of

396   most concern for the reindeer husbandry, shows spatial and temporal variability

397   (www.rovdata.no; see also Supplement S7). Predators affect reindeer populations negatively for

398   the obvious reason that they kill individuals. This, however, does not necessarily mean that

399   predation may be strong enough to regulate populations–for that to occur the rate of predation

400   must reach a certain magnitude. In a study from one Sameby (Njarke) in Sweden, Åhman et al.

401   (2014) investigated population changes using mark-recapture method and concluded that

402   predation was the most plausible cause of high female mortality and a subsequent population

403   collapse in one of two sub-herds within the district. Others, however, conclude that predation

404   has initiated local or regional collapses in Sweden (Danell 2010). In large-scale analyses, Hobbs et

405   al. (2012) found that while predation by lynx and wolverine negatively affected both population

406   growth and harvest, the standardized negative effect of predation was smaller than that of

407   latitude at of latitude (both growth rates and harvest was smaller in the North than in the South:

408   see also Næss and Bårdsen 2015 for similar analysis from Norway). They also report the

409   occurrence of negative density dependence on population growth and effects of climate (using

410   the North Atlantic Oscilliation Index: Hobbs *et al.* 2012). These analyses show that predation

411   affects both harvest and population growth, but that predation alone does not tell the full story

412   (see also Tveraa *et al.* 2014 for similar analyses from Norway). Moreover, the number of lynx in

413   the reindeer husbandry area in Sweden has not changed significantly since 1995, whereas the

414   number of wolverines has increased (family groups) while the number of reindeer has increased

415   (at least since 2000; Supplement S7). In sum, even though predation per definition affects prey

416   negatively this effect seems not to be strong enough to induce large-scale population collapses in

417   Sweden.

418

419   **Modernization and changes in policy**

420   Legislation and policy may have major influence on both the strategies applied by herders and the

421   dynamics of the reindeer herd. Reindeer herding in Sweden is governed by the Reindeer

422   Husbandry Act, which regulates who has access to land for reindeer grazing and the organization

423   of the Sameby (Anonymous 1971). The County Administrative Boards defines the borders

424   between the administrative units and a maximum 'ceiling' on how many animals each unit are

425   allowed to have, which represents a major regulative force within the system. Since 1973, the

426 Swedish state supports harvest of reindeer by paying a 'slaughter support' for all reindeer being

427 slaughtered at approved slaughterhouses. Consequently, the reindeer husbandry in Sweden has

428 been subject to substantial changes from the earlier study period until present day.

429 Potential negative impacts, such as increased frequency of winter warm spells, losses and

430 fragmentation of habitat and predation, on the reindeer husbandry may be compensated for by

431 other changes such as better protection against harsh winters, modernization, changes in policy,

432 earlier springs and increased plant production. For instance, Turunen et al.'s (2016:15) study from

433 Finland found that: "[t]o cope with the impacts of adverse climatic conditions, herders increase

434 control over their herds, intensify the use of pasture diversity, take reindeer into enclosures

435 and/or start or intensify supplementary feeding". Supplementary feeding, which was

436 commercially developed in the 1960s (Staaland and Sletten 1991), has been increasingly utilized in

437 Sweden at least from the early 1980's. From 1987, the herders also used feeding to reduce

438 radioactive contamination in reindeer because of the Chernobyl Accident in 1986 (Åhman 1999).

439 The production of reindeer pellets in Sweden has since then increased dramatically, from an

440 annual production of <2 kg to ca. 30 kg per reindeer (pers. comm., Lantmännen and

441 Fodercentralen). Supplementary feeding, which generally is performed during late winter, is

442 known for increasing female reproductive allocation (e.g. increased reproductive success and calf

443 body mass: e.g. Bårdsen 2009, Bårdsen *et al.* 2008, Bårdsen *et al.* 2009) with an consequent

444 positive effects on herd growth (Ballesteros *et al.* 2013). To increase the production, partly

445 necessarily due to increased costs as an effect of modernization by the use of machines and other

446 technical devices, there has also been a transition in herd structure. In 1945-1965, herds usually

447 consisted of 1 male per 2-3 females while few calves were harvested (Norsk-svensk

448 reinbeitekommisjon 1967). At present, however, an average herd in Sweden consists of 9:1

449 female:male ratio, where 72% of the harvested individuals are calves (Supplement S7). In sum,

450 while modernization and herding strategies (see Turunen *et al.* 2016:Table 8 for a list of herder-

451 responses to bad weather conditions) may affect population growth positively, and thus

452 compensate for the negative effects discussed above, they are both costly and labor intensive.

