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# The changing contribution of top-down and bottom-up limitation of mesopredators during 220 years of land use and climate change

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## Summary

1. Apex predators may buffer bottom-up driven ecosystem change, as top-down suppression may dampen herbivore and mesopredator responses to increased resource availability. However, theory suggests that for this buffering capacity to be realized, the equilibrium abundance of apex predators must increase. This raises the question: will apex predators maintain herbivore/mesopredator limitation, if bottom-up change relaxes resource constraints?

2. Here, we explore changes in mesopredator (red fox *Vulpes vulpes*) abundance over 220 years in response to eradication and recovery of an apex predator (Eurasian lynx *Lynx lynx*), and changes in land use and climate which are linked to resource availability.

3. A three-step approach was used. First, recent data from Finland and Sweden were modelled to estimate linear effects of lynx density, land use and winter temperature on fox density. Second, lynx density, land use and winter temperature was estimated in a 22 650 km<sup>2</sup> focal area in boreal and boreo-nemoral Sweden in the years 1830, 1920, 2010 and 2050. Third, the models and estimates were used to project historic and future fox densities in the focal area.

4. Projected fox density was lowest in 1830 when lynx density was high, winters cold and the proportion of cropland low. Fox density peaked in 1920 due to lynx eradication, a mesopredator release boosted by favourable bottom-up changes – milder winters and cropland expansion. By 2010, lynx recolonization had reduced fox density, but it remained higher than in 1830, partly due to the bottom-up changes. Comparing 1830 to 2010, the contribution of top-down limitation decreased, while environment enrichment relaxed bottom-up limitation. Future scenarios indicated that by 2050, lynx density would have to increase by 79% to compensate for a projected climate-driven increase in fox density.

5. We highlight that although top-down limitation in theory can buffer bottom-up change, this requires compensatory changes in apex predator abundance. Hence apex predator recolonization/recovery to historical levels would not be sufficient to compensate for widespread changes in climate and land use, which have relaxed the resource constraints for many herbivores and mesopredators. Variation in bottom-up conditions may also contribute to context dependence in apex predator effects.

**Key-words:** ecosystem processes, historical ecology, historical maps, intraguild killing, trophic interactions, wildlife monitoring, wildlife restoration

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## Introduction

Ecosystem structure is determined by an interplay between top-down and bottom-up processes, where the latter are linked to resource availability and primary productivity (Oksanen *et al.* 1981; Power 1992). Primary productivity is in turn affected by climate change and land cover conversion linked to anthropogenic land use (Foley *et al.* 2005; Haberl *et al.* 2007; Heimann & Reichstein 2008).

Top-down forces are linked to consumption and interference competition, and their importance in structuring ecosystems has been revealed when apex consumers have been reduced, lost from or reintroduced to ecosystems world-wide (Estes *et al.* 2011; Ripple *et al.* 2014). Loss of apex predators can cause herbivore release (Hairston, Smith & Slobodkin 1960), mesopredator release (Soulé *et al.* 1988), trigger trophic cascades (Pace *et al.* 1999) and lead to alternative ecosystem states (Estes *et al.* 2011).

It has also been suggested that apex predators can 'buffer' herbivore and mesopredator responses to bottom-up driven ecosystem change by dampening population fluctuations and changes in equilibrium abundance due to changing resource conditions (Post *et al.* 1999; Wilmers, Post & Hastings 2007; Pasanen-Mortensen, Pykönen & Elmhagen 2013; Pasanen-Mortensen & Elmhagen 2015). However, realization of this top-down ecosystem function requires that apex predators respond numerically or behaviourally to the bottom-up change (Oksanen *et al.* 1981; Post *et al.* 1999; Elmhagen *et al.* 2010). This can be prevented by anthropogenic limitation of apex predators, below the density where they carry out structurally important top-down functions (Soulé *et al.* 2005). Still, theory on interactions between top-down and bottom-up effects remains poorly tested and little understood (Ripple *et al.* 2014).

The Eurasian lynx (*Lynx lynx*, hereafter lynx) limits red fox (*Vulpes vulpes*, hereafter fox) density in Eurasia, thus functioning as apex predator and mesopredator respectively (Pasanen-Mortensen, Pykönen & Elmhagen 2013). Fox density can decrease drastically at high lynx density (Matyushkin & Vaisfeld 2003), probably because of interspecific killing to reduce competition, as lynx seldom eat the foxes they kill (Sunde, Overskaug & Kvam 1999; Hellid, Liberg & Gløersen 2006). However, at low prey densities, lynx prey upon foxes (Mattisson *et al.* 2011). In the absence of lynx, the fox is released from top-down limitation and instead limited bottom-up (Elmhagen *et al.* 2010; Pasanen-Mortensen, Pykönen & Elmhagen 2013; Pasanen-Mortensen & Elmhagen 2015). High primary productivity and crop fields have positive effects by increasing prey abundance, while harsh winters have negative effects, e.g. through direct and indirect effects on prey productivity and accessibility (Hersteinsson & MacDonald 1992; Kurki *et al.* 1998; Bartoń & Zalewski 2007; Pasanen-Mortensen, Pykönen & Elmhagen 2013; Pasanen-Mortensen & Elmhagen 2015).

Here we explore the hypothesis that top-down limitation buffer, i.e. compensate for, changes in bottom-up

forces which relax resource constraints for mesopredators. Specifically, we test how changes in lynx abundance, land use and climate manifest themselves on fox abundance in an anthropogenic landscape over 220 years. Thus, we investigate to what extent buffering is presently occurring, and what would be required for buffering to be a factor in the future. We use a three-step approach where we (i) analyse present-day effects of lynx, land use and winter temperature on fox density in a reference area, (ii) assess changes in lynx density, land use and winter temperature in a projection area from 1830 to 2050 and (iii) use the outcomes of step 1 and 2 to project fox density in the projection area in 1830, 1920, 2010 and 2050, thereby exploring changes in the contributions of top-down and bottom-up limitation over time.

