

Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients

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Summary

1. The Mesopredator Release Hypothesis (MRH) suggests that top predator suppression of mesopredators is a key ecosystem function with cascading impacts on herbivore prey, but it remains to be shown that this top-down cascade impacts the large-scale structure of ecosystems.
2. The Exploitation Ecosystems Hypothesis (EEH) predicts that regional ecosystem structures are determined by top-down exploitation and bottom-up productivity. In contrast to MRH, EEH assumes that interference among predators has a negligible impact on the structure of ecosystems with three trophic levels.
3. We use the recolonization of a top predator in a three-level boreal ecosystem as a natural experiment to test if large-scale biomass distributions and population trends support MRH. Inspired by EEH, we also test if top-down interference and bottom-up productivity impact regional ecosystem structures.
4. We use data from the Finnish Wildlife Triangle Scheme which has monitored top predator (lynx *Lynx lynx*), mesopredator (red fox *Vulpes vulpes*) and prey (mountain hare *Lepus timidus*) abundance for 17 years in a 200 000 km² study area which covers a distinct productivity gradient.
5. Fox biomass was lower than expected from productivity where lynx biomass was high, whilst hare biomass was lower than expected from productivity where fox biomass was high. Hence, where interference controlled fox abundance, lynx had an indirect positive impact on hare abundance as predicted by MRH. The rates of change indicated that lynx expansion gradually suppressed fox biomass.
6. Lynx status caused shifts between ecosystem structures. In the ‘interference ecosystem’, lynx and hare biomass increased with productivity whilst fox biomass did not. In the ‘mesopredator release ecosystem’, fox biomass increased with productivity but hare biomass did not. Thus, biomass controlled top-down did not respond to changes in productivity. This fulfils a critical prediction of EEH.
7. We conclude that the cascade involving top predators, mesopredators and their prey can determine large-scale biomass distribution patterns and regional ecosystem structures. Hence, interference within trophic levels has to be taken into account to understand how terrestrial ecosystem structures are shaped.

Key-words: carnivores, interference competition, intraguild predation, linear mixed effect models, path analysis

Introduction

Large carnivores have a key function in terrestrial ecosystems when they suppress herbivores and indirectly prevent over-

grazing, but also when they suppress mesocarnivores and indirectly prevent excessive predation on mesocarnivore prey. Both these top-down cascades may impact local ecosystem structures and biodiversity (McLaren & Peterson 1994; Crooks & Soulé 1999; Terborgh *et al.* 2001; Sinclair, Mduma & Brashares 2003; Hebblewhite *et al.* 2005; Johnson, Isaac &

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Fisher 2007). However, classical ecosystem theory explains the regional structure of ecosystems only in terms of energy flows between trophic levels. It assumes that trophic levels act as homogenous units and that predation is the sole mechanism by which predators impact ecosystem structure (Hairston, Smith & Slobodkin 1960; Fretwell 1977; Oksanen *et al.* 1981; Oksanen & Oksanen 2000). Classical theory thereby overlooks suppression of mesocarnivores, which rarely involve significant levels of consumption (Palomares & Caro 1999). It is essential to explore alternative routes which may affect ecosystem structure (Berger, Gese & Berger 2008). The aims of this document are: (i) to test if the recolonization of a large carnivore reduces mesocarnivore abundance and has cascading effects on herbivore prey, and (ii) to apply classical ecosystem theory to this route of control and test if it impacts the large-scale structure of ecosystems.

Hairston *et al.* (1960) suggested that predators generally suppress herbivore densities and that plants therefore escape herbivore control. Fretwell (1977) added that the strength of top-down control and the number of trophic levels are determined by ecosystem productivity. These ideas were given a mathematical foundation as the Exploitation Ecosystems Hypothesis (EEH) (Oksanen *et al.* 1981; Oksanen & Oksanen 2000). For three-level ecosystems, EEH predicts that plants and predators are limited bottom-up by resource availability whilst herbivores are limited top-down by predation. This results in a regional ecosystem structure where predator and plant biomass increase with productivity, whilst herbivore biomass does not. Higher productivity may sustain additional trophic levels. In four-level ecosystems, which primarily are found in aquatic environments, secondary predators are sustained through predation on primary predators. Consequently, the biomass of secondary predators and herbivores increase with productivity, whilst the biomass of primary predators and plants do not (Fig. 1; Fretwell 1977; Oksanen *et al.* 1981; Oksanen & Oksanen 2000).

Exploitation Ecosystems Hypothesis regards trophic levels as the smallest ecosystem unit and exploitation, i.e. consump-

tion of individuals in lower trophic levels, as the mechanism which shapes ecosystem structure. In contrast, the Mesopredator Release Hypothesis (MRH) suggests that interference causes top predator suppression of mesopredators, which indirectly leads to increased prey abundance (Soulé *et al.* 1988; Crooks & Soulé 1999; Palomares & Caro 1999; Johnson *et al.* 2007; Ludwig 2007; Rayner *et al.* 2007; Thompson & Gese 2007; Berger *et al.* 2008; Ritchie & Johnson 2009). Furthermore, the strength of top predator control of mesopredators may increase with ecosystem productivity (Elmhagen & Rushton 2007). We suggest this could result in 'interference ecosystems' where interference divides the predators into two functional groups, top predators and mesopredators. A second route of control could form where some herbivores, the prey of mesopredators, are released from top-down control (Fig. 1). Within this route, the community structure would resemble a four-level exploitation ecosystem. That is, mesopredator biomass should be regulated top-down and not respond to changes in productivity, whilst the biomass of herbivore prey should increase with productivity. Where mesopredator release has occurred, the control mechanisms and community structure should be shifted. In these 'mesopredator release ecosystems', mesopredator biomass should increase with productivity, whilst prey biomass should not.

