

Please cite this paper as:

Elmhagen, B. and Rushton, S. P. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* **10**: 197-206.

Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up?

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Abstract

It has been argued that widespread extinctions of top predators have changed terrestrial ecosystem structures through mesopredator release, where increased abundances of medium-sized predators have detrimental effects on prey communities. This top-down concept has received much attention within conservation biology, but few studies have demonstrated the phenomenon. The concept has been criticized since alternative explanations involving bottom-up impacts from bioclimatic effects on ecosystem productivity and from anthropogenic habitat change are rarely considered. We analyse the response of a mesopredator (the red fox) to declines in top predators (wolf and Eurasian lynx) and agricultural expansion over 90 years in Sweden, taking bioclimatic effects into account. We show a top-down mesopredator release effect, but ecosystem productivity determined its strength. The impacts of agricultural activity were mediated by their effects on top predator populations. Thus, both top-down and bottom-up processes need to be understood for effective preservation of biodiversity in anthropogenically transformed ecosystems.

Keywords

Bioclimatic region, bottom-up, ecological communities, linear mixed effect models, mesopredator release, path analysis, species interactions, structural equation modelling, top predators, top-down.

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INTRODUCTION

Top-down trophic control is stronger in aquatic than terrestrial ecosystems (Shurin *et al.* 2002) and only a small number of trophic cascades involving terrestrial mammals have been described (Schmitz *et al.* 2000). Nevertheless, mammalian top predators are considered to be major determinants of trophic structure and biodiversity in terrestrial ecosystems (McLaren & Peterson 1994; Palomares & Caro 1999; Sæther 1999; Terborgh *et al.* 1999, 2001; Sinclair *et al.* 2003, Hebblewhite *et al.* 2005). As well as impacting herbivore communities, they kill predators in lower trophic levels (Palomares & Caro 1999). Reductions in top predator abundances can therefore cause a mesopredator release, where increased abundances of medium-sized predators have detrimental impacts on the underlying

prey community (Soulé *et al.* 1988; Crooks & Soulé 1999). The concept of mesopredator release has received much attention within conservation biology, to explain abnormally high mesopredator abundances and declines in the abundance or diversity of prey, and it has formed an argument for restoration of top predator populations to regain pristine ecosystem structures (Palomares & Caro 1999; Sæther 1999; Terborgh *et al.* 1999).

Evocations of the mesopredator release hypothesis have often been made *post hoc*, when large predators are already rare or extinct and there are effectively no data available with which to test the hypothesis (Sæther 1999; Terborgh *et al.* 1999). In effect, past processes have been inferred from snapshots of current form. The whole concept of

mesopredator release as a driver of ecosystem structure is in fact rather simplistic. It assumes that the role of man is that of an apex predator with top-down effects cascading via top predators, but ignores bottom-up effects arising from anthropogenic transformation of the landscapes in which the mesopredators are found (Litvaitis & Villafuerte 1996; Larivière 2004). Furthermore, the top-down hypothesis takes no account of the fact that the trophic structure of ecological communities depends on ecosystem productivity and that the strength of trophic interactions is unlikely to be the same in all ecosystems (Oksanen & Oksanen 2000). The relative impact of top-down (predation) and bottom-up (food/nutrient) processes in determining the structure of terrestrial ecosystems remains largely untested and controversial (Litvaitis & Villafuerte 1996; Pace *et al.* 1999; Larivière 2004).

It has been argued that the rise to present dominance of the red fox (*Vulpes vulpes* L.) in the Scandinavian predator community occurred because of mesopredator release (Lindström 1989a; Sæther 1999). Wolves (*Canis lupus* L.) and Eurasian lynx (*Lynx lynx* L.) were widely distributed in Scandinavia in the early 19th century before persecution had reduced both species to near-extinction by 1920 (Flagstad *et al.* 2003; Rueness *et al.* 2003). The Eurasian lynx occupies a similar top position in the ecosystem as the wolf, since they both specialize on ungulate prey when these are available. The red fox in contrast is a generalist predator on smaller prey and a scavenger (Jedrzejewski *et al.* 1989). Both wolves and lynx also kill red foxes (Palomares & Caro 1999). It has been suggested that the near-extinction of top predators released red foxes and had cascade effects on lower trophic levels (Sæther 1999), since predation by red foxes now suppresses populations of small game prey such as grouse and hare (*Lepus timidus*) as well as smaller predators such as pine marten (*Martes martes* L.) (Lindström *et al.* 1994, 1995). Furthermore, competition following a range expansion of the red fox has been argued as a factor causing the near extinction of the arctic fox (*Alopex lagopus* L.) in Scandinavia (Tannerfeldt *et al.* 2002). However, the 19th century was also characterized by rapid human population growth and agricultural expansion. The resultant mixed agricultural landscapes now holds the highest population densities of red foxes in Scandinavia since their prey here are most abundant (Angelstam *et al.* 1984; Kurki *et al.* 1998), suggesting that the expansion of agriculture may have favoured foxes through fragmentation of relatively unproductive forest landscapes. This anecdotal evidence suggests that both top-down and bottom-up processes have affected the trophic structure of this terrestrial ecosystem.

The near-extinction of top predators and the concurrent transformation of the landscape in Scandinavia provide a natural experiment where key top-down and bottom-up

drivers of mesopredator dynamics changed over time. Here we use human census, headage and agricultural data collected by Swedish government authorities from 23 counties over 90 years (1828-1917) and Linear Mixed Effects models to investigate the relative impact of bottom-up agricultural change and top-down mesopredator release on the red fox at the national scale as they happened. The study area, Sweden, was 450 000 km² and comprised 4 bioclimatic regions representing a marked productivity gradient ranging from nemoral (deciduous broad-leaf forest), through boreo-nemoral (mixed forest) and boreal (coniferous taiga forest) regions to alpine tundra. We also use the large scale data set to test the hypothesis that top-down constraint of mesopredators depended on the bioclimatic gradient of ecosystem productivity. Specifically, we address the hypothesis that changes in trophic structure were greatest in productive regions, since these had the potential to sustain high densities of both top predators and red foxes and this was where changes in agricultural activity were most marked. We show that the growth rates of red fox populations depended on both top-down and bottom-up processes and that these depended on bioclimatic region.