## Materials and methods

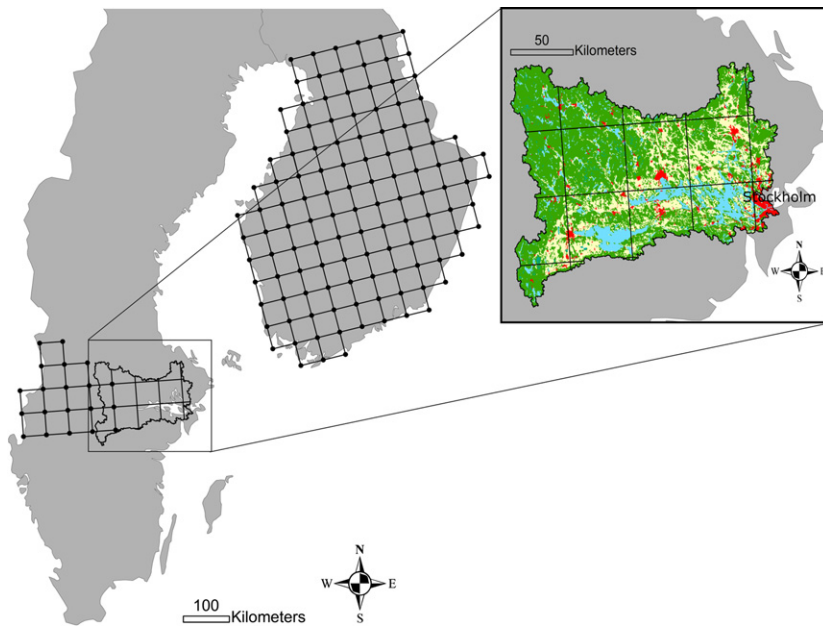
### REFERENCE AND PROJECTION AREAS

Assuming that present-day relationships between mesopredators and drivers of mesopredator abundance can be used to project changes in mesopredator abundance over time (space-for-time substitution), a reference area was used to analyse fox responses to present-day spatial variation in lynx, land use and winter temperature, and a projection area was used to project temporal variation in fox abundance in relation to changes in these drivers.

The reference area consisted of Finland (59°50'N–65°50'N and 21°5'E–31°36'E) and central Sweden (58°59'N–60°55'N and 11°41'E–15°9'E; Fig. 1). The Finnish area, covering 273 500 km<sup>2</sup>, is dominated by boreal coniferous and boreo-nemoral forests, and agriculture is mainly located to the south and west. The Swedish area covers 27 500 km<sup>2</sup> of the boreal and boreo-nemoral forest zone with agricultural areas mainly located to the south. Lynx are present almost throughout both areas, although the density varies (Elmhagen *et al.* 2010; Zetterberg & Svensson 2012).

Delimitation of the reference area was based on availability of suitable data. Data were available also north of the Finnish reference area, but this region was excluded as lynx were very rare and habitat conditions were too different from the Swedish region. Grey wolves (*Canis lupus*) are locally present; however, as previous European studies do not indicate any strong effect of foxes by wolves (Pasanen-Mortensen, Pykönen & Elmhagen 2013; Dorresteijn *et al.* 2015), and as wolf density is low, potential effects of wolves on foxes were not considered. Neither is the potential impact of fox hunting included, as the incentive for fox hunting has changed over time due to changes in the socio-economic circumstances and the bounty system. Hence, today's hunting effort and hunting bag data are not comparable to the historical.

The projection area consisted of the Norrström drainage basin (NDB) in central Sweden (58°51'N–60°18'N and 14°26'–18°19'E; Fig. 1). It covers 22 650 km<sup>2</sup> of boreal and boreo-nemoral forests, large lakes, cities and agricultural fields. NDB has gone through substantial changes in potential drivers of fox density since the mid-1800s (Elmhagen *et al.* 2015): lynx were eradicated in the early 1900s but is now recolonizing the area, the agrarian revolution has shifted the land use from subsistence to industrial agriculture and silviculture, and the yearly mean temperature has increased by 1.6 °C.



**Fig. 1.** 50 × 50 km squares in the reference area (marked corners, Sweden in west, Finland in east) and in the projection area, Norrström drainage basin (unmarked corners).

## STEP 1 – PRESENT-DAY FOX LIMITATION

### Species data

Data on fox and lynx abundance in Finland (1989–2005; <https://riistakolmiot.fi/>) and Sweden (2001–2003) were compiled from line transect surveys using the wildlife triangle method developed within the Finnish Wildlife Triangle Scheme (Lindén *et al.* 1996). Each winter, the number of animal tracks crossing a triangular transect of 3 × 4 km were counted within 48 h after snowfall, or 24 h after a pre-survey where all tracks were marked to separate new tracks from old. The counts were transformed to number of crossings/10 km/24 h and to grids of 50 × 50 km squares, using counts from all years and triangles within a square (Lindén *et al.* 1996; Wallgren *et al.* 2009). Squares with <2 triangles per 50 × 50 km, or with all triangles strongly aggregated, were excluded ( $n = 1$  in Finland,  $n = 4$  in Sweden). In total, the study included 95 squares and 1046 wildlife triangles in Finland, and 11 squares and 163 wildlife triangles in Sweden (Fig. 1, data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dk6v5>).