Large-scale data and substantial variation in baseline productivity are required to test EEH (Power 1992). Such data are hard to obtain and terrestrial trophic cascades have generally been studied on small spatial scales (Borer *et al.* 2005). Likewise, intraguild predation, mesopredator release and associated cascades have been rarely studied on the scales required to investigate the effect of interference on large-scale community structures (Elmhagen & Rushton 2007; Vance-Chalcraft *et al.* 2007). Here, we use a unique Finnish data set to analyse species biomass distributions and population trends over 17 years in a 200 000 km² study area which covers a distinct bioclimatic productivity gradient. We have the Eurasian lynx (*Lynx lynx* Linnaeus, 1758), the red fox

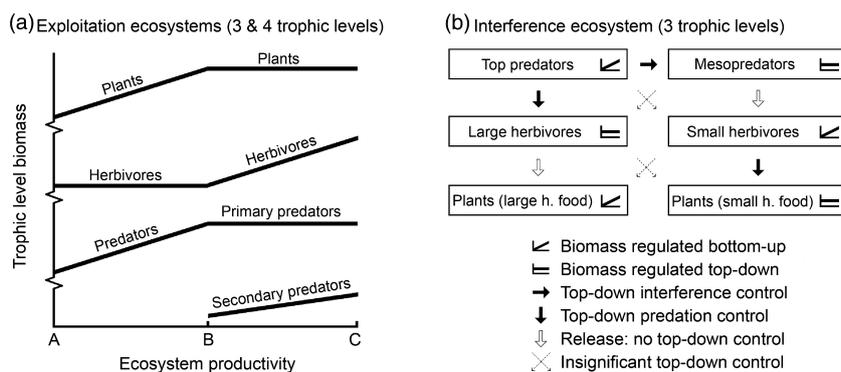


Fig. 1. Conceptual sketch illustrating predictions for exploitation and interference ecosystems. (a) In three-level exploitation ecosystems, predator and plant biomass increase with productivity, whilst herbivore biomass does not (A–B). At higher productivity (B–C), secondary predators form a fourth trophic level which causes cascading shifts in trophic control and biomass distributions in lower levels. (b) In three-level interference ecosystems, there are two routes of control. Top predators suppress large herbivores and mesopredators and indirectly release small herbivores and some plants from top-down control. Hence, trophic levels do not respond uniformly to top-down and bottom-up control. A prerequisite is that exploitation efficiencies differ between functional groups, e.g. that top predators do not significantly suppress small herbivores.

(*Vulpes vulpes* Linnaeus, 1758) and the mountain hare (*Lepus timidus* Linnaeus, 1758) that represent top predators, mesopredators and herbivores, respectively. Lynx is the dominant top predator in Finland and the red fox is the dominant mesopredator (Helle *et al.* 1996). Both predators prey on hare (Pulliainen, Lindgren & Tunkkari 1995; Kauhala, Laukkanen & von Rege 1998). The lynx was close to extinction in the 1950s, but immigrants from Russia re-established a population in eastern Finland in the 1960s. In the 1990s, there was a rapid increase in lynx numbers and distribution, most likely due to lowered hunting pressure after Finland entered the European Union and signed the Habitat Directive (Kojola 2004; Ludwig 2007).

The ongoing recolonization of lynx serves as a natural experiment which allows us to contrast regions which differ in top predator status. This is in full agreement with MRH, which often is evoked to predict how large carnivore management affect mesopredator abundances (Prugh *et al.* 2009). EEH on the other hand, assumes the top trophic level to be unexploited and consequently, that top predator biomass increases with productivity (Fretwell 1977). This may not be the case during recolonization and otherwise when top predators are managed. However, EEH implies that relatively low top predator densities should suffice to control mesopredators at low productivities, whilst higher top predator densities should be required at higher productivities (Fig. 1). Hence, during the early stages of recolonization when top predator densities are generally low, the impact of top predator control should be stronger in low productivity regions. Specifically, we therefore test:

1. If species distribution patterns support the mesopredator release model of control, i.e. if lynx biomass is negatively

related to fox biomass, whilst fox biomass is negatively related to hare biomass, when the effect of ecosystem productivity is taken into account. The analysis comprises the entire study area, i.e. both high and low productivity regions. Top predator control should therefore be stronger at low productivities.

2. If large-scale ecosystem structures are those predicted for (i) an interference ecosystem and (ii) a mesopredator release ecosystem, i.e.
 - (i) If lynx and hare biomass increase with ecosystem productivity, whilst fox biomass do not, in the least productive half of the study area where relatively low lynx densities should be sufficient to control fox biomass.
 - (ii) If fox biomass increase with ecosystem productivity, whilst lynx and hare biomass do not, in the most productive half of the study area where relatively high lynx densities should be required to control fox biomass.
3. If the increase and expansion of the lynx population in 1989–2005 gradually reverses the impact of mesopredator release on foxes and hares. The analysis comprises the entire study area, so top predator control should be stronger at low productivities.

Materials and methods

The study area consisted of Finland south of Finnish Lapland, which corresponds to the present distribution of lynx (Fig. 2a). The virtual absence of lynx in Lapland may in part be related to low habitat suitability, as lynx always was rare in this region (Kojola 2004). In addition, present-day management has aimed to keep lynx densities low in Lapland to avoid depredation on semi-domesticated reindeer (Ministry of Agriculture and Forestry 2007).

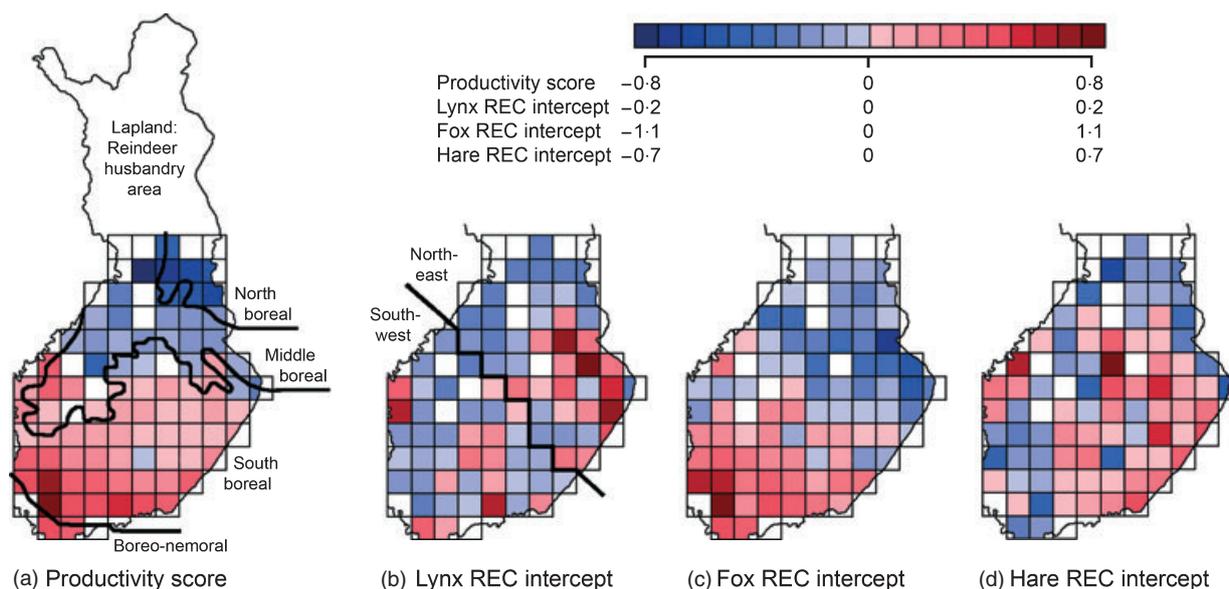


Fig. 2. Spatial variation in (a) the bioclimatic productivity score and (b–d) the RECs-intercept which represent biomass distributions. RECs-intercept show how much the biomass in each square deviates from the average biomass. The colour banding from blue (below average) to red (above average) represents the trend from low to high values. Taking productivity into account, lynx suppressed fox, whilst fox suppressed hare. Lynx had a stronger negative impact on fox biomass in relatively unproductive squares. White squares were excluded from the analyses (see Method). Vegetation zones after Ahti *et al.* (1968) are superimposed in (a). The north-eastern and south-western subregions are indicated in (b).