453

454 **FUTURE PROSPECTS**

455 In Fennoscandia there is currently a debate on whether the reindeer husbandry as a livelihood is

456 threatened and for Sweden there has been a growing concern of the reindeer husbandry as being

457 in a state of crisis. While livelihood as a concept is multifaceted and relates to e.g. living

458 conditions, opportunities and capabilities for well-being, resilience and resource base (Shigaeva *et*

459 *al.* 2007) reindeer herders are primarily pastoralists, i.e. people who depend on livestock for most

460 of their income (Berhanu *et al.* 2007, Næss and Bårdsen 2010). In the present study, we found no

461 evidence of any population collapses within the Swedish Reindeer Husbandry since World War

462 II. Furthermore, no evidence of collapses, or crisis, was found when we analysed of the number

463 of owners and slaughtered calved as well as meat production and average carcass mass in Sweden

464 from 1995 and onwards (Supplement S7). We lack data on the spatiotemporal development of

465 several important confounders that potentially could affect our results. This, however, is not that

466 important as the overall impact of most of the co-occurring changes (as discussed above) was *a*

467 *priori* expected to negatively affect population growth even though modernization and changes in

468 policy could potentially have positive impacts. We thus wonder: Why did we not find evidence of

469 population declines when in fact the most apparent changes in the husbandry are expected to

470 affect the number of reindeer negatively? Future studies should look into this question, and the

471 extent in which other indicators of livelihood threats are supporting the hypothesis that the

472 Swedish Reindeer Husbandry are collapsing or in a state of crisis. In particular, we welcome

473 similar analyses as the ones we have performed at level of the individual herder (termed sub-

474 population above).

475

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488

489   *Compliance with Ethical Standards*

490   The use and presentation of the data for the period 1995-2012 has been approved by the Sami

491   Parliament of Sweden. The authors declare that they have no conflict of interest.

492

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763

Figures

Fig. 1. Temporal trends in reindeer abundance (N: A-B) and growth rate (λ: C-D) for each

population (grey lines) for the two periods: past (1945-1965) and present (1995-2012). Thick

blue lines shows the median and the 25th and 75th percentiles for each year. Map of the study

area (E) and the 51 current populations, or Sameby (a geographical unit compromising of

herders that utilize a given area). The study area expands from central to northern Sweden

(www.sametinget.se/underlag). Source: National Geodata (www.geodata.se/en). The current

sizes of each Sameby range from ca. 755 km² to 22 500 km².

Fig. 2. Estimated average coefficients, with precision (± 1 SE; Supplement S4:Table S4.1-2

provided test statistics), from the second-order autoregressive (AR) models fitted to each

population and time period (1945-1965 and 1995-2012) separately.

Fig. 3. Visualization of data, i.e. estimates from the Ricker model, and model predictions,

including precision (± 1 SE), from the model presented in Table 1. We provide estimates

from the present (1995-2012) on the Y-axis whereas estimates from the past (1945-1965) are

provided on the X-axis.

Fig. 4. Visualization of data, i.e. estimates from the autoregressive model, and model predictions,

including precision (± 1 SE), from the model presented in Table 2 (see legends under Fig. 3

for details).

Fig. 5. Median lambdas (A) and density (B) across years for each population, based on data where

we could provide estimates for both periods, and the lack of relationship between them in the

analysis of growth (coefficients and their SEs are provided on the plot: $F_{1,34} = 0.123$; $P =$

0.730) and positive for density ($F_{1,34} = 50.050$; $P > 0.001$). Only four populations revealed

consistent negative growth, i.e. had negative lambdas for both the 25th and the 75th quantiles

within the same period (grey circles), whereas two had consistent growth (red circles).