METHODS

The data

We retrieved data on the number of wolves, lynx and red foxes killed in each county from 1828 to 1917 from Sweden's Official Statistics (Sveriges Officiella Statistik 1870-1917, 1879). Swedish authorities also collected data on the amount of cereal seed (wheat, rye, barley, oats and mixed seed) used for sowing in each county (Sveriges Officiella Statistik 1827-1860, 1866-1917). We used this as an index of the proportion of land under arable cultivation. From 1866, there were data also on the area of arable land. We analysed the relationship between the amount of seed used and the reported area of arable land in each county in 1870, 1880, 1890, 1900 and 1910. There was a consistent, strong positive correlation between these variables (Pearson's $R = 0.93-0.95$, $N = 23$, all $P < 0.0001$) indicating that seed use provided a good index of the proportion of arable land in the landscape. Finally, we included the number of human inhabitants in each county in the analyses since this variable may impact on the intensity of predator persecution. We retrieved data on the number of people in each county every five years from Sweden's Statistical Database (<http://www.scb.se>). All data – predators killed, barrels of seed used and human population – were standardized by area before the analyses (number per 1000 km²).

There were gaps in all data series except that of human population (Fig. 1). The hunting records contained gaps in

particular in the 1840s and 1870-1875. The gaps in the 1840s were not explained, whilst the latter gap was caused by a reorganization of data collection procedures. This also applied to the seed data. Up until 1860, data were reported every five years as the yearly average for the period, whilst data were reported every year after 1866 (Fig. 1; Gadd 1999; Medin 1999). We did not extrapolate data to cover intervening years but used the data available to model rates of change in each variable over the study period.

The productivity gradient

Sweden stretches 1570 km from south to north. The length of the growing season ranges from an average of 220 days per year in the nemoral broad-leaf forests of south-western Sweden to 100 days in the alpine tundra in the north-west (SMHI 1961-1990). To achieve a variable which represents

this gradient in ecosystem productivity, we performed a Detrended Correspondence Analysis of the percentage distribution of different bioclimatic regions (alpine tundra, north boreal, south boreal, boreo-nemoral, nemoral) in each county (Fig. 2b). The resultant bioclimatic variable represented a trend from large positive values in the most productive counties to large negative values in the least productive counties. The first axis of this ordination explained 87% of the variation in cover of each bioclimatic region and so was considered to capture the bioclimatic variation across counties. The bioclimatic axis scores were significantly correlated with the latitude of the county centroids ($R = -0.90, P < 0.001$).

Model building strategy

We used Linear Mixed Effect models to investigate the rate of change with time in the number of foxes, lynx and wolves killed, the amount of seed used and human population size. The number of lynx and wolves (top predators) killed were pooled in each county since preliminary analyses showed that they followed similar trends.

A progressive model building strategy (Pinheiro & Bates 2000) was used to develop models for each variable. We started with simple models assuming no random effects, a linear (or curvilinear where appropriate) relationship between response and time with independent errors. Models were made more complex with the inclusion of random effects for the intercept and time covariate and appropriate error structures. Analyses showed that residuals were serially correlated for some models, necessitating the use of off-diagonal error components in the error matrices of final models. Models with autoregressive error structures were used for the models relating seed use, top predator and red fox variables to time since the likelihood ratio tests showed that these provided better fits to the data than did models assuming an independent error structure. As we had data available for each of the 23 counties present in Sweden, we investigated the variation in rates of change for each variable at the county level, with county modelled as a random effect. However, the model for top predators did not include the southernmost county since wolf and lynx already were extinct here by the start of the study period. In effect, we produced models describing the average (fixed effects) rate of change with time for each variable for Sweden as a whole and random effects which showed how the rates of change in each county deviated from that general trend.

We used likelihood ratio tests to compare and then identify the best models during the modelling building process. Assumptions of normality in the within group errors and the random effects were assessed using qq-plots following Pinheiro and Bates (2000). Analyses were undertaken using the nlme package in R (Ihaka & Gentleman 1996).