THE DATA

Winter track count data collected within the Finnish Wildlife Triangle Scheme were used as indices of lynx, fox and hare biomass. The scheme is a long term, large-scale survey which provides yearly estimates of the distribution and relative abundance of game species. The methods are described in detail by Lindén *et al.* (1996).

A wildlife triangle is a permanent line transect route of 12 km (4×3 km). Triangle locations represent different forest habitats in proportion to local occurrence. Each winter, 800–900 triangles distributed throughout Finland are surveyed by local hunters who count the number of fresh tracks crossing the transect. The count is either done 1–2 days after a snow fall or 24 h after a pre-check where all old tracks are marked. For each species, the data are compiled by the Finnish Game and Fisheries Research Institute as the number of crossings per 24 h per 10 km. Comparisons of relative species abundance are routinely made on a larger scale (50×50 km squares) using the average numbers of crossings per 24 h per 10 km. This appears to be a reasonable correlate of population size (Lindén *et al.* 1996) and should therefore reflect population biomass.

Thus, the unit used in statistical modelling was the average number of crossings per 24 h per 10 km, for each species, in each 50×50 square, each year. The final models used data collected during 9123 triangle surveys carried out in 82 squares in 1989–2005. This corresponds to a total of 109 000 km of transect line surveyed, or an average of 6.5 triangles surveyed per square and year.

ECOSYSTEM PRODUCTIVITY

The net primary production in Finland is primarily limited by temperature and solar radiation (Nemani *et al.* 2003). The study area encompassed boreo-nemoral and boreal vegetation zones which differ in climate and land cover (Fig. 2a, Ahti, Hämet-Ahti & Jalas 1968). The gradual transition from boreo-nemoral to north boreal zones reflects a gradient of decreasing ecosystem productivity, where the mean annual temperature decreases from 6 to 0 °C.

A score reflecting the bioclimatic productivity gradient was assigned to each 50×50 square (Fig. 2a). The productivity scores were obtained from the first axis of a Detrended Component Analysis of the proportion of different land covers in each square. Land cover data were retrieved from the EU Corine data base and the proportions of broad-leaved forests, mixed forests, coniferous forests, agricultural land, wetlands and shrubs were calculated for each square. Agricultural land was included because it is the most productive land covers that tend to be converted to arable land. The productivity scores agreed well with the productivity gradient suggested by the vegetation zones (Fig. 2a). They were also correlated to the average temperature sums in the growing season ($N = 82$, $R = 0.88$, $P < 0.001$), i.e. to the sum of temperatures all days in the year when $t \geq 5$ °C, averaged for 1989–2005. We are therefore confident that the scores reflect the gradient of ecosystem productivity in the study area.

STATISTICAL MODELLING

The wildlife triangle data were used as indices of species biomass to build linear mixed effect (LME) models which described population trends and biomass distributions. For each species, the retrieved LME model expressed the population trend as two fixed effects and 2×82 random effect coefficients (RECs). The fixed effects described the average population trend in the study area as a fitted regression line, where the fixed effect for intercept showed the average biomass

during the study period and the fixed effect for time showed the average rate of change. 50×50 km square was modelled as a random effect. The RECs consequently described to what extent the populations in each of the 82 squares deviated from the average. For example, a high positive REC-intercept implied that the biomass in that square was high above the average.

The LME models were developed using a progressive model building strategy (Pinheiro & Bates 2000). Likelihood ratio tests were used to compare and then identify the best models. Assumptions of normality in the within group errors and random effects were assessed with qq-plots following Pinheiro & Bates (2000). All 50×50 km squares south of Finnish Lapland were included in the first models ($N = 96$), but 14 squares were excluded during model building to achieve models which fulfilled assumptions of normality. The excluded outliers were 13 squares where lynx tracks never were recorded and one square with exceptionally high hare abundance. Furthermore, anomalies in the 1997 hare data caused the first hare model to deviate from assumptions of normality. Because there was no ecological explanation for the anomalies, hare data from this year were excluded. For all species, the final (best) models used centred and log-transformed ($\ln(x + 1)$) data from 82 squares (Fig. 2). All final models included random effects for the intercept and time covariate and autoregressive-moving average (ARMA) error structures to handle serial correlation in the residuals. LME modelling was undertaken using the nlme package in R (Ihaka & Gentleman 1996).

The 50×50 grid square is an arbitrary sampling unit considering the long-distance movement patterns of lynx. Given this and the distinct spatial component where lynx were recolonizing from a core area, there might have been spatial as well as temporal dependencies in the models. Whilst ARMA error structures were included in the LME models, it was not possible to include elements for spatial dependencies in the same model. The extent of spatial autocorrelation in the residuals was therefore tested separately for each species, each year, using Mantel tests (ecodist package in R; Goslee & Urban 2007). There was significant autocorrelation only in 9 of 51 cases (P -level 0.05, not corrected for multiple testing) and the extent of spatial autocorrelation did not change over time for any species. This indicates that spatial autocorrelation in the residuals was not a major problem.

The RECs from the final LME models were used in further analyses to test hypotheses 1 and 3; if biomass distributions (RECs-intercept) and population trends (RECs-time) supported MRH. Relationships between the variables were investigated through Structural Equation Modelling (SEM), specifically path analysis (Fox 2002). Path analysis partitions relationships between variables along hypothetical pathways of interaction which are identified *a priori*, and the variances and covariances of the variables are used to test for causal relationships. The models are fitted by maximum likelihood. A full *a priori* model was developed for each hypothesis and then compared to simpler models where non-significant pathways were excluded. Models were rejected if their covariance structure differed from that of the data. The best, parsimonious, model was identified as that with the smallest Bayesian Information Criterion (BIC) where all pathways were significant (Fox 2002). The models were fitted in R using the sem library (Fox 2002). The path analysis approach is appropriate when the ecological processes under study, e.g. species interactions, are sufficiently known to construct *a priori* path diagrams (Palomares *et al.* 1998; Elmhagen & Rushton 2007).