The mean track counts were transformed to densities ( $n \text{ km}^{-2}$ ) using Prikloński's formula (Prikloński 1965; Goszczyński 1989; Bartoń & Zalewski 2007; Pasanen-Mortensen, Pykönen & Elmhagen 2013):

$$\frac{\text{T.I.} \times (\pi/2)}{\text{DMD}}$$

where T.I. is tracking index ( $n$  tracks per km per 24 h) and DMD is average daily moving distance. Data on DMD of fox (9.1 km) and lynx (10.2 km) in Russia were used (Goszczyński 1986).

### Land use

A positive association exists between fox density and cropland, while there is a negative association with grasslands (Pasanen-Mortensen & Elmhagen 2015). Croplands has expanded in the

reference area, while other open habitats, e.g. grasslands and wetlands, have declined in extend. To estimate the impact of cropland and other open habitats on fox, the proportions of these land covers were assessed from Corine Land Cover 2000 with 100 m resolution ([www.eea.europa.eu](http://www.eea.europa.eu)) for each 50 × 50 km square (data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dk6v5>). Only Corine land cover classes found in both the reference and projection areas were included. All land cover classes that imply crop production were included in the proportion of 'cropland'. Other classes of open habitat (peat bogs, inland marshes and pastures) were sparse, and grouped to represent 'other open habitats'.

### Climate

Mean winter temperatures were assessed from CRU TS 3.10 ([www.cgiar-csi.org](http://www.cgiar-csi.org); Harris *et al.* 2013). Temperatures from December to February in 1990–2006 were used for the Finnish squares, and in 1991–2003 for the Swedish squares (data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dk6v5>).

### Fox limitation models

Potential bottom-up effects on fox abundance may be difficult to assess in the presence of lynx, as strong top-down limitation can prevent fox abundance from varying in response to climate conditions and land use (Pasanen-Mortensen, Pykönen & Elmhagen 2013; Pasanen-Mortensen & Elmhagen 2015). However, a previous study showed that fox abundance was related to ecosystem productivity in southern Finland, likely because lynx abundance was relatively low (Elmhagen *et al.* 2010). The impact of lynx abundance, winter temperature and proportion of cropland (including a second-degree polynomial, Pasanen-Mortensen & Elmhagen 2015) and open habitat on fox density was therefore assessed in two linear models, expected to capture different aspects of fox limitation (Table 1). The first model was based on an analysis of all data ( $n = 106$  squares, hereafter regional model), while the second model was based on a data subset



including only southern Finland ( $n = 43$ , hereafter local model). We assumed that the local model would better capture potential relationships between fox density and bottom-up variables, as indicated by Elmhagen *et al.* (2010).

As species abundance data were used, heteroscedasticity was expected, as well as spatial autocorrelation due to dependence between nearby squares. Heteroscedasticity is usually handled by transforming a skewed response variable to meet the assumption of homoscedasticity in ordinary least squares regression. However, transforming count data can induce bias in models (O'Hara & Kotze 2010). We therefore analysed the data with generalized least squares (GLS). GLS allows for heteroscedasticity by recognizing the explanatory variable that causes heteroscedasticity and include it into the model as a variance covariate with an assumption of the variance structure. Also a spatial residual correlation structure can be included to account for spatial autocorrelation (Zuur *et al.* 2009).

Heteroscedasticity was tested for using Breusch–Pagan test (Breusch & Pagan 1979), and a variance structure was included when heteroscedasticity was significant. A spatial correlation structure was included when this improved model fit. The correlation structures were chosen based on Akaike information criterion (AIC; Zuur *et al.* 2009).

Backward elimination based on AIC was applied to select variables to include in the regional and local model. Backward elimination was chosen rather than model selection from a large number of *a priori* models for two reasons: First, our full model included variables which previously have been shown to affect fox abundance. Second, model selection takes into account only statistical performance and tends to find the statistically most parsimonious model, i.e. one which includes as few variables as possible. This is not always the ecologically most feasible model when it comes to understanding cases where several ecological processes contribute to the response (Sand *et al.* 2012). In our case, where the research question focuses on multiple ecological processes which all changed extensively during the study period and are known *a priori* to affect fox abundance, backward elimination was deemed a more considerate way of analysing the empirical data and produce parameters for projections.

The best regional model included a power variance structure with winter temperature as variance covariate, and a Gaussian spatial correlation structure. The best local model included neither variance nor correlation structures.

**Table 1.** Full models and models after backwards elimination. Null models are included for comparison. A second-degree polynomial was included for cropland

	AIC	$\Delta_i$	$w_i$
Regional model			
Lynx density + cropland <sup>2</sup> + winter temperature	-414	3.19	0.169
Lynx density + winter temperature	-418	0	0.831
Null model	-256	163	$3.64 \times 10^{-36}$
Local model			
Lynx density + cropland <sup>2</sup> + winter temperature + open habitat	-139	2.65	0.210
Lynx dens + cropland + winter temperature + open habitat	-142	0	0.790
Null model	-112	30.5	$1.93 \times 10^{-36}$

## STEP 2 – CHANGES IN LYNX DENSITY, LAND USE AND CLIMATE

A grid of  $50 \times 50$  km squares ( $n = 18$ ; Fig. 1) was created for NDB and used in step 2 and 3.