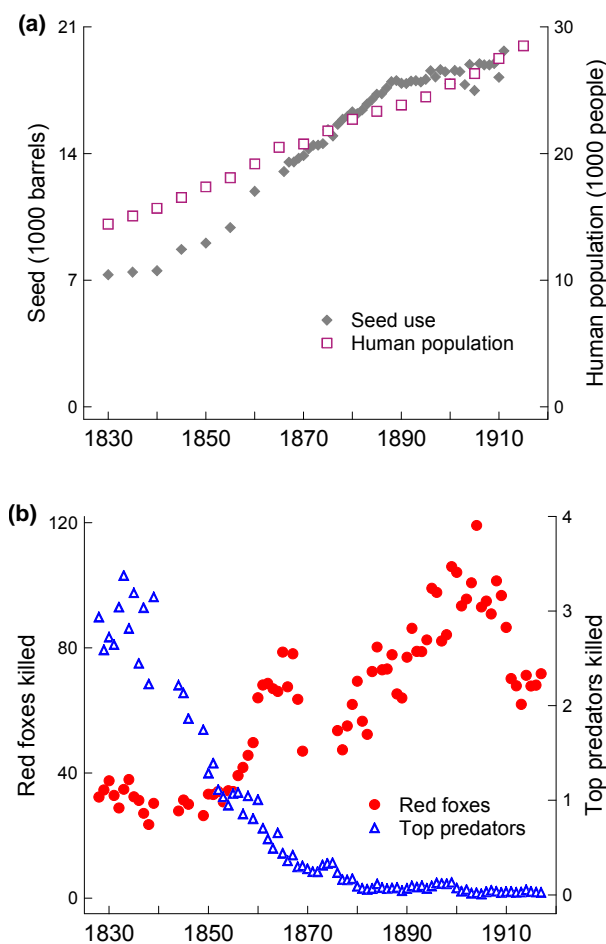


Figure 1 Changes in (a) human population size, (a) seed use, (b) red foxes killed and (b) top predators killed when averaged over all counties in Sweden during the study period. All variables are standardized by area (no. per 1000 km²).

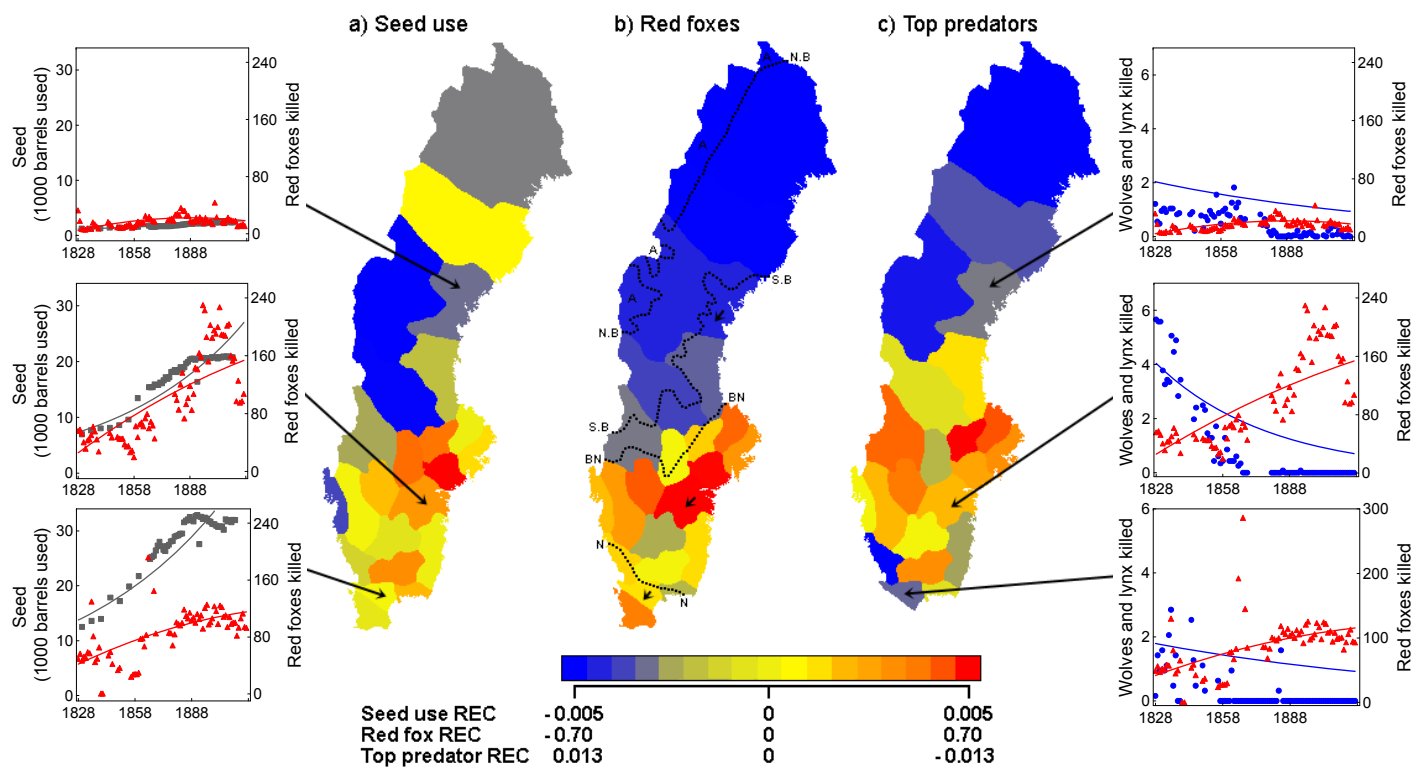


Figure 2 Spatial variation in the RECs of each county relating to rates of change in (a) barrels of seed used, (b) red foxes killed and (c) top predators killed. The colour banding from blue through green to red represents the trend from lower to higher than average rates of change in each parameter. Rates of change were generally higher in the south. For top predators, the highest rates of change had negative RECs, as they represent a decline. Examples of the actual trends in each variable standardized by area (no. per 1000 km²) are shown for three counties with fitted regression lines (red = red fox; grey = seed used; blue = top predators). Top predators had already been eradicated from the southernmost county by 1828 and they were close to extinction in the other nemoral counties. The relatively low rates of change in seed use in the nemoral (southern) counties reflects a reduced agricultural expansion in a region where a large proportion of suitable land already was under cultivation, and the low rates of decline in top predators reflect the final extinction of already decimated populations. Map (b) also illustrates the bioclimatic regions in Sweden. The dotted lines are the northern borders of the nemoral (N), boreo-nemoral (BN), south boreal (S.B) and north boreal (N.B) regions. Areas of alpine tundra are marked with A.