Both full models assumed that ecosystem productivity was an exogenous variable, whilst the species variables were endogenous variables. *A priori* theory, EEH, predicts that species biomass is regulated bottom-up when released from top-down control. Hence, pro-

ductivity had the potential to impact all species bottom-up and these pathways were included. The top-down control mechanisms suggested by MRH had *a priori* support as fox predation can suppress hare abundance (Kauhala & Helle 2000) and lynx can kill foxes to an extent where fox abundance is suppressed (Helldin, Liberg & Glöersen 2006; Ludwig 2007). Because lynx prey on hares (Pulliainen *et al.* 1995) a top-down pathway between lynx and hare was included in the models. The alternative, a bottom-up relationship between hare and lynx, had no *a priori* support as lynx and hare dynamics are unrelated (Kauhala & Helle 2000). If anything, this supports the top-down cascade suggested by MRH; lynx and hare dynamics should not be linked if the net impact of lynx is to release hare from top-down control.

We used robust regression to test hypothesis 2, the relationship between productivity scores and RECs-intercept for lynx, fox and hare in two subregions representing interference and mesopredator release ecosystems. We assumed that an interference ecosystem structure would exist in the least productive half of the study area, the north-eastern subregion, whilst we expected a mesopredator release ecosystem in the more productive south-west (Fig. 2b). In addition, ANCOVA with subregion as a factor was carried out to test if the relationship between species biomass and productivity differed between subregions. ANCOVA used the same data as the robust regressions, i.e. with significant outliers excluded. The base package in R was used for all tests.

Results

Linear mixed effect modelling of the winter track data confirmed that the recolonizing lynx population was increasing, but revealed declining trends in fox and hare (Table 1). The fitted regression lines (Table 1) correspond to untransformed intercept values of 0.10 lynx crossings per 24 h per 10 km, 4.0 fox crossings per 24 h per 10 km and 15.61 hare crossings per 24 h per 10 km. The annual increase in the lynx population was 11.5%, whilst the yearly decline in fox and hare was 0.87% and 0.82%, respectively. RECs-time and RECs-intercept were correlated in all species (lynx $r = 0.99$, fox $r = 0.93$, hare $r = 0.51$, all $P < 0.001$). Thus, rates of increase in lynx were higher where lynx biomass was high, whilst rates of decline in fox and hare were higher where fox and hare biomass was low.

The biomass distributions of lynx, fox and hare supported the MRH model of top-down control (Hypothesis 1, Fig. 2b–d). A correlation matrix between RECs-intercept and the productivity scores indicated that the biomass of all species increased with productivity. However, lynx and fox biomass were negatively related, whilst lynx and hare biomass were positively related. There was no relationship between hare and fox biomass (Table 2). In contrast to simple correlations, SEM takes into account the combined effects of several predictors on each variable. The lynx–hare and fox–hare pathways were not significant at $P < 0.05$ in the full model. However, the fox–hare pathway turned significant when the lynx–hare pathway, which had the highest P -value in the full model, was removed. The parsimonious model thereby revealed a top-down causal pathway where lynx biomass had a significant negative impact on fox biomass, whilst fox biomass had a significant negative impact on

Table 1. The fixed effects for intercept (biomass distribution) and time (rate of change) for the best LME models for each species

	Regression coefficients			d.f.	Order of ARMA error structure	Deviance explained (d^2)
	Value	T	P			
Lynx				1287	2	0.40
Intercept	0.099	10.40	< 0.0001			
Time	0.0087	6.23	< 0.0001			
Red fox				1287	4	0.58
Intercept	1.61	33.28	< 0.0001			
Time	−0.014	−3.96	0.0001			
Hare				1205	4	0.41
Intercept	2.81	73.49	< 0.0001			
Time	−0.023	−5.44	< 0.0001			

LME, linear mixed effect; ARMA, autoregressive-moving average.

Table 2. Pearson's correlations between the productivity scores and the RECs-intercept (biomass)

Variable	Lynx RECs		Fox RECs		Hare RECs	
	R	P	R	P	R	P
Productivity scores	0.23	0.038	0.67	< 0.001	0.30	0.005
Lynx RECs			−0.28	0.011	0.38	< 0.001
Fox RECs					−0.038	0.73

Significant correlations at $P < 0.05$ are highlighted in bold. All $N = 82$.

RECs, random effect coefficients.

hare biomass (Fig. 3). Although productivity had a significant positive impact on the biomass of all species, top-down control implied that fox biomass was lower than expected from productivity where lynx biomass was high, whilst hare biomass was lower than expected from productivity where fox biomass was high. The impact of top-down control was mediated by ecosystem productivity and stronger at low productivities (Figs 2 and 3).

The large-scale ecosystem structures supported Hypothesis 2. In the north-east, lynx and hare biomass increased significantly with productivity, whilst fox biomass did not (Fig. 4a–c). In the south-west, lynx biomass no longer increased significantly with productivity, indicating that lynx biomass was relatively low considering the productivity of the ecosystem. Instead, fox biomass increased significantly with productivity, whilst hare biomass did not (Fig. 4d–f). Significant interactions between subregion and productivity in ANCOVA confirmed that the slope of the regression lines differed between subregions for fox ($F = 66.43$, $P = 0.00062$) and hare ($F = 5.99$, $P = 0.015$). The interaction tended to be significant for lynx ($F = 3.83$, $P = 0.074$).

The long-term population trends supported the MRH prediction that lynx recolonization gradually led to suppression of fox biomass, but the expected increase in hare biomass failed to appear (Hypothesis 3, Fig. 5). Simple correlations