### Lynx estimates

Yearly bounty records from 1830 to 1839, from the counties covering NDB, were used to estimate lynx density in 1830 (Sweden's Official Statistics 1870–1917, 1879, <http://www.scb.se/en/>). On average  $135 (\pm 30$  SD) lynx were killed annually in the counties during this period, and there was no tendency of increase or decrease over time. In present-day Sweden, a cull of 16–20% is expected to maintain the lynx population at a constant level, as it corresponds to the yearly population growth (Andrén *et al.* 2006). For each county, lynx density in 1830 was therefore estimated assuming a cull of 20% (population kept at a constant level). Because of the uncertainty in the estimate, lynx density was also estimated for a cull of 10% (weakly limited) and 30% (decreasing population). Finally, lynx density in NDB was estimated based on the proportion of each  $50 \times 50$  km square covered by each county (data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dk6v5>).

From 1909, after a period when few lynx were killed annually, no more lynx were killed in the counties included in NDB (Sweden's Official Statistics 1870–1917, 1879), and lynx can be considered extirpated. Hence, lynx density was set to zero in all squares in the 1920s models.

Legal protection of lynx in Sweden 1928–1942 and 1991–1994 allowed recovery from a small northern population. To assess lynx density in 2010, data on family groups from the county administration boards from the winters 2003/2004 and 2005–2010 were used (Viltskadecenter 2004, 2006, 2007; Svensson 2008, 2009; Svensson & Hedmark 2010; <http://www.viltskadecenter.se>). The number of lynx can be roughly estimated by multiplying the number of family groups with a factor of 5.95 ( $\pm 0.64$  SD, Andrén *et al.* 2002). This information was used to estimate lynx density in each county, and then allocated to the squares.

The future development of the lynx population in NDB is unknown and depends largely on political decisions. For the 2050 projections, we used different lynx density scenarios, including a mean of 5.6 lynx/1000 km<sup>2</sup>, a decline to 0, 2.5 or 5 lynx/1000 km<sup>2</sup>, or an increase to 7.5 or 10 lynx/1000 km<sup>2</sup>, assuming 10 lynx/1000 km<sup>2</sup> to be reasonable as it is similar to the estimated density in 1830 assuming a stable population. The change in lynx density was calculated by assuming an equal change in each square compared to 2010 (but never below 0).

### Land use model

To estimate the proportion of cropland in the past, a landscape model was developed based on the strong relationship between soil type and land use (Cousins 2009; Cousins & Vanhoenacker 2011). Cadastral maps from 1897 to 1901 at a scale of 1 : 50 000 (<http://www.lantmateriet.se/sv/>) covering parts of NDB were used together with a digital soil and bedrock database from the Geological Survey of Sweden (<http://www.sgu.se/en/products/>) in the model. We used 100 random point samples across NDB, and the relationship between land use and soil types was analysed. Soil types are strongly correlated with land use in southern Scandinavia

because of the redistribution of soils due to land uplift after the last Ice Age ( $R^2 = 90\%$ ; Cousins 2009), thus 100 sample points were deemed sufficient for the historical model building. The digital soil and bedrock database was used to create a land use model for 1830 and 1920. The model for 1920 assumes that all soils like clays and silts, and peatland within open areas, had been turned into crop production, as this was the general pattern in this region by 1930 (Morell 2001). This development was enabled by the agricultural revolution, i.e. after introducing heavier ploughs, techniques to drain land more effectively and artificial fertilizers (Morell 2001). In 1830, crop fields were small and located on well-drained soils, whereas heavier soils were used for mowing or grazing (Cousins 2009). To estimate the proportion of croplands in 1830, the ratio between cropland and meadows in 1865 data from Sweden's Official Statistics (1868) was used and superimposed on the 1920 landscape model (data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.dk6v5>).

Today there are only remnants of meadows and peatlands left in the landscape, and forest grazing – which was commonly practised up until the 1920s – has been abandoned. Due to this difference between past and present land use, it was unreliable to use estimates of open habitat (other than cropland) impact on fox from step 1 together with modelled proportions of historical open habitat for the fox abundance projections. To project fox abundance in 1830 and 1920, we instead used data on open habitats in 2010 (peat bogs, inland marshes and pastures) to represent a minimum proportion of open habitats.

To assess open habitats and cropland in NDB squares in 2010, Corine Land Cover 2000 ([www.eea.europa.eu](http://www.eea.europa.eu)) was used (data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dk6v5>). For the scenarios of 2050, the 2010 land cover was also used, which can be considered a conservative model (Elmhagen *et al.* 2015).

### Winter temperature model

Winter temperatures for each NDB square were estimated using data from temperature stations operated between 1800 and 2010 (Swedish Meteorological and Hydrological Institute, <https://opendata-catalog.smhi.se/explore/>). A linear model was fitted for temperature as a function of elevation, latitude and distance to the sea for each winter month (December–February) based on the 1980–2000 period with around 40 active temperature stations. Assuming that these relationships between temperature and elevation, latitude and distance to sea did not change over time, the same models were used to interpolate mean winter temperature

for each square between the active temperature stations for the winters of 1831–1840, 1921–1930 and 2001–2010. The residuals between the linear models and the observed temperatures from active weather stations for each time period were spatially interpolated via ordinary kriging (R-gstat package, Pebesma 2004) and added to the linear model results.

The annual mean temperature in NDB is expected to increase by 1.6 °C until 2041–2070 (Elmhagen *et al.* 2015). The change in mean winter temperature has not been estimated, but we assumed an increase in winter temperature by 1.5 °C in each square from 2010 to 2050.

### STEP 3 – FOX PROJECTIONS

For each time step and NDB square, fox densities were deterministically projected using a linear model with intercept and parameter estimates obtained from the best regional and local GLS models (step 1), together with the estimated lynx density, winter temperature and proportion of cropland and open habitat (step 2). The area weighted mean fox density for the entire NDB was also calculated. Additionally, the uncertainty of the variables in step 1 was taken into account by conducting stochastic projections for each square using the parameter estimates and standard errors from the best GLS models to generate random deviates. The number of simulations were weighted by the sizes of the squares ( $n_{\max} = 100\,000$  and  $n_{\min} = 282$ ).