Causal relationship between variables

The outputs from the LME-models were interpreted in the following way. The regression coefficients for the fixed effect (time) in the models were an estimate of the mean rate of decline or increase for Sweden as a whole in each variable. The coefficients of random effects for the time covariate for each county represented the difference in rate of change of the response variable relative to the average of the whole country. Long-term trends in hunting records may be affected both by changes in population sizes and by changes in hunting effort because of, for example, changes in hunting methods, bounty systems and fur prices. We assumed that these changes in hunting effort were similar all over Sweden. As such they would not impact on the differences in random effects for counties, but rather on the trend for Sweden as a whole as represented by the fixed effects. We consequently tested if the “rate” coefficients of the random effects for the counties for the fox model were correlated with those of the other models, i.e. if the deviations of the individual counties in the rates of change in

the number of foxes killed were related to the deviations in rates of change in top predator killed, seed use and human population density. To test if ecosystem productivity affected rates of change in the variables, we also correlated the random effects against the bioclimatic axis achieved through the DCA analysis.

We used Structural Equation Modelling (SEM) and path analysis (Fox 2002) to investigate the causal relationships between the variables using the covariance matrix derived from the random effects. Path analysis is a method for partitioning relationships amongst variables on the basis of hypothetical pathways of interaction that are identified *a priori*. The paths between variables are relationships which are expressed in equation form, where the response variables are driven by one or more predictor variables, and the response variables in one equation may form predictors in others, thereby forming sequences of causal relationships. SEM tests whether the variables in the path are interrelated by examining the variances and covariances of the variables. Models are fitted by maximum likelihood. By comparing

goodness of fit criteria (GFI) and Bayes Information Criterion (BIC) estimated for each model it is possible to compare competing models of the underlying processes and identify the parsimonious model for the available data (Fox 2002). SEM and path analysis has previously been used to investigate intraspecific relationships between predators and was then recommended for other cases where the knowledge of the natural history of the system is sufficient to construct *a priori* path diagrams (Palomares *et al.* 1998).

We developed a full model and then compared this with simpler models which did not include pathways for which the association was shown to be non-significant. We assessed the extent to which covariance structure of the model differed from a fully saturated model using χ^2 and rejected any model where the covariance structure of the model was different to that of the data. The best pathway model was identified as that with the smallest BIC where all interaction paths were significant (Fox 2002). The models were fitted in R using the sem library (Fox 2002).

The full model assumed that there were two exogenous variables. These were the bioclimatic axis representing county level productivity and human population growth rate. The remaining rates of change in seed use and predators killed were assumed to be endogenous variables whose values were determined by the pathways in the model. We assumed that productivity would impact on all endogenous variables, since high productivity should facilitate arable activities and sustain higher densities of predators. A rapidly growing human population should have a positive impact on seed use and could impact on the number of predators killed. Any increase in rates of expansion in agricultural activity should impact on rates of expansion of foxes through improving habitat quality through increased food availability (Angelstam *et al.* 1984; Kurki *et al.* 1998) and negative effects on top predators by increased exposure to human hunters, in effect habitat loss or degradation, as today (IUCN Cat Specialist Group 2002; Mech & Boitani 2004).

Finally, we assumed that declines in top predators would impact on the number of foxes killed due to decreased predation pressure, i.e. mesopredator release (Palomares & Caro 1999). Our assumption that agricultural expansion had different effects on foxes and top predators is also based upon differences in the hunting methods used and the general vulnerability of the species to human control. Fragmented landscapes should have facilitated wolf hunting in particular, since a common 19th century hunting method was to have beaters drive wolves towards hunters. The hunting success for foxes on the other hand should have been relatively independent of landscape composition, since foxes were often trapped. Furthermore, top predators are known to be vulnerable to human persecution (IUCN Cat Specialist Group 2002; Mech & Boitani 2004), whilst red foxes are notorious for being hard to control and fox hunting

Table 1 The fixed effects for time for the best models for each of the variables.

	Regression coefficients			Order of AR error structure*	Deviance explained (d ²)
	T	d.f.	P		
Red foxes**					
time	5.31	1602	< 0.0001	6	0.70
time ²	-2.35	1602	0.0187		
Top predators	-8.86	1533	< 0.00001	3	0.71
Seed use	18.27	1169	< 0.00001	1	0.99
Human population	10.51	389	< 0.00001	-	0.998

The fixed effects for time (average rate of change) for the best models for each of the variables red foxes, top predators, seed use and human population. All regression coefficients were significantly different from zero.

* All variables but human population showed serial dependency in the residuals. Hence, these models included autoregressive (AR) error structures of different orders.

** The best fox model included a quadratic variable for time, representing an unimodal response to time with a small post peak decline.

bags hence tend to reflect fox densities but not impact on them (Kurki *et al.* 1998, Baker & Harris 2006).

RESULTS

General trends in the data

Despite an emigration of approximately 1 million people to North America, the human population in Sweden doubled from 2.8 to 5.6 million during the study period and the increase was close to linear. Seed use increased exponentially until the 1890s when the increase levelled off (Fig. 1a). The annual kill of top predators in Sweden declined exponentially. In contrast, the annual kill of foxes increased over time, but the increase levelled off around the turn of the century (Fig. 1b). The fixed effects (average rate of change) for the best LME-models utilized log-transformed data for all variables but foxes killed for which the best model included a quadratic variable for time effectively representing an unimodal response with a small post peak decline (Table 1). For the fox we only considered the random effect coefficients for the linear component in the subsequent analyses since these represent the linear component (the growth component) of the data.

Impacts on red foxes and relationships between the variables

The random effects coefficients (RECs) for the rates of change of all of the red fox, top predator, seed use and human variables differed between the counties, indicating that there was considerable spatial variation in the dynamics of each parameter (Fig. 2).

Table 2 Correlations between the bioclimatic variable and the rate of change variables.