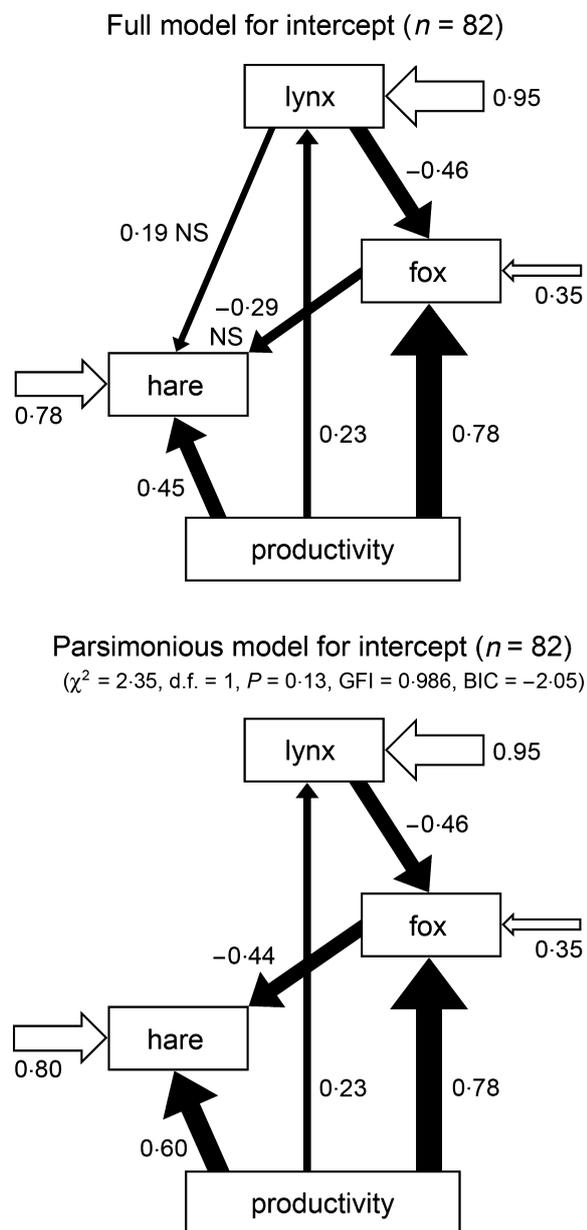


Fig. 3. The *a priori* (full) and parsimonious models used in SEM for RECs-intercept. The parsimonious model shows that lynx had a negative impact on fox whilst fox had a negative impact on hare. The top-down impact of lynx was mediated by productivity and stronger at low productivity. Black arrows indicate causal paths and standardized path coefficients. Outlined arrows indicate residual errors for the response variables. GFI = goodness-of-fit index, BIC = Bayesian Information Criterion, NS = not significant.

indicated that rates of increase in the lynx population were higher in productive squares, whilst rates of decline in fox were higher in unproductive squares. There was a significant negative correlation between rates of increase in lynx and rates of decline in fox. The rates of decline in hare were not related to the other variables (Table 3). SEM confirmed that high rates of increase in lynx corresponded to high rates of decline in fox. The impact was mediated by productivity and stronger at low productivities (Figs 5 and 6). The full model indicated that rates of decline in hare were lower where lynx

showed high rates of increase, and that hare declined less at low productivities. However, both these pathways drifted out of significance when the fox–hare pathway, which was not significant in the full model, was removed. Hence, the parsimonious model did not explain any variation in rates of decline in hare biomass (Fig. 6).

Discussion

This article is the first to demonstrate that the cascade involving top predators, mesopredators and their prey can transform large-scale biomass distribution patterns and shape regional ecosystem structures. In contrast to trophic cascades and predictions of traditional ecological theory, this cascade was triggered by interference interactions between top predators and mesopredators as predicted by MRH. For the study area as a whole, biomass distribution patterns supported the existence of a top-down route of control where high lynx biomass suppressed fox biomass, whilst high fox biomass suppressed hare biomass. When the study area was subdivided, we found two different ecosystem structures. First, an interference ecosystem where lynx suppression of foxes allowed hare biomass to escape top-down control and increase with productivity. Second, a mesopredator release ecosystem where fox biomass was regulated bottom-up and increased with productivity whilst hare biomass was regulated top-down. Thus, we show that changes in top predator status can cause shifts between top-down and bottom-up regulation of mesopredators and their prey.

The predicted impacts of interference and mesopredator release on large-scale ecosystem structures were derived from EEH. EEH was developed for endotherm communities but the theory suggests that interference, modelled as intraguild predation, has negligible effects on herbivore biomass in three-level boreal ecosystems (Oksanen *et al.* 1981; Oksanen & Oksanen 2000). In contrast, a recent meta-analysis showed that unidirectional intraguild predation among terrestrial invertebrates generally release shared prey from top-down suppression, as intermediate predators are more effective predators on the shared prey (Vance-Chalcraft *et al.* 2007). Such cascades may be wide-spread also in endotherm communities, since an increasing number of studies show that mesopredator release causes prey suppression whilst interference indirectly release prey (Prugh *et al.* 2009; Ritchie & Johnson 2009). In our study system, both lynx and foxes prey on hares (Pulliainen *et al.* 1995; Kauhala *et al.* 1998). In the north-eastern subregion where lynx indirectly released hare from top-down control, hare constitutes 86% of the lynx diet (Pulliainen *et al.* 1995). However, the fixed effects for intercept indicated that foxes were on average 40 times more abundant than lynx. This may explain why foxes were more effective predators on hares than lynx were.

Exploitation Ecosystems Hypothesis and intraguild predation theory suggest that intermediate predators are suppressed through intraguild predation. MRH accepts additional interference mechanisms such as intraguild killings and avoidance (Palomares & Caro 1999). EEH assumes

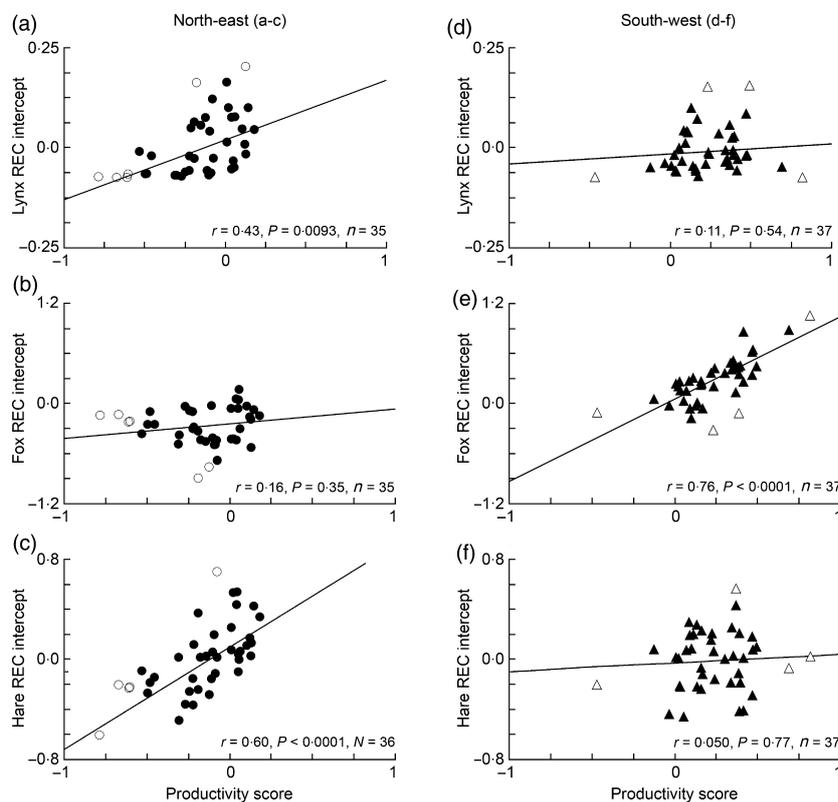


Fig. 4. Robust regressions between productivity scores and RECs-intercept for lynx, fox and hare. (a–c) In the north-east where lynx was relatively abundant, lynx and hare biomass increased with ecosystem productivity. (d–f) In the south-west where lynx was relatively rare considering the high productivity, only fox biomass increased with productivity. Outlined markers indicate outliers which were excluded from the regressions.