Fig. 6. Spline correlograms for (A) population-specific population growth rates [$\lambda_t = \log_e(N_{t+1}) \div$
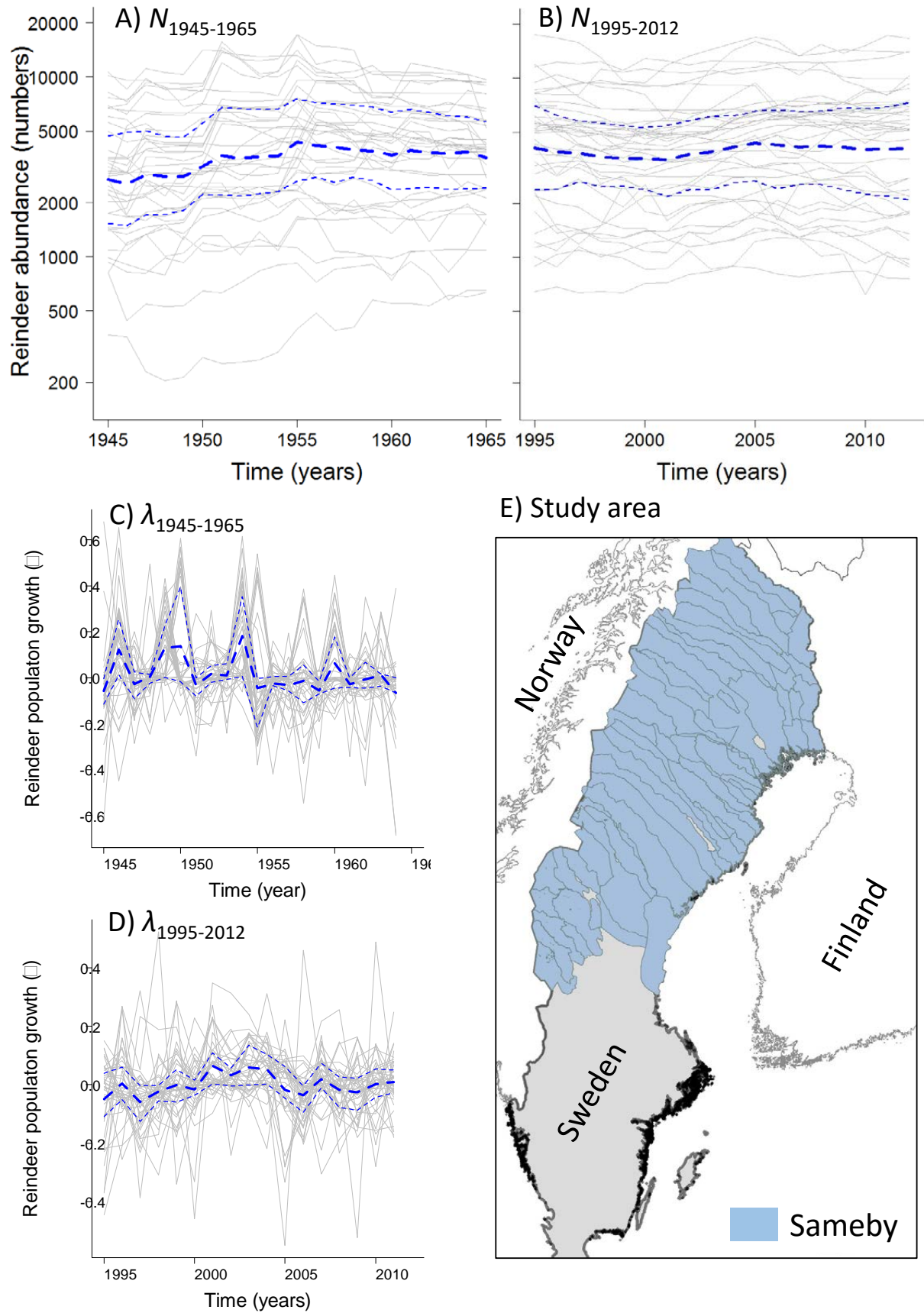
$\log_e(N_t)$] and (B) population density as a function of distance (m).
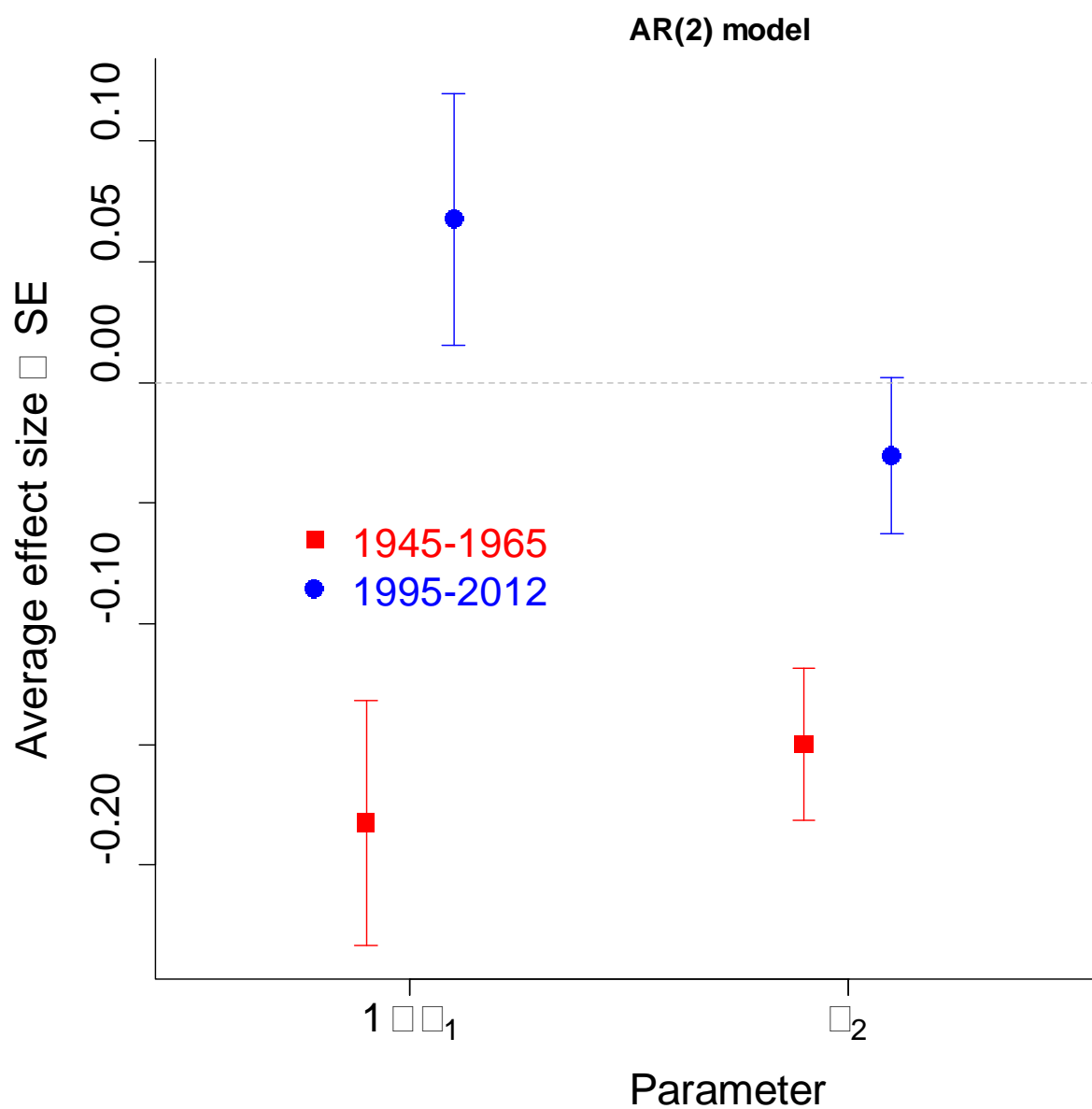