Variables	Human population		Seed use		Top predators killed		Red foxes killed	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Bioclimatic axis	- 0.29	0.18	0.53	0.011	- 0.34	0.12	0.79	< 0.0001
Human population			- 0.27	0.23	0.12	0.61	- 0.27	0.22
Seed use					- 0.46	0.030	0.63	0.0016
Top predators killed							- 0.55	0.0079

Pearson's correlations between the bioclimatic axis and the rate of change variables. The correlations were performed between the first axis of a Detrended Correspondence Analysis of the bioclimatic template and the random effects coefficients of the rate equations for the other variables. Significant correlations at $P < 0.05$ level are highlighted in bold. Top predators were already extinct in the southernmost county by the start of the study period, hence $N = 22$ in all correlations.

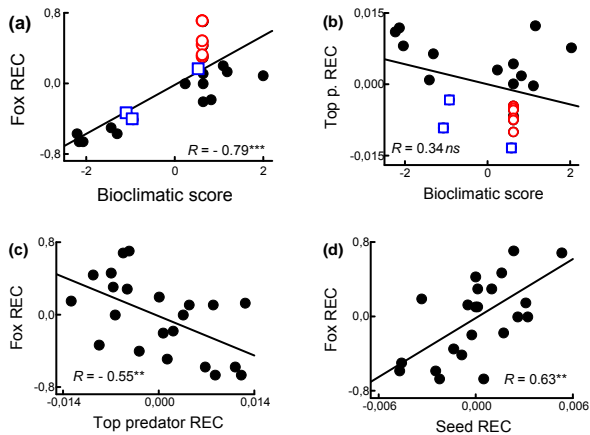


Figure 3 Correlations between RECs of red foxes killed and (a) the bioclimatic axis, (c) top predator RECs and (d) seed use RECs, and the correlation between (b) top predator RECs and the bioclimatic axis. The highest rates of decline in top predators were concentrated to the boreo-nemoral (bioclimatic score 0.62) and south boreal regions. In the boreo-nemoral region, these high rates of decline corresponded well with high rates of increase in red foxes (a, b; six data points marked as red circles). High rates of decline of top predators in the south boreal region did not correspond with such increases in red foxes (a, b; three data points marked as blue squares)

RECs for foxes killed and the amount of seed used were positively related to the bioclimatic variable, indicating that both rates of change were higher in productive southern Sweden (Table 2; Fig. 3). The RECs for foxes and seed use were positively correlated with each other, suggesting that the rate of fox expansion was linked to the rate of agricultural expansion. The RECs for top predators killed were negatively correlated with the RECs for seed use, indicating that the rate of decline in top predators was linked to agricultural expansion, but the rate of decline was not correlated with the bioclimatic axis (Table 2; Fig. 3). The RECs for foxes killed were negatively correlated with those for top predators killed, indicating that rates of increase in red foxes were most rapid where rates of decline in top predators also was the most rapid (Table 2; Fig. 3). The RECs for rates of change in the human population were not related to those of seed use or either predator, suggesting

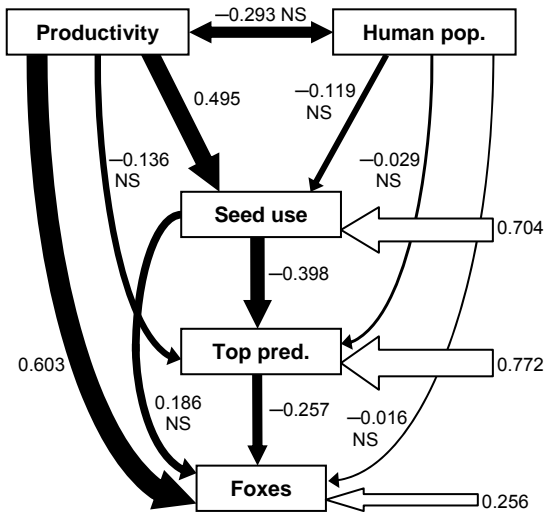
that these processes were not strongly linked (Table 2). In other words, the change in the number of foxes killed was faster in more productive regions where seed use also increased most rapidly. However, the rates of increase in foxes were most accelerated in boreo-nemoral counties which also showed the highest rates of decline in top predators (Fig. 2 and 3).

We investigated the causal relationships between the variables using SEM and path analysis. Standardized coefficients on each pathway of the full model (which had a χ^2 of zero) are shown in Fig. 4(a) and the parameter estimates for the model are given in Table 3. None of the pathways involving human population growth rate were significant, so this variable was removed from all subsequent models, leaving only one exogenous variable, landscape productivity. Likewise, the pathway between productivity and top predators was not significant and was also removed. The pathway between seed use and top predator changes was not significant at $P < 0.05$ in the null model but became so in the parsimonious model after the other pathways had been removed (Table 3). The parsimonious model, where the BIC was the lowest, included all of the endogenous variables. Productivity had significant direct effects on fox population growth rate and rate of increase in seed use. Changes in top predators also had significant direct effects on fox population growth rate, whilst the effect of agricultural expansion on red foxes was indirect through its effect on top predators (Fig. 4b).

For the most parsimonious model (Fig. 4b) the direct contribution of the exogenous variable landscape productivity to rates of change in fox population was 0.701, whilst the indirect effects through, seed usage and decline in top predators was $0.531 * -0.463 * -0.324 = 0.079$. The ratio of the relative contribution of direct versus indirect effects of the exogenous variables to the change in fox population growth rate was therefore $0.701/0.079$ indicating that productivity by itself had a greater direct impact (9.7 times) than the indirect route through mesopredator release. Nonetheless this indicates that both bottom-up (productivity) and top-down (decline in top predators as driven by seed use and productivity) processes were responsible for the observed patterns of fox population growth rates.