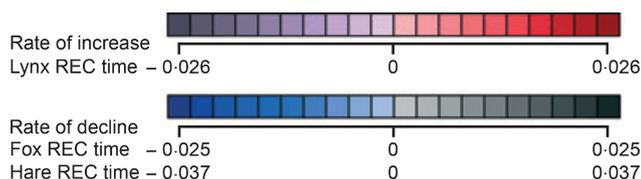
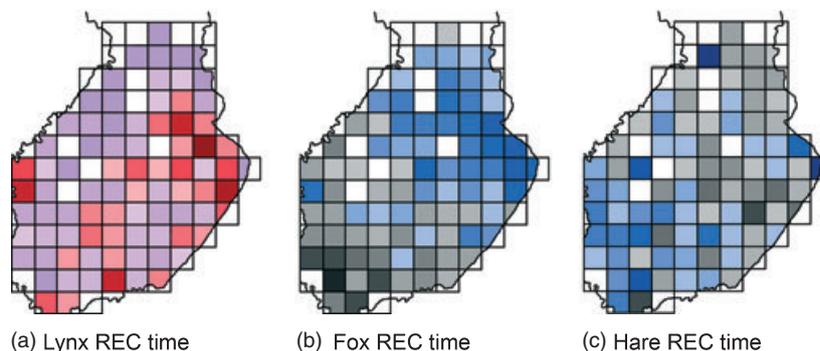


Fig. 5. Spatial variation in RECs-time which represent population trends. Purple-red colour banding represents rates of increase, whilst blue-black colour banding represents rates of decline. Red shades indicate high (above average) rates of increase, whilst blue shades indicate high rates of decline (above average) in fox and hare. In the unproductive east, high rates of increase in lynx corresponded to high rates of decline in fox. In the productive south, fox showed low rates of decline also where rates of increase in lynx were high.



linear food chains where secondary predators sustain themselves on primary predators. MRH allows for branched food chains and omnivory, where both top predators and mesopredators may sustain themselves on herbivore prey. Top predators may, or may not, feed on mesopredators (Prugh *et al.* 2009). Polis & Strong (1996) pointed out that important trophic links may be insignificant from a dietary perspective, because predators sometimes exert strong top-down control of prey which constitutes only a few per cent of their diets. Similarly, MRH and this study indicate that ecosystem links emanating from interference can represent key ecosystem

functions with strong impacts on ecosystem structure, although they are energetically negligible. For example, lynx often leave the foxes they kill uneaten, which indicates that interference in part results from intraguild killings motivated by other interests than food acquisition (Sunde, Overskaug & Kvam 1999). Moreover, fox constitutes a negligible few per cent of lynx diets (Pulliainen *et al.* 1995). Intraguild killings appear sufficient to explain the negative impact of lynx recolonization on foxes in Fennoscandia (Helldin *et al.* 2006). However, avoidance may reinforce the effects of intraguild killings and the habitat choice of a subdominant predator

Table 3. Pearson's correlations between the productivity scores and RECs-time

Variable	Lynx RECs (increase)		Fox RECs (decline)		Hare RECs (decline)	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Productivity scores	0.23	0.042	0.61	< 0.001	-0.05	0.65
Lynx RECs (incr.)			-0.33	0.028	0.17	0.13
Fox RECs (decl.)					-0.019	0.86

Note that RECs for lynx show rates of increase, whilst the RECs for foxes and hares show rates of decline. Hence, for example, the positive correlation between lynx and the productivity scores indicates high rates of increase in productive squares, whilst the positive correlation between fox and the productivity scores indicates high rates of decline in low productivity squares. Significant correlations at $P < 0.05$ are highlighted in bold. All $N = 82$. RECs, random effect coefficients.

may match predation risk rather than resource distribution (Thompson & Gese 2007). In extreme cases, the dynamics of a subdominant predator may be driven by avoidance alone (Shirley *et al.* 2009).

The Finnish lynx population increased by 11.5% per year, a rate very similar to the 11% annual increase observed in boreal Sweden, where lynx also expanded its distribution in the 1990s (Liberg & Andrén 2006). The long-term population trends confirmed that the increase and expansion of the Finnish lynx population gradually suppressed the fox population, but the predicted indirect effect on hare failed to appear. Instead the hare population declined, independent of the trends in the predator populations. It is well-established that red fox predation can drive hare dynamics and suppress hare abundance in present-day Fennoscandia (e.g. Lindström *et al.* 1994; Kauhala & Helle 2000). Hence, a recent change in the ecosystem may have caused hare to decline, e.g. indirect effects of the unusually mild winters in the 1990s and 2000s (Kauhala & Helle 2007). However, the full path model suggested that rates of decline in hare were lower where lynx showed high rates of increase. This relationship hints at the possibility that the increase in lynx had an indirect positive impact on hare, but if so, it was too weak to outweigh the negative impact of the factor which drove the decline. The lynx–hare relationship also drifted out of significance in the parsimonious model.

This study investigated both pattern and process, i.e. biomass distributions and long-term trends. The positive correlation between RECs-intercept and RECs-time showed that lynx increased more where it was relatively abundant. This should be expected under an assumption of logistic population growth during recolonization. Furthermore, lynx females disperse shorter distances than males and tend to settle close to their natal home range (Liberg & Andrén 2006). A bias towards migrating males may therefore have slowed down growth rates in squares where lynx was absent or rare at the start of the study period. RECs-intercept and RECs-time were correlated also in fox, reflecting the substantial impact of lynx on fox, where fox distribution patterns and