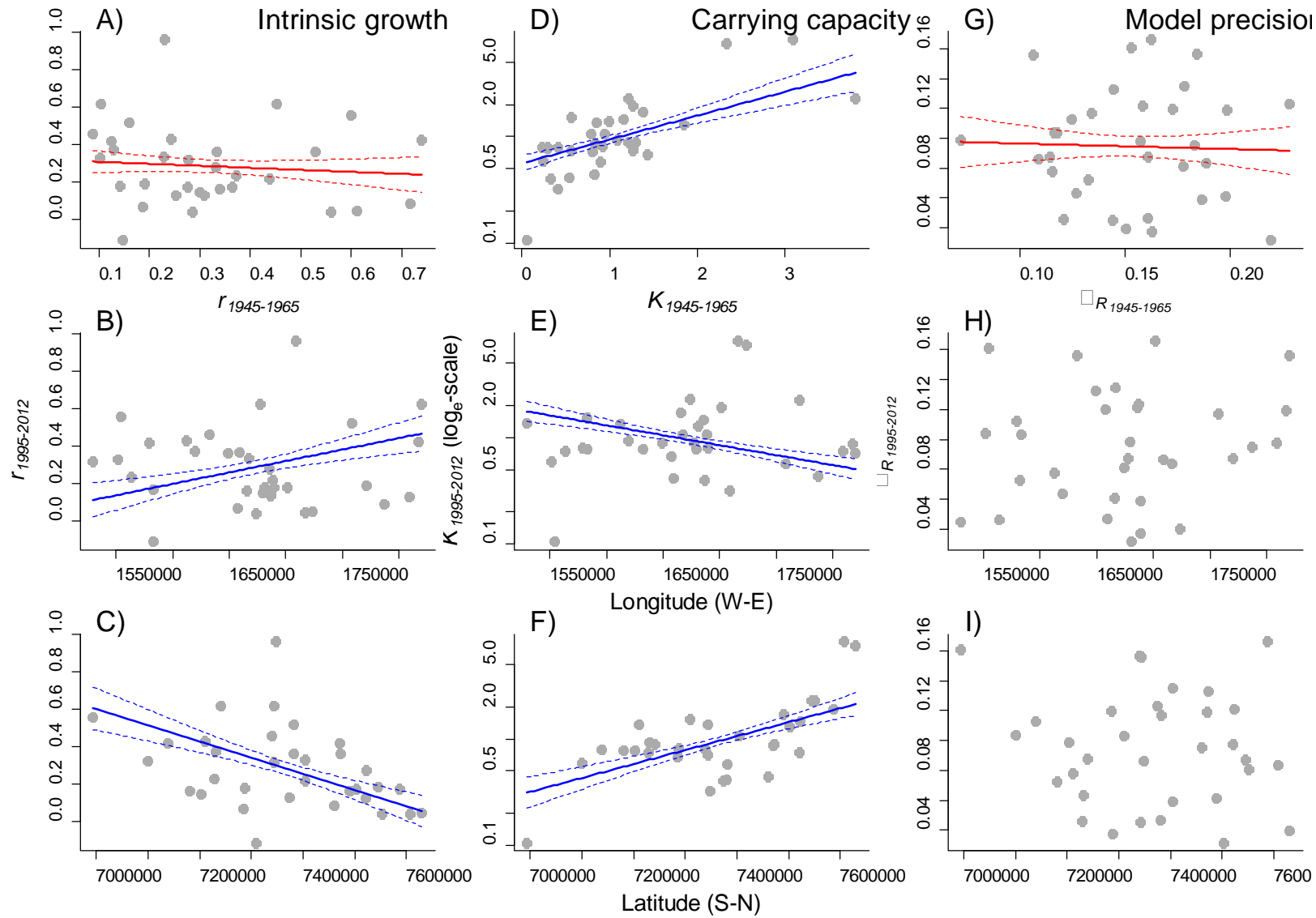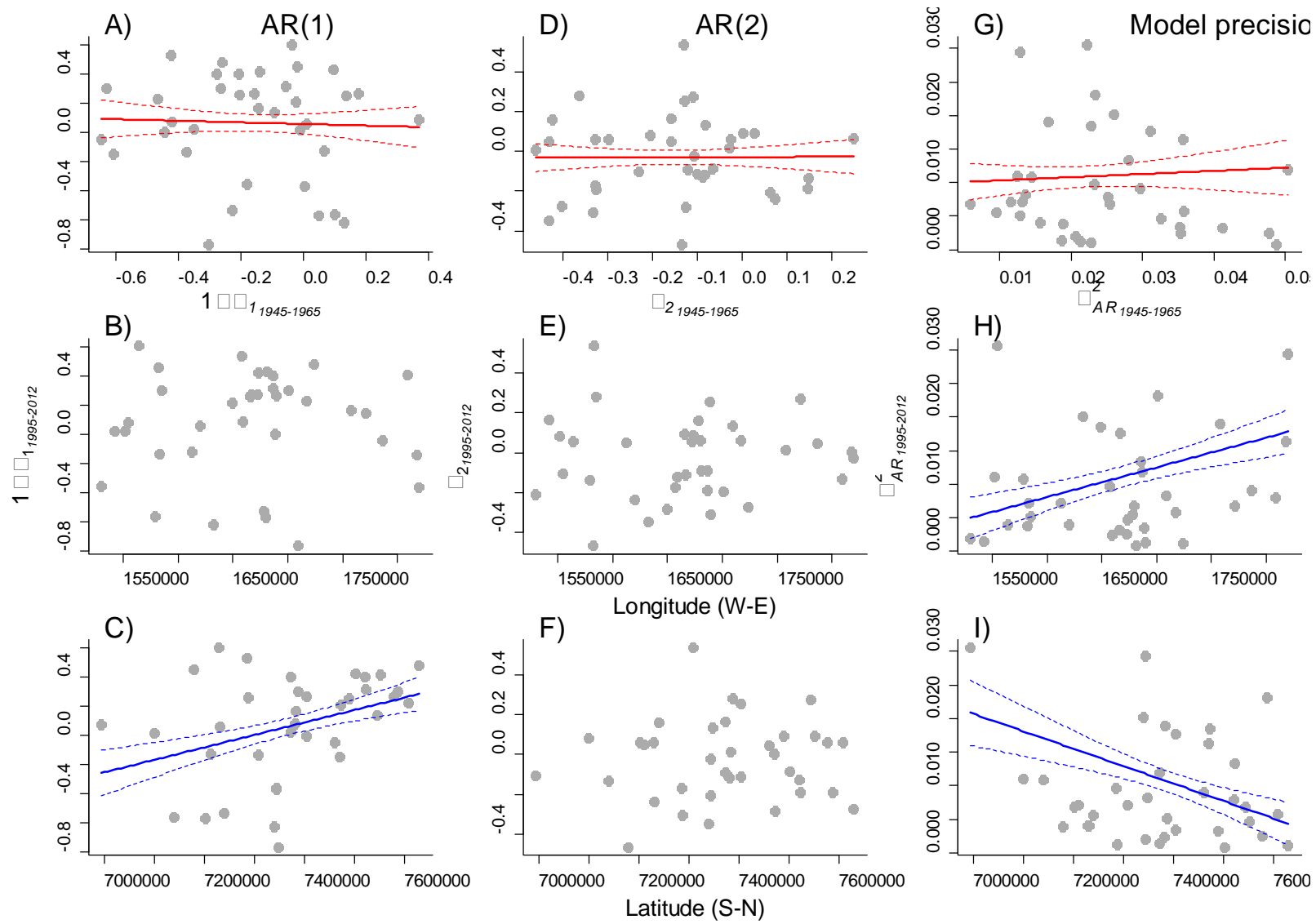
Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