(a) Full model

$\chi^2 = 0$, $df = 0$, $P =$ Not applicable, $GFI = 1$, $BIC = 0$



(b) Parsimonious model

$\chi^2 = 4.41$, $df = 3$, $P = 0.62$, $GFI = 0.92$, $BIC = -14.13$

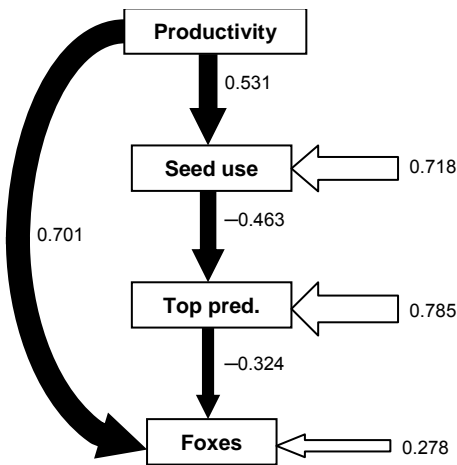


Figure 4 The *a priori* models used in path analyses and summaries of path analysis results. Single-pointed black arrows indicate causal paths and path coefficients. Single-pointed outlined arrows indicate residual errors for the response variables. The full model (a) assumes that background productivity (the bioclimatic axis) and human population growth are the major drivers of change in seed use, top predators killed and red foxes killed. Note that the value assigned to the productivity – human population growth rate path (the double-pointed black arrow) is the correlation coefficient. The parsimonious model (b) assumes that productivity impacts directly on the rate of increase in red foxes and indirectly through the increased seed use and its negative impacts on top predators. $GFI =$ Goodness of Fit Index, $BIC =$ Bayesian Information Criterion, $NS =$ Not Significant.

Table 3 Parameter Estimates from the Structured Equation Modeling Analysis of the pathways for the full (null) model.

Relationship	Estimate	Std Err.	z	Pr(> z)
Prod.–seed use	0.0010	0.00040	2.6	0.0097
Prod.–top pred	-0.00085	0.0014	-0.6	0.55
Prod.–foxes	0.21	0.047	4.5	0.000064
Human–seed use	-0.097	0.15	-0.6	0.53
Human–top pred	-0.071	0.49	-0.1	0.88
Human–foxes	-2.2	15.8	-0.1	0.89
Human–prod.	-0.0011	0.00087	-1.3	0.20
Seed use–top pred	-1.2	0.68	-1.7	0.081
Seed use–foxes	31.2	23.6	1.3	0.18
Top pred–foxes	-14.5	7.1	-2.0	0.040
Prod.	1.5	0.46	3.2	0.0012
Human	0.0000098	0.0000030	3.2	0.0012
Seed use	0.0000045	0.0000014	3.2	0.0012
Top pred.	0.000044	0.000014	3.2	0.0012
Foxes	0.046	0.014	3.2	0.0012

Significant pathways at $P < 0.05$ level are highlighted in bold. The pathway between seed use and top predators was not significant in this model but became so in the parsimonious model after the other pathways had been removed.

DISCUSSION

These analyses are the first to demonstrate the combined role of top-down mesopredator release and bottom-up habitat change on mesopredators as they occurred. Unlike previous research they have been undertaken at a large scale (Schmidt 2003) – a scale appropriate for analysing the underlying population processes of large vertebrates (man and top predators) – and they are the only analyses that have considered the bottom-up impact of productivity along a bioclimatic gradient at the landscape scale. We found a distinct mesopredator release effect in response to declining top predator populations, but baseline ecosystem productivity appeared to set an upper limit to the impact. Thus, the most rapid rates of decline in top predators coincided with much accelerated red fox growth rates in the productive boreo-nemoral region, whilst the release effect appeared negligible in low productivity boreal and alpine areas. Rates of expansion within agriculture were most pervasive in productive bioclimatic regions and had a direct negative impact on top predators.

Data necessary to study processes acting on large spatial and temporal scales are hard to obtain. Historic data may lack the precision of data obtained from controlled experiments and hunting records may reflect changes in hunting effort rather than changes in population sizes (Myrberget & Pedersen 1993). We therefore need to consider how the quality of the data may have influenced the results. Until the early 19th century, pastoral agriculture was the norm in Sweden. Livestock grazed in the forests in summer, hay was gathered from meadows and bogs, whilst there were only

small patches of arable field. The 19th century mechanization and rationalizations meant that obstacles in the fields, for example patches of trees, were removed and water bodies were drained. Previously unsuitable land could be cultivated and fragmented patches of arable land were merged into large fields. This led to a shift from pastoral to arable agriculture and the proportion of arable land in the landscape increased (Slotte 2001). The increase in seed use reflects these changes. The fact that agricultural yield increased faster than the population consuming it in the mid 19th century (Fig. 1a) is supported by the fact that Sweden temporarily achieved an exportable surplus of cereal crops during this period (Gadd 1999; Medin 1999). However, the seed use data for the first third of our study period were reported only as five-year averages. It is possible that the seed models were less accurate as a result of the coarse nature of these data. This might explain why a direct effect of seed use on foxes was not significant. Wolf and lynx were eliminated from all but the three northernmost counties where they were near-extinct at the end of the study period (Flagstad *et al.* 2003; Rueness *et al.* 2003). This implies a strong relationship between data describing the decline in top predators killed and the decline in actual population sizes. For red foxes, there is no substantial information about long-term trends in 19th century populations independent of the hunting records. However, rates of change in human population density, which we hypothesized to have affected hunting efforts, did not impact on rates of change in foxes killed. Instead, rates of change in foxes were associated with the rates of decrease in top predator populations, ecosystem productivity and, indirectly, to rates of increase in seed use. These trends were evident in all counties sampled, in effect repeated 23 times in a study area of 450 000 km², providing strong evidence that the trends we observed in the data were real and not artefact.