The probability that the stochastically projected fox density was higher/lower in the next period was estimated, where a probability of 0.50 means that there is an equal probability of increase and decrease between the two periods, i.e. a random change.

Additionally, historical data retrieved from Sweden's Official Statistics (1827–1860, 1870–1917, 1866–1917, 1879) on seed use and bounties paid for lynx and fox were plotted for comparison with the 1830–1920 projections. We expected these data to reflect expansion of cropland and changes in species densities.

ArcGIS 10.2.1 (ESRI 2010), and Geospatial Modelling Environment 0.7.2 (Beyer 2012) and R 2.15.3 (R Core Team 2013) were used for the study.

## Results

### STEP 1 – PRESENT-DAY FOX LIMITATION

In the best GLS regional model, fox density was determined by lynx (negative relationship) and winter

	Estimate	Std. coeff	Std. error	<i>t</i> -value	<i>P</i> -value
<b>Regional model</b>					
Intercept	0.22	–	0.045	5.0	<0.0001
Lynx density	–0.0043	–0.20	0.00098	–4.4	<0.0001
Winter temperature	0.012	0.35	0.0042	2.8	0.0056
<b>Local model</b>					
Intercept	0.26	–	0.042	6.1	<0.0001
Lynx density	–0.0082	–0.38	0.0017	–4.8	<0.0001
Winter temperature	0.020	0.39	0.0057	3.5	0.0012
Cropland	0.26	0.55	0.050	5.2	<0.0001
Open habitat	–0.94	–0.34	0.23	–4.1	0.0002

**Table 2.** Effects of lynx, winter temperature, and proportion of cropland and open habitat on red fox density from GLS regional and local models

**Table 3.** Means of modelled and estimated variables in NDB

Variable	1830	1920	2010
Lynx/1000 km <sup>2</sup>	7 <sup>10</sup> , 11 <sup>20</sup> or 21 <sup>30</sup>	0	5.6
Cropland (%)	15	22	23
Open habitat (%)	min 2.3	min 2.3	2.3
Temperature December–February (°C)	−3.9	−3.3	−2.4

Culling rate used to estimate lynx density in 1830 (10, 20 or 30%).

temperature (positive relationship, Tables 1 and 2), where winter temperature had the stronger effect (Table 2). In the best GLS local model, fox density was determined by lynx and open habitat (negative relationships), and by proportion cropland and winter temperature (positive relationships, Tables 1 and 2). Cropland had the strongest effect, and open habitat the weakest (Table 2).

#### STEP 2 – CHANGES IN LYNX DENSITY, LAND USE AND CLIMATE

In 1830, mean lynx density was high (7–21 lynx/1000 km<sup>2</sup>), regardless of which culling rate it was estimated from (Table 3). There were no lynx in NDB in 1920. By 2010, the lynx had recolonized, but densities were generally lower than in 1830 (49% lower based on 20% culling rate, Table 3, Fig. 2).

In 1830, 15% of the NDB's landscape was covered by cropland, with a variation of 5–40% across the squares. In 1920, the proportion of cropland had increased to 22% in the region but to more than 50% in some parts, and to 23% in 2010 (Table 3, Fig. 2).

If the number of foxes killed reflects fox population size, changes in fox bounty records from 1830 to 1920 indicated an increase which coincided with the decrease in lynx and also an increase in seeds used for sowing fields (Fig. 3).

Mean winter temperature was lowest in 1830 (−3.9 °C) and increased by 1.5 °C over time to −3.3 °C in 1920 and −2.4 °C in 2010 (Table 3, Fig. 2).

#### STEP 3 – FOX PROJECTIONS

Deterministic and stochastic projected fox density was lowest in 1830, highest in 1920 and intermediate in 2010, irrespective of estimated lynx density in 1830, and of which model (regional or local) the projections were based on (Table 4, Fig. 2). The relative changes in fox density were higher in projections based on the local model, which took into account changes in fox density in response to changes in land use. The probability of change was hence higher for stochastic projections based on the local model (Appendix S1, Supporting Information).

According to deterministic and stochastic projections of fox density in response to a 1.5 °C increase in winter temperature, fox density will increase between 2010 and 2050 for lynx density scenarios with 0–7.5 lynx/1000 km<sup>2</sup>. In the highest lynx density scenario, where lynx density was assumed to increase by 79% (from 5.6 to 10 lynx/1000 km<sup>2</sup>), the negative effect of lynx on fox fully compensated for the positive effect of climate warming (Table 4 and Appendix S1).

As the coefficient for lynx was higher in the local than the regional model, changes in lynx density rendered a larger effect on fox in the projections based on the local model. However, the impact of lynx was counteracted by the simultaneous positive impact of climate, which also was stronger in the local than the regional model, and additionally by the positive effect of cropland. Local model projections thus rendered larger quantitative changes, while both models rendered similar qualitative changes in fox density between time steps.