$\lambda_{1995-2012} = -0.0005(0.0045)-0.0921(0.2641) \cdot \lambda_{1945-1965}$ ($R^2 = 0.004$) $D_{1995-2012} = 0.4100(0.1042)+0.6439(0.0910) \cdot D_{1945-1965}$ ($R^2 = 0.595$)
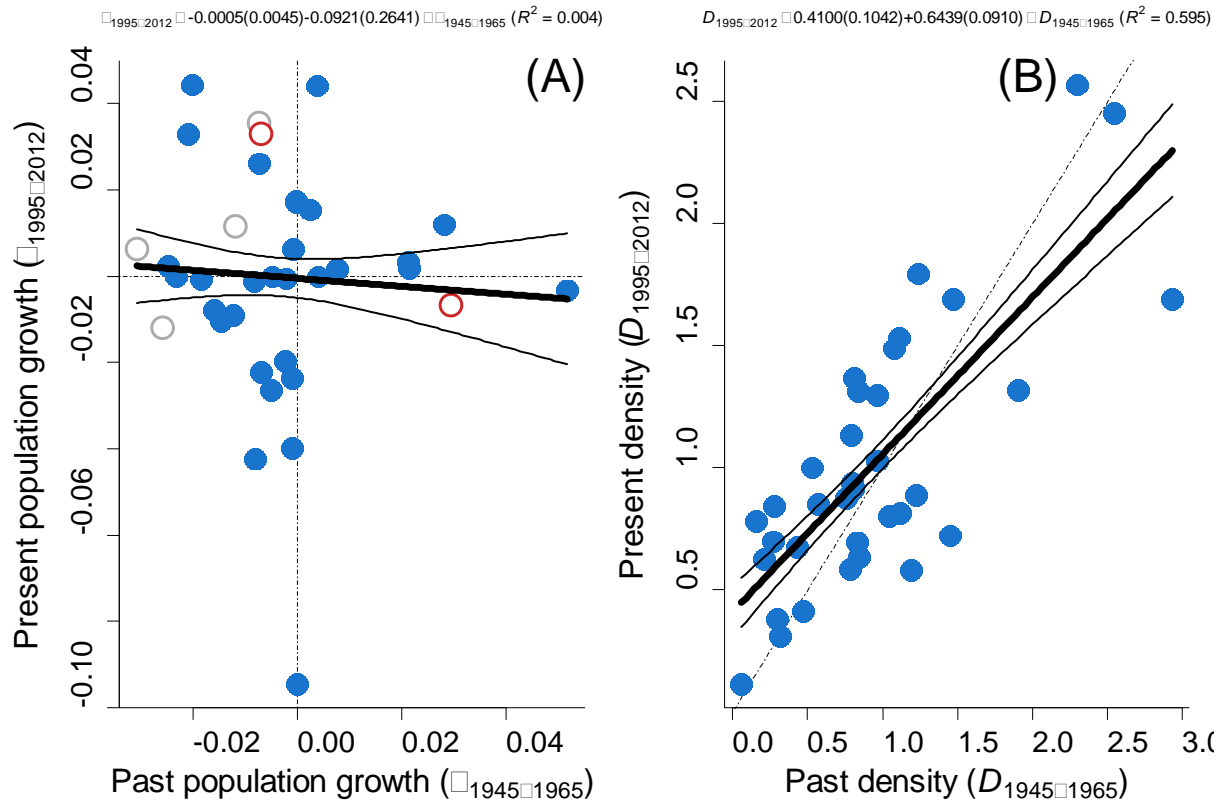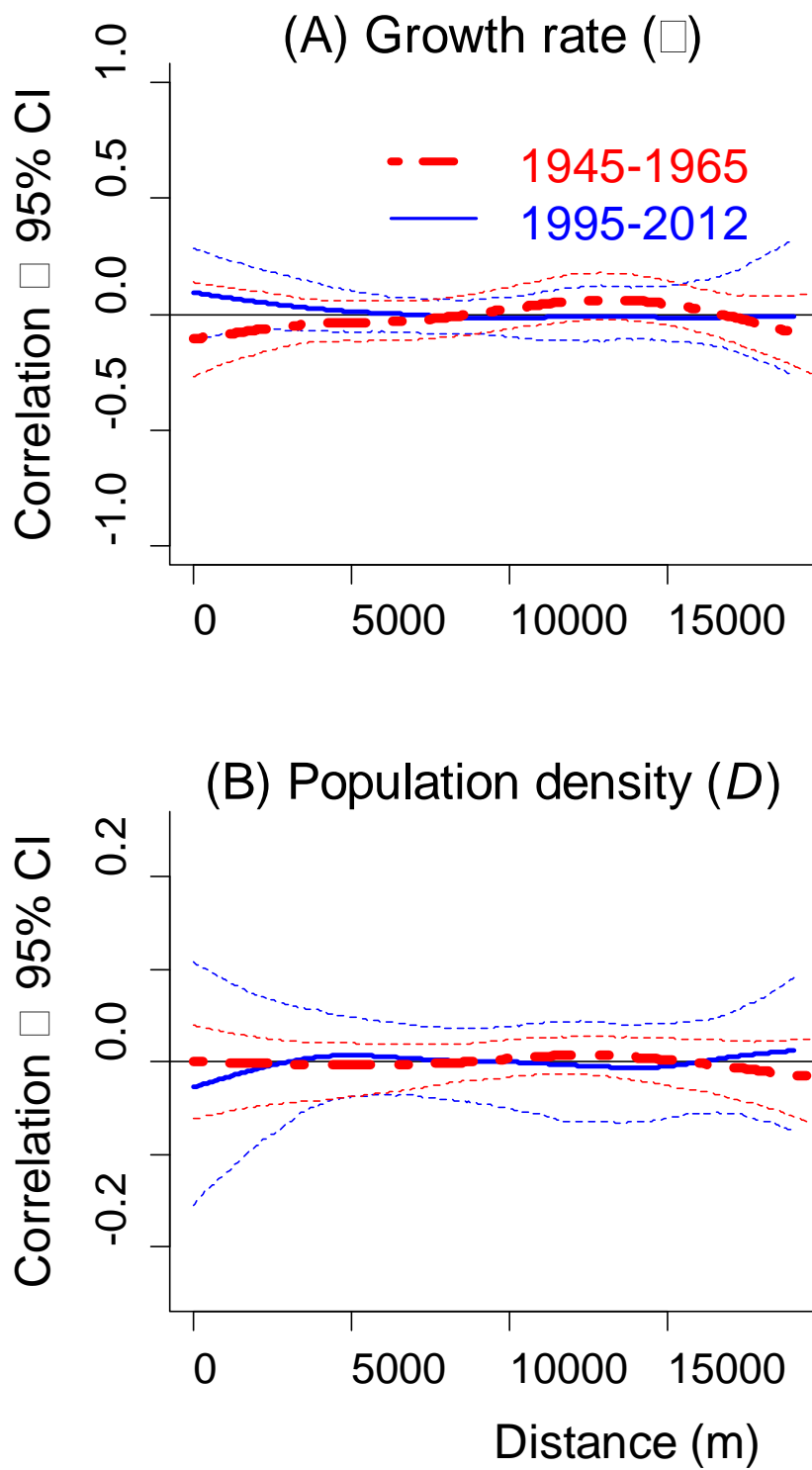