This study covered a spatial scale where top-down and bottom-up impacts on predators could be compared in different bioclimatic regions. Rates of decline in top predators were only indirectly related to ecosystem productivity, via agricultural expansion. This pattern has a historic explanation. Top predators had already been exterminated in the southernmost county by 1828 and neighbouring populations were severely diminished. Nemoral counties were therefore characterized by low rates of decline, which made the simple correlation between top predators and baseline productivity non-significant. In contrast, top predators remained abundant in several boreo-nemoral counties in 1828, subsequently characterized by rapid rates of decline. It was also here that rates of increase in red foxes killed were most rapid. The lowest rates of change in foxes were found in the low productivity boreal and alpine regions. Although southern boreal counties showed relatively rapid rates of decline in top predators,

there was no corresponding increase in foxes, indicating that the top-down constraint was less important than bottom-up control through baseline productivity.

The distinct response by red foxes to top predator extinction in the boreo-nemoral region supports the mesopredator release hypothesis. Mesopredators are suppressed in the presence of top predators and cannot exploit the productivity potential of the ecosystem, but they increase when the top-down restraint disappears. In low productivity ecosystems however, a lack of a mesopredator release could reflect reduced interaction between top predators and mesopredators at low population densities, with top-down suppression being non-existent. Alternatively, low productivity may simply limit mesopredator abundances, leaving no capacity for mesopredator populations to grow when top predators are removed.

We suggest that the “bioclimatic” impact on the mesopredator release effect in Sweden represents fundamental differences in the population ecology of foxes and their prey. In present-day Sweden, the productive boreo-nemoral region sustains dense, socially regulated red fox populations and fox reproductive success is stable because the region offers an abundant and diverse prey community (Angelstam *et al.* 1984; Lindström 1989b). This implies a potential for strong effects of top-down control, since top predator extinction may have caused a shift to bottom-up control, similar to effects found in small-scale experiments (Schmitz *et al.* 2006). In the boreal and alpine regions in contrast, red foxes depend on cyclic rodents as prey and this is reflected both in reproductive success and fox population dynamics (Angelstam *et al.* 1984; Lindström 1989b). The rodent cycle is driven by highly specialized small mustelid predators (Hanski *et al.* 2001), but may not be substantially influenced by foxes since a drastic decline in red fox numbers due to an epidemic of fatal mange in the 1970s did not affect the rodent cycle in Sweden (Lindström *et al.* 1994). Such asymmetrical relationships with strong bottom-up effects by rodents on foxes, but little effect of foxes on rodents, also exists in Arctic ecosystems where arctic foxes exploit lemming peaks and fluctuate violently in response to them, whilst small mustelids drive the cycle (Gilg *et al.* 2003). Thus, a pervasive impact of bottom-up control on red foxes in northern Sweden implies that fox populations regularly decline due to food shortage. Hence, we suggest that most of the productivity potential already was exploited when top predators declined in the 19th century and the release effect was therefore negligible.

What are the implications of our findings? A comparison of historic (mainly 19th century) and present distributions of mammal species on six continents showed that their combined distributions had declined by 68% and that population extinctions were concentrated to regions with high human densities or intense human activities such as

agriculture and hunting (Ceballos & Ehrlich 2002). This indicates that alterations of ecosystem structures involving both top-down and bottom-up anthropogenic impacts are widespread. Understanding top-down and bottom-up control mechanisms is necessary for effective management of ecosystems in order to preserve biodiversity. This will be increasingly important as species distributions, species associations and ecosystem structures change in response to climate change (Burns *et al.* 2003). It has been suggested that over-abundant mesopredator populations should be managed by top predator reintroductions to re-establish top-down control (Terborgh *et al.* 1999). We suggest that this is a simplistic conclusion and that a broader perspective is needed to preserve biodiversity in anthropogenically altered ecosystems. Firstly, reintroducing top predators to ecosystems where they have been eradicated may suppress mesopredator populations. However, if overabundance of mesopredators results from decreased bottom-up control, this may not be a sufficient remedial management action. Secondly, if the relative impact of top-down and bottom-up regulation depends on bioclimatic region and the underlying mesopredator-prey dynamics, it cannot be assumed that reintroductions of top predators will have the same impact in all ecosystems. Finally, the impact of top predators on ecosystem structures depends on top predator densities. Proper trophic cascades in terrestrial ecosystems, i.e. cascades with effects extending from top predator to plant levels, have only been shown for wolves in North American national parks (McLaren & Peterson 1994; Pace *et al.* 1999; Post *et al.* 1999; Hebblewhite *et al.* 2005). These cases are unique in the sense that they represent ecosystems left relatively much to regulate themselves. Hardly any protected areas in Europe are 'pristine' or large enough to sustain viable top predator populations and conservation plans generally rely on management of top predators in multi-use landscapes where there may be conflicts with human activities (Linnell *et al.* 2001). These strategies may allow for conservation of the top predator species in focus, but the top predator densities tolerated by land users may not have strong effects on ecosystem structures.

In conclusion, this paper provides good evidence that both top-down and bottom-up processes are important determinants of mesopredator numbers. They also demonstrate that bioclimatic region – effectively ecosystem productivity – determines the relative strength of the trophic interactions. These findings increase our understanding of trophic control in terrestrial ecosystems and have implications for conservation schemes. Studies on model ecosystems have shown that diverse predator communities can dampen cascade effects on lower trophic levels (Finke & Denno 2004). Our analyses indicate that the impacts of top predators in constraining mesopredator populations will depend on ecosystem productivity. In productive ecosystems, restoration of top

predators may buffer against other anthropogenically induced changes to mesopredator populations and facilitate the preservation of species on lower trophic levels, but this may not be the case in unproductive ecosystems.