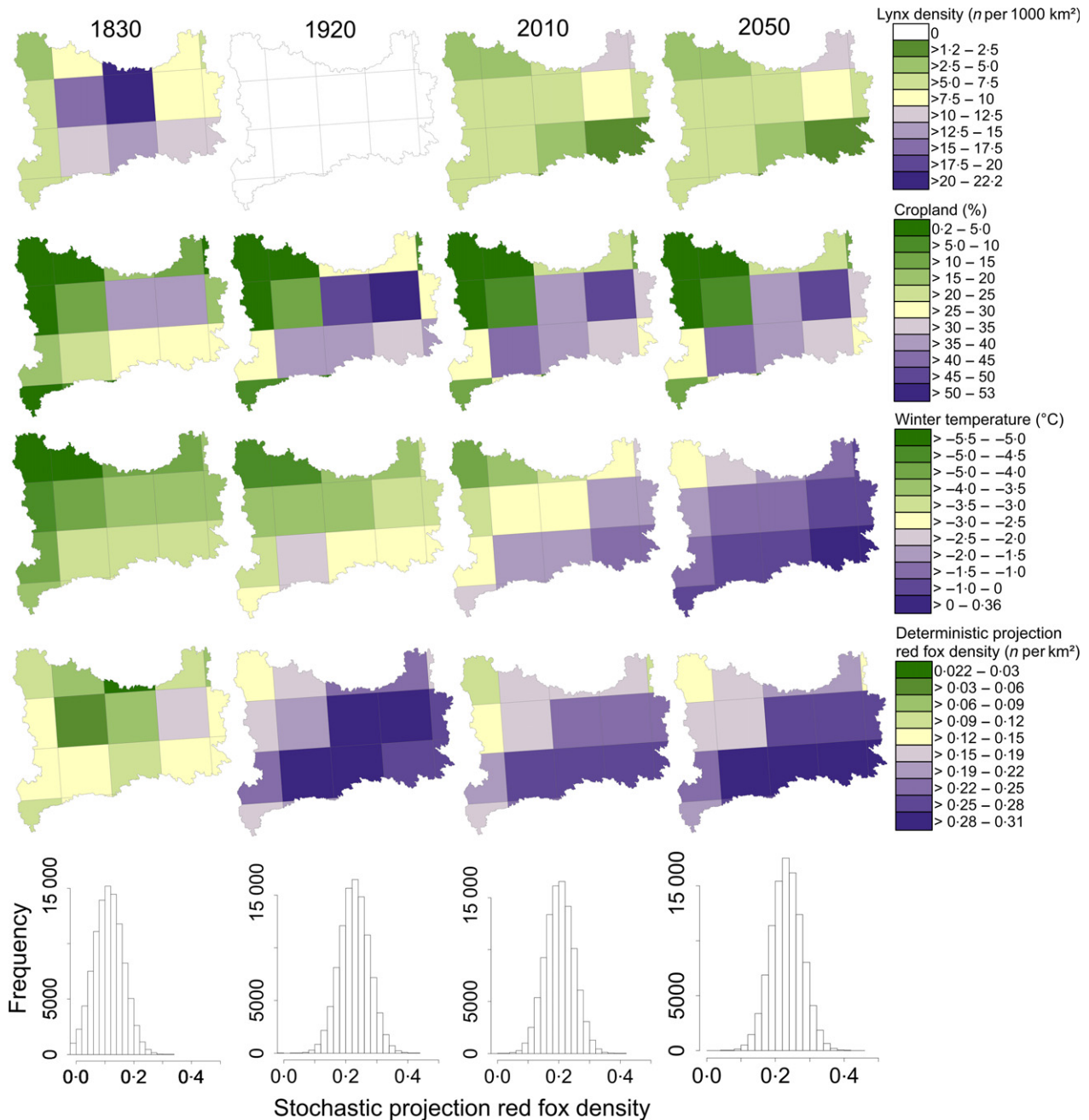
Although deterministic projections produced clear patterns of change in fox density over time, the stochastic projections showed that given the uncertainties in the parameter estimates, relatively substantial changes in the drivers were required to produce a high (>90%) probability of increase/decline in fox density. For example, deterministic projections based on the local model suggested that fox density doubled between 1830 and 1920 due to additive effects of lynx extirpation and environmental enrichment, and 95% of the stochastic projections suggested that fox density increased (Table 4, Fig. 4 and Appendix S1). lynx density estimated from 20% culling rate.

In contrast, the deterministic decline in fox density between 1920 and 2010, when lynx recolonization and warmer winters acted antagonistically, was less certain and only 65% of the stochastic projections resulted in fox decline (Table 4, Fig. 4 and Appendix S1; local model, lynx density estimated from 20% culling rate).

Likewise, future projections based on the local model showed a distinct deterministic pattern; fox density increased in response to milder winters unless lynx increased to a level where these antagonistic effects cancelled each other out, while the stochastic projections showed a high (88%) probability of fox increase only in the scenario where lynx were absent (Table 4, Appendix S1). Overall, the deterministic trends illustrate the conceptual outcome of simultaneous changes in top-down and bottom-up drivers over time (Fig. 4).

## Discussion

When projecting red fox abundance, we found an increase due to mesopredator release resulting from reduction of lynx, and due to environment enrichment resulting from land use and climate changes over time. Theoretically, bottom-up changes that increases primary productivity also increases the biomass at higher trophic levels



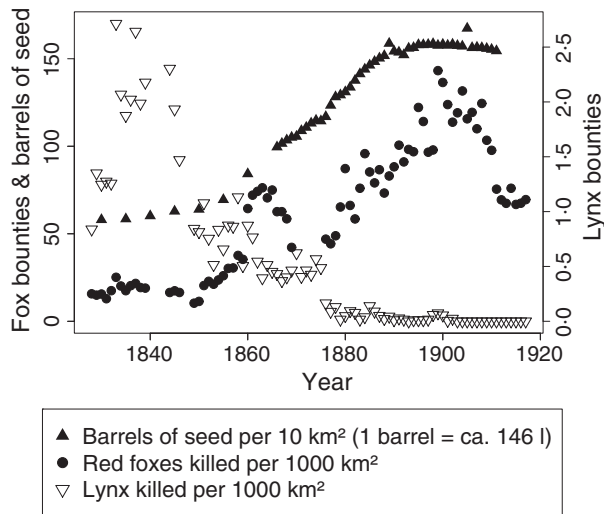
**Fig. 2.** Estimated lynx density (assuming 20% culling rate in 1830), proportion of cropland and winter temperature. Deterministically projected red fox density and frequency distributions of stochastically projected fox density in 1830 (assuming 20% lynx culling rate), 1920, 2010 and 2050 (assuming lynx density and proportion cropland as in 2010, and 1.5  $^{\circ}\text{C}$  increase in winter temperatures) based on the best GLS local model.