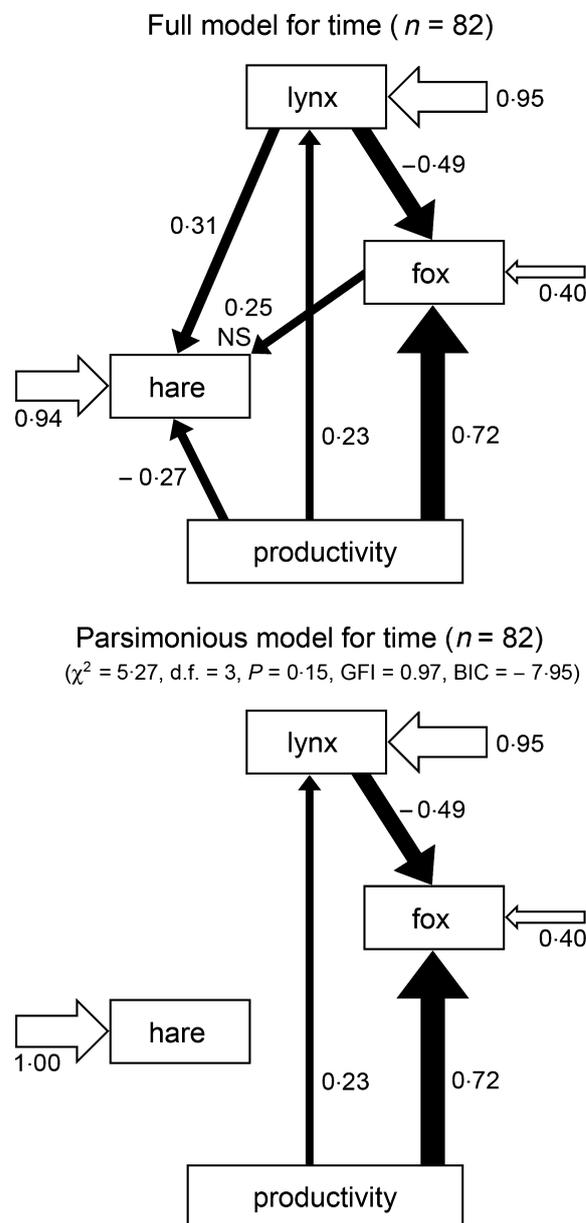


Fig. 6. The *a priori* (full) and parsimonious models for RECs-time. The parsimonious model shows that lynx expansion gradually suppressed fox, but the top-down impact was mediated by productivity and stronger at low productivity. The decline in hare was not driven by the variables under study. Black arrows indicate causal paths and standardized path coefficients. Outlined arrows indicate residual errors for the response variables. GFI = goodness-of-fit index, BIC = Bayesian Information Criterion, NS = not significant.

rates of change mirrored those of lynx. In hare however, the correlation between RECs-intercept and RECs-time was relatively weak. This corroborates the results of the path analyses, which showed that top-down control had an impact on hare biomass distribution, but not on recent population trends. When our study began, the biomass distribution of hare had 30 years to adjust to the gradual change in predator biomass distributions following the early recolonization of lynx. Despite the recent decline in the hare population, these relative biomass distributions are likely to have persisted,

since rates of decline in hare did not differ significantly between different parts of the study area.

Exploitation Ecosystems Hypothesis stipulates that the impact of the top trophic level should increase with productivity. This should cause a critical prediction to be fulfilled; the biomass of trophic levels regulated top-down should be held constant in relation to productivity (Oksanen *et al.* 1981; Oksanen & Oksanen 2000; Aunapuu *et al.* 2008). Lynx recolonization of Finland started in the east, but the productivity gradient had a south-western to north-eastern direction. For the north-eastern subregion, this implied that the most productive squares were colonized first, whilst the least productive squares were colonized first in the south-western subregion. Lynx expansion to the west thus provided a natural experiment where lynx biomass increased significantly with productivity only in the north-eastern subregion. The experiment was not perfect since recolonization was ongoing and there consequently was a lot of noise in the correlations. Despite this, the slope of the lynx-productivity regression lines tended to differ significantly between subregions. Furthermore, the path analyses showed that lynx regulation of fox biomass was stronger at low productivities, i.e. in the north-east. Taken together, this appears sufficient to shape the regional ecosystem structures as predicted by EEH theory. The critical prediction that biomass regulated top-down should be unrelated to productivity was satisfied for fox in the north-east and for hare in the south-west. Furthermore, hare biomass increased significantly with productivity in the north-east, whilst fox biomass did in the south-west.

This study focused on the route of control from large carnivores, via mesocarnivores, to medium-sized prey. The more explored route of control is the one where large carnivores suppress ungulates with cascading effects on forage plants (e.g. McLaren & Peterson 1994; Post *et al.* 1999; Hebblewhite *et al.* 2005; Wilmers *et al.* 2006). In boreal North-America, the large-scale biomass distributions of these groups follow the predictions of EEH for three-level ecosystems (Crête & Manseau 1996; Crête 1999). The above studies may therefore illustrate two parallel routes of control in 'interference ecosystems'. When interference divides the predators into functional groups which control different categories of prey, trophic levels may not respond homogeneously to top-down and bottom-up regulation (Fig. 1). Such interference ecosystems may characterize parts of boreal Fennoscandia. Lynx specialize on small ungulate prey where these are available (Jedrzejewski, Jedrzejewska & Szymura 1989). Small ungulates were absent from large parts of the Finnish study area, where moose (*Alces alces* Linnaeus, 1758) is the only native ungulate. However, south boreal Sweden, which was recolonized by lynx in the 1990s, provided high densities of roe deer (*Capreolus capreolus* Linnaeus, 1758). Lynx preyed primarily on roe deer, but suppressed foxes and roe deer alike. Meanwhile, grouse and hare showed increasing trends, indicating that small game had been released from fox control (Helldin 2004; Helldin *et al.* 2006). Parallel routes of control where some herbivores are controlled top-down whilst others are controlled bottom-up have previously been

described for the complex Serengeti ecosystem (Sinclair *et al.* 2003). This study indicates that such patterns exist also in fairly simple ecosystems in boreal Europe.

Mesopredator Release Hypothesis and EEH are not mutually exclusive theories. An interference ecosystem may be equivalent to a four-level exploitation ecosystem, if intraguild predation dominates the interference interactions and intraguild prey is dietary important. Likewise, the total biomass of trophic levels may conform to the predictions of EEH, even though the biomass of some functional groups shows opposite patterns. To sort out the mishmash of overlapping theories lies beyond the scope of this article. However, EEH inspired us to test the combined influence of top-down and bottom-up regulation processes on the cascade involving top predators, mesopredators and their prey. Our main results support the existence of a species cascade with substantial impacts on species biomass distributions and large-scale ecosystem structures. Finke & Denno (2004) found that increased predator diversity weakened top-down control of herbivores and the indirect effect on plants. By separating the predator guild into different functional groups, MRH pinpoints a mechanism behind such patterns. We conclude that top-down interference as well as bottom-up ecosystem productivity must be taken into account to understand patterns of trophic control and the processes that shape terrestrial ecosystem structures.