Fig. 5.

Fig. 6.

Tables

Table 1. Estimates from linear models relating present (1995-2012) estimates from the Ricker model, (A) intrinsic growth, (B) carrying capacity ($\log_e$-scale) and (C) model uncertainty, to their past (1945-2012) values, potential covariates (latitude and longitude) and interactions (see Supplement S4 for details). Please note that all predictors were centred, i.e. subtracting the average, which means that the intercept represents model predictions for the average across all predictors (see Fig. 3 for a visualization of the data and model predictions).

Parameter	Ricker model estimates				Partial R^2
	Estimate	SE	t	P	
(A) Intrinsic growth, r					
Intercept	0.272	0.035	7.871	<0.001	
$r_{1945\text{-}1965}$	-0.107	0.211	-0.510	0.614	0.009
Longitude, S-N (X)	1.221×10^{-06}	5.909×10^{-07}	2.067	0.048	0.128
Latitude, W-E (Y)	-8.632×10^{-07}	2.903×10^{-07}	-2.974	0.006	0.234
(F = 3.201; df = 3,29; P = 0.038; R^2 = 0.249)					
(B) Carrying capacity, $\log_e(K)$					
Intercept	0.008	0.085	0.092	0.927	
$K_{1945\text{-}1965}$	0.516	0.144	3.583	0.001	0.307
Longitude, S-N (X)	-4.309×10^{-06}	1.420×10^{-06}	-3.035	0.005	0.241
Latitude, W-E (Y)	3.019×10^{-06}	8.697×10^{-07}	3.472	0.002	0.294
(F = 20.480; df = 3,29; P < 0.001; R^2 = 0.679)					
(C) Sigma, σ_R					
Intercept	0.095	0.007	14.095	<0.001	
Sigma$_{1945\text{-}1965}$	-0.037	0.193	-0.192	0.849	
(F = 0.037; df = 1,31; P = 0.849; R^2 = 0.001)					

Table 2. Estimates from linear models relating present (1995-2012) estimates from the autoregressive model, (A) direct density dependence (the first-order AR coefficient), (B) delayed density dependence (the second-order AR coefficient) and (C) model uncertainty, to their past (1945-2012) values, potential covariates (latitude and longitude) and interactions (see Supplement S4 for details). See Table 1 for details and Fig. 4 for a visualization of the data and model predictions.

Parameter	Autoregressive (AR) model estimates				Partial R^2
	Estimate	SE	t	P	
(A) The first-order AR coefficient [AR(1)], $1-\beta_1$					
Intercept	0.068	0.058	1.185	0.244	
$AR(1)_{1945\text{-}1965}$	-0.055	0.242	-0.227	0.822	0.002
Latitude, W-E (Y)	8.559×10^{-07}	3.835×10^{-07}	2.232	0.033	0.131
($F = 2.607$; df = 2,33; $P = 0.089$; $R^2 = 0.136$)					
(B) The second-order AR coefficient [AR(2)], β_2					
Intercept	-0.030	0.035	-0.876	0.387	
$AR(2)_{1945\text{-}1965}$	0.008	0.195	0.041	0.967	
($F = 0.002$; df = 1,34; $P = 0.967$; $R^2 < 0.001$)					
(C) Sigma², σ_{TS}^2					
Intercept	0.011	0.002	7.036	<0.001	
$Sigma^2_{1945\text{-}1965}$	0.047	0.136	0.346	0.731	0.004
Longitude, S-N (X)	4.434×10^{-08}	1.910×10^{-08}	2.319	0.027	0.148
Latitude, W-E (Y)	-2.560×10^{-08}	1.160×10^{-08}	-2.205	0.035	0.136
Latitude × Longitude	-1.769×10^{-06}	1.040×10^{-06}	-1.706	0.098	0.086
($F = 2.575$; df = 4,31; $P = 0.057$; $R^2 = 0.249$)					