(Oksanen *et al.* 1981). Consequently, land use and climate changes that increases ground primary productivity should favour mesopredators through increased prey availability and thereby relaxed resource constraints.

According to the projections, recolonizing lynx suppressed fox abundance in 2010. However, the contribution of this top-down force in limiting mesopredator abundance was lower in 2010 than in 1830, not only because of lower lynx abundance in 2010 but also because of environment enrichment. The impact of recolonizing lynx on

fox abundance was thus counteracted by the changes that had occurred in land use and climate. While a previous study has shown that apex predators, especially ambush predators, can buffer fluctuations in prey abundance (Wilmer, Post & Hastings 2007), we found that lynx abundance would have to be two times higher in 2050 than in 1830 to fully buffer against the environment enrichment over time and prevent a long-term increase in fox density (Fig. 4). This suggests that apex predator recolonization/recovery to historical levels would be insufficient to





**Fig. 3.** Red fox and Eurasian lynx bounty records and seed use in NDB. Coincident with the increase in seed use, the number of killed lynx decreased, while the number of killed foxes increased.

compensate for bottom-up changes of ecosystems that favour mesopredators. In a similar manner, primary productivity seems to influence the impact of top-down forces

such that lynx and grey wolf have less impact on roe deer abundance in more productive ecosystems (Melis *et al.* 2009), and the strength of negative cascading effects of large mammalian herbivores weakens in more productive ecosystems (Daskin & Pringle 2016).

Semi-natural grasslands-producing livestock fodder was an important component in the 19th century landscape. A previous study comprising parts of NDB showed that the proportion of grasslands declined by 90% from the early 1900s to the early 2000s, primarily replaced by coniferous forest (Cousins *et al.* 2015). Because grasslands are few and scattered in present-day Sweden and Finland, their potential effect on fox could not be estimated, but grasslands generally have a negative effect on fox density in Eurasia (Pasanen-Mortensen & Elmhagen 2015). However, rodents are an important food source for foxes (Lindström 1989), and in the Palearctic, rodent densities are higher in natural and semi-natural open habitats than in forests (Jędrzejewski *et al.* 1996). This suggests that the transition from semi-natural grasslands to forest might have been unfavourable for foxes.

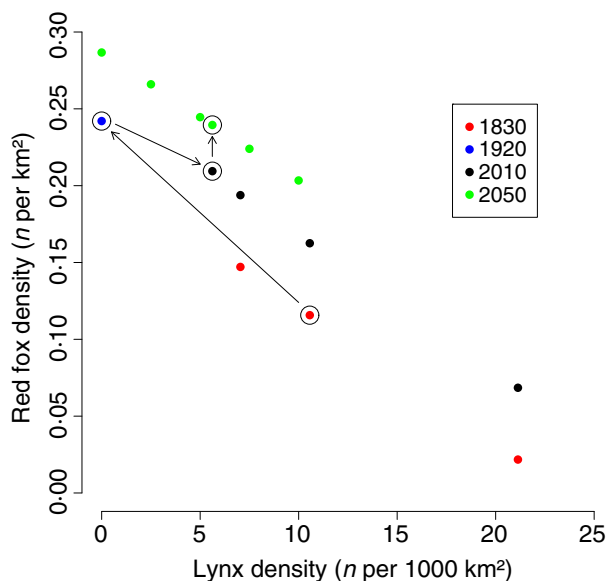
An assumption in this study was a linear (constant) effect of lynx on fox density. However, the relationship

**Table 4.** Projected red fox density ( $n\ km^{-2}$ ) over time in NDB using the best GLS models

	Deterministic projections			Stochastic projections	
	Min	Max	Area weighted mean	Mean	SD
<b>Regional model</b>					
1830, 10% lynx culling	-0.012	0.14	0.080	0.088	0.052
1830, 20% lynx culling	0.080	0.16	0.13	0.13	0.049
1830, 30% lynx culling	0.11	0.17	0.15	0.15	0.048
1920	0.17	0.20	0.18	0.19	0.047
2010	0.15	0.21	0.17	0.17	0.046
2010, lynx as 1830 10% culling	0.0029	0.16	0.097	0.11	0.050
2010, lynx as 1830 20% culling	0.095	0.18	0.15	0.15	0.047
2010, lynx as 1830 30% culling	0.13	0.19	0.16	0.17	0.046
2050, +1.5 °C, lynx absent	0.19	0.23	0.21	0.21	0.045
2050, +1.5 °C, 2.5 lynx/1000 km <sup>2</sup>	0.18	0.23	0.20	0.20	0.045
2050, +1.5 °C, 5 lynx/1000 km <sup>2</sup>	0.17	0.23	0.19	0.19	0.045
2050, +1.5 °C, lynx as 2010	0.17	0.22	0.19	0.19	0.045
2050, +1.5 °C, 7.5 lynx/1000 km <sup>2</sup>	0.16	0.22	0.18	0.18	0.045
2050, +1.5 °C, 10 lynx/1000 km <sup>2</sup>	0.15	0.20	0.17	0.17	0.046
<b>Local model</b>					
1830, 10% lynx culling	-0.15	0.12	0.022	0.025	0.061
1830, 20% lynx culling	0.022	0.19	0.12*	0.11	0.052
1830, 30% lynx culling	0.081	0.21	0.15	0.14	0.050
1920	0.14	0.31	0.24*	0.23	0.048
2010	0.11	0.28	0.21*	0.20	0.047
2010, lynx as 1830 10% culling	-0.12	0.18	0.068	0.075	0.058
2010, lynx as 1830 20% culling	0.055	0.25	0.16	0.16	0.050
2010, lynx as 1830 30% culling	0.11	0.27	0.19	0.19	0.048
2050, +1.5 °C, lynx absent	0.18	0.35	0.29	0.28	0.044
2050, +1.5 °C, 2.5 lynx/1000 km <sup>2</sup>	0.17	0.33	0.27	0.26	0.045
2050, +1.5 °C, 5 lynx/1000 km <sup>2</sup>	0.14	0.31	0.24	0.24	0.045
2050, +1.5 °C, lynx as 2010	0.14	0.31	0.24*	0.23	0.045
2050, +1.5 °C, 7.5 lynx/1000 km <sup>2</sup>	0.12	0.29	0.22	0.22	0.046
2050, +1.5 °C, 10 lynx/1000 km <sup>2</sup>	0.10	0.27	0.20	0.20	0.048