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References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, **5**, 169–211.
- Aunapuu, M., Dahlgren, J., Oksanen, T., Grelman, D., Oksanen, L., Olofsson, J., Rammul, Ü., Schneider, M., Johansen, B. & Hygen, H.O. (2008) Spatial patterns and dynamic responses of arctic food webs corroborate the exploitation ecosystems hypothesis (EEH). *American Naturalist*, **171**, 249–262.
- Berger, K.M., Gese, E.M. & Berger, J. (2008) Indirect effects and traditional trophic cascades: a test involving wolves, coyotes and pronghorn. *Ecology*, **89**, 818–828.
- Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D. & Halpern, B.S. (2005) What determines the strength of a trophic cascade? *Ecology*, **86**, 528–537.
- Crête, M. (1999) The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. *Ecology Letters*, **2**, 223–227.
- Crête, M. & Manseau, M. (1996) Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. *Evolutionary Ecology*, **10**, 51–62.
- Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563–566.
- Elmhagen, B. & Rushton, S.P. (2007) Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters*, **10**, 197–206.
- Finke, D.L. & Denno, R.F. (2004) Predator diversity dampens trophic cascades. *Nature*, **429**, 407–410.
- Fox, J. (2002) *An R and S-PLUS Companion to Applied Regression*. Sage, Thousand Oaks, CA.

- Fretwell, S.D. (1977) The regulation of plant communities and the food chains exploiting them. *Perspectives in Biology and Medicine*, **20**, 169–185.
- Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1–19.
- Hairston, N.G.F., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421–424.
- Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E. & Paquet, P.C. (2005) Human activity mediates a trophic cascade caused by wolves. *Ecology*, **86**, 2135–2144.
- Helldin, J.O. (2004) *Lynx Predation on red fox and its Secondary Effect on Prey Populations*. Report, Swedish University of Agricultural Sciences, Riddarhyttan.
- Helldin, J.O., Liberg, O. & Glöersen, G. (2006) Lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*) in boreal Sweden – frequency and population effects. *Journal of Zoology*, **270**, 657–663.
- Helle, E., Helle, P., Lindén, H. & Wikman, M. (1996) Wildlife populations in Finland during 1990–1995, based on wildlife triangle data. *Finnish Game Research*, **49**, 12–27.
- Ihaka, R. & Gentleman, R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 229–314.
- Jedrzejewski, W., Jedrzejewski, B. & Szymura, A. (1989) Food niche overlaps in a winter community of predators in the Białowieża Primeval Forest, Poland. *Acta Theriologica*, **34**, 487–496.
- Johnson, C.N., Isaac, J.L. & Fisher, D.O. (2007) Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society of London B*, **274**, 341–346.
- Kauhala, K. & Helle, P. (2000) The interactions of predator and hare populations in Finland – a study based on wildlife monitoring counts. *Annales Zoologici Fennici*, **37**, 151–160.
- Kauhala, K. & Helle, P. (2007) Metsäjäniskanta pienentynyt voimakkaasti. *Riista- ja kalatalous Selvityksiä*, **3**, 1–12. In Finnish with English summary.
- Kauhala, K., Laukkanen, P. & von Rege, I. (1998) Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. *Ecography*, **21**, 457–463.
- Kojola, I. (2004) Finland. *Status and Conservation of the Eurasian Lynx (Lynx Lynx) in Europe in 2001* (eds M. Von Arx, C. Breitenmoser-Würsten, F. Zimmermann & U. Breitenmoser), pp 78–85. Kora Bericht No. 19, Muri.
- Liberg, O. & Andrén, H. (2006) *The Lynx Population in Sweden 1994–2004. An Evaluation of Census Data and Methods*. Report, Wildlife Damage Center & Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan.
- Lindén, H., Helle, E., Helle, P. & Wikman, M. (1996) Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. *Finnish Game Research*, **49**, 4–11.
- Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J.E. (1994) Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. *Ecology*, **75**, 1042–1049.
- Ludwig, G.X. (2007) *Mechanisms of Population Declines in Boreal Forest Grouse*. PhD thesis, University of Jyväskylä, Jyväskylä.
- McLaren, B.E. & Peterson, R.O. (1994) Wolves, moose, and tree rings on Isle Royal. *Science*, **266**, 1555–1557.
- Ministry of Agriculture and Forestry. (2007) *Management Plan for the Lynx Population in Finland*. Ministry of Agriculture and Forestry 1b/2007, Vammalan Kirjapaino Oy.
- Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B. & Running, S.W. (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, **300**, 1560–1563.
- Oksanen, L. & Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist*, **155**, 703–723.
- Oksanen, L., Fretwell, S.D., Arruda, J. & Niemelä, P. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240–261.
- Palomares, E. & Caro, T.M. (1999) Interspecific killing among mammalian carnivores. *American Naturalist*, **153**, 492–508.
- Palomares, F., Ferreras, P., Travaini, A. & Delibes, M. (1998) Co-existence between Iberian lynx and Egyptian mongooses: estimating interaction strength by structural equation modelling and testing by an observational study. *Journal of Animal Ecology*, **67**, 967–978.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-effects Models in S and S-Plus*. Springer Verlag, New York.
- Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813–846.
- Post, E., Peterson, R.O., Stenseth, N.C. & McLaren, B.E. (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature*, **401**, 905–907.
- Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology*, **73**, 733–746.
- Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009) The rise of the mesopredator. *BioScience*, **59**, 779–791.
- Pulliaainen, E., Lindgren, E. & Tunkkari, P.S. (1995) Influence of food availability and reproductive status on the diet and body condition of the European lynx in Finland. *Acta Theriologica*, **40**, 181–196.
- Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K. & Clout, M.N. (2007) Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 20862–20865.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.
- Shirley, M.D.F., Elmhagen, B., Lurz, P.W.W., Rushton, S.P. & Angerbjörn, A. (2009) Modelling the spatial population dynamics of arctic foxes (*Vulpes lagopus*): the effects of red foxes and microtine cycles. *Canadian Journal of Zoology*, **87**, 1170–1183.
- Sinclair, A.R.E., Mduma, S. & Brashares, J.S. (2003) Patterns of predation in a diverse predator-prey system. *Nature*, **425**, 288–290.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Soric, M. & Hill, S. (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, **2**, 75–92.
- Sunde, P., Overskaug, K. & Kvam, T. (1999) Intraguild predation of lynxes on foxes: evidence of interference competition? *Ecography*, **22**, 521–523.
- Terborgh, J., Lopez, L., Nuñez, P.V., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. & Balbas, L. (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1926.
- Thompson, C.M. & Gese, E.M. (2007) Food webs and intraguild predation: community interactions of a native mesocarnivore. *Ecology*, **88**, 334–346.
- Vance-Chalcraft, H.D., Rosenheim, J.A., Vonesh, J.R., Osenberg, C.W. & Sih, A. (2007) The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology*, **88**, 2689–2696.
- Wilmers, C.G., Post, E., Peterson, R.O. & Vucetich, J.A. (2006) Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters*, **9**, 383–389.

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