Culling rate used to estimate lynx density in 1830: 10, 20 or 30%.

\*The scenarios shown in Fig. 2.



**Fig. 4.** Effect of environmental enrichment due to climate and land use changes on red fox density, relative to the effect of lynx. Projected fox density is plotted against lynx density for each time step and scenario (Table 4; local model, area weighted mean fox density). Rings indicates scenarios in Fig. 2.

between top-down effects of apex predators and habitat productivity could be asymptotic, where the top-down effect weakens at high productivity (Ripple *et al.* 2014). For example, the effect of lynx predation on roe deer in Europe appears to be stronger at low habitat productivity (Melis *et al.* 2009). Likewise, lynx may prey on foxes to a larger extent in low-productive ecosystems when access to preferred herbivore prey is limited (Mattisson *et al.* 2011). In our study, a nonlinear top-down effect of lynx on fox could have two implications. First, projections may underestimate the negative effect of lynx in the 1830 projections, as roe deer was eradicated in NDB in the mid-1800s (Liberg *et al.* 2010). Hence lynx were restricted to a diet composed of smaller prey species, such as hare and galliformes, and competition between lynx and fox may have been higher than in present-day Sweden and southern Finland, where small ungulates are available. Second, if the top-down effect weakens at high productivity, we might overestimate the buffering capacity of lynx. A weaker top-down effect of lynx on fox at higher productivity may be similar to the effect of fox hunting in relation to productivity. Fox removal has been shown to decrease fox density at northern latitudes in Finland, but not at southern latitudes (Kauhala 2004), which could suggest that the effect of hunting weakens at high productivity.

Potential effects of fox hunting were not included in this study as data are too uncertain to use for modelling. Foxes were however hunted during the entire study period, and a speculation is that fox hunting was more intense in 1830,

and that it also could have had a stronger effect on fox populations in the low-productive ecosystem.

While loss of apex consumers has led to trophic downgrading (Estes *et al.* 2011), the resulting trophic cascades has raised a call for trophic rewilding (Svenning *et al.* 2016). The context dependence of apex predator effects, i.e. dependence on ecosystem productivity, must however be taken into account if apex predators are used in ecosystem restoration programmes (Ritchie *et al.* 2012). In our projections, the contribution of top-down limitation of mesopredators by a given number of apex predators became a less influential determinant of fox abundance as changes in bottom-up drivers pushed the ecosystem towards a more productive state. For the buffering capacity of apex predators to be realized, apex predator density must thus also be able to respond to environment enrichment. This is in accordance with theory predicting that predator density must increase with increasing productivity to maintain prey and mesopredator density at the same level as at lower productivity (Oksanen *et al.* 1981; Elmhagen *et al.* 2010).

Global changes in climate and land use can cause increased primary productivity (Nemani *et al.* 2003; Haberl *et al.* 2007), implying widespread environmental enrichment through bottom-up processes. We suggest that environmental enrichment is an overlooked mechanism causing increases of mesopredator and herbivore densities unless apex predators can respond numerically or behaviourally to the environment enrichment. This does not necessarily mean that increased apex predator abundance always is an optimal management measure – again awareness of ecosystem context is important, as increased apex predator abundance may have negative effects on other parts of transformed ecosystems (see e.g. Wittmer, Sinclair & McLellan 2005; Serrouya *et al.* 2011).

Apex predators such as large carnivores have declined world-wide, but they also have recolonized some ecosystems (Ripple *et al.* 2014). In Europe they have, and are currently, returning to highly anthropogenic ecosystems (Chapron *et al.* 2014). Our study highlights that recolonizing apex predators cannot be expected to set back an ecosystem to the previous structure if they return to an environmentally enriched ecosystem at the same abundance as before enrichment. Moreover, the results suggests that in ecosystems with extant apex predators, their contribution to the total limitation of mesopredators or prey will decrease if environmental enrichment is ongoing and the apex predators cannot respond numerically or behaviourally to this change.

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## Data accessibility

Data available from the Dryad Digital Repository, <https://doi.org/10.5061/dryad.dk6v5> (Pasanen-Mortensen *et al.* 2017).

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Appendix S1.** Relative change in projected red fox density between time steps and probability of change between time steps. A probability of 0.50 means an equal probability of increase and decrease between the two time steps, i.e. a random change.