ACKNOWLEDGEMENTS

We thank Martin Embley, Diane Srivastava, John Fryxell and three anonymous referees for constructive comments on the manuscript. B.E. and this research were funded by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning.

REFERENCES

- Angelstam, P., Lindström, E. & Widén, P. (1984). Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, 62, 199-208.
- Baker, P.J. & Harris, S. (2006). Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? *Eur. J. Wild. Res.*, 52, 99-108.
- Burns, C.E., Johnston, K.M. & Schmitz, O.J. (2003). Global climate change and mammalian species diversity in U.S. national parks. *Proc. Nat. Acad. Sci.*, 100, 11474-11477.
- Ceballos, G. & Ehrlich, P.R. (2002). Mammal population losses and the extinction crisis. *Science*, 296, 904-907.
- Crooks, K.R. & Soulé, M.E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, 400, 563-566.
- Finke, D.L. & Denno, R.F. (2004). Predator diversity dampens trophic cascades. *Nature*, 429, 407-410.
- Flagstad, Ø., Walker, C.W., Vilà, C., Sundqvist, A.K., Fernholm, B., Hufthammer, A.K. *et al.* (2003). Two centuries of the Scandinavian wolf population: patterns of genetic variability and migration during an era of dramatic decline. *Mol. Ecol.*, 12, 869-880.
- Fox, J. (2002). *An R and S-PLUS Companion to Applied Regression*. Thousand Oaks, CA: Sage.
- Gadd, J.O. (1999). Präster och landshövdingar rapporterar. Allmän jordbruksstatistik 1802-1864. [Priests and county governors report. General statistics of agriculture 1802-1864. In Swedish] In: *Svensk jordbruksstatistik 200 år [Swedish agricultural statistics 200 years]*. Statistics Sweden. pp. 29-48.
- Gilg, O., Hanski, I. & Sittler, B. (2003). Cyclic dynamics in a simple vertebrate predator-prey system. *Science*, 302, 866-868.
- Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. (2001). Small-rodent dynamics and predation. *Ecology*, 82, 1505-1520.
- Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M. *et al.* (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, 86, 2135-2144.
- Ihaka, R. & Gentleman, R. (1996). R: A language for data analysis and graphics. *J. Comput. Graph. Stat.*, 5, 229-314.
- IUCN Cat Specialist Group. (2002). *Lynx lynx*. 2006 IUCN Red List of Threatened Species. www.iucnredlist.org.
- Jedrzejewski, W., Jedrzejewska, B. & Szymura, A. (1989). Food niche overlaps in a winter community of predators in the Bialowieza Primeval Forest, Poland. *Acta Theriol.*, 34, 487-496.
- Kurki, S., Nikula, A., Helle, P. & Lindén, H. (1998). Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. *J. Anim. Ecol.*, 67, 874-886.
- Larivière, S. (2004). Range expansion of raccoons in the Canadian prairies: review of hypotheses. *Wildl. Soc. Bull.*, 32, 955-963.

- Lindström, E. (1989a). The role of medium-sized carnivores in the Nordic boreal forest. *Finn. Game. Res.*, 46, 53-63.
- Lindström, E. (1989b). Food limitation and social regulation in a red fox population. *Holarct. Ecol.*, 12, 70-79.
- Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L. *et al.* (1994). Disease reveals the predator: Sarcoptic mange, red fox predation, and prey populations. *Ecology*, 75, 1042-1049.
- Lindström, E.R., Brainerd, S.M., Helldin, J.O. & Overskaug, K. (1995). Pine marten – red fox interactions: a case of intraguild predation? *Ann. Zool. Fenn.*, 32, 123-130.
- Linnell, J.D.C., Swenson, J.E. & Andersen, R. (2001). Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? *Biodiv. Cons.*, 9, 857-868.
- Litvaitis, J.A. & Villafuerte, R. (1996). Intraguild predation, mesopredator release and prey stability. *Conserv. Biol.*, 10, 676-677.
- McLaren, B.E. & Peterson, R.O. (1994). Wolves, moose, and tree rings on Isle Royal. *Science*, 266, 1555-1557.
- Mech, L.D. & Boitani, L. (2004). Grey wolf *Canis lupus*. In: *Canids: Foxes, wolves, jackals and dogs – status survey and conservation action plan*. (eds. Sillero-Zubiri, C., Hoffmann, M. & Macdonald, D.W.). IUCN/SSC Canid Specialist Group. pp. 124-129.
- Medin, K. (1999). Statistiska centralbyrån tar över. Allmän jordbruksstatistik 1865-1920. [Statistics Sweden takes over. General statistics of agriculture 1865-1920. In Swedish] In: *Svensk jordbruksstatistik 200 år [Swedish agricultural statistics 200 years]*. (eds. Gadd, C.J. & Jorner, U.) Statistics Sweden. pp. 49-85.
- Myrberget, S. & Pedersen, H.C. (1993). Using historical data in studies on cycles in small rodent and small game populations: a reply. *Oikos*, 66, 547-550.
- Oksanen, L. & Oksanen, T. (2000). The logic and realism of the hypothesis of exploitation ecosystems. *Am. Nat.*, 155, 703-723.
- Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, 14, 483-488.
- Palomares, E. & Caro, T.M. (1999). Interspecific killing among mammalian carnivores. *Am. Nat.*, 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. *J. Anim. Ecol.*, 67, 967-978.
- Pinheiro, J.C. & Bates, D.M. (2000). *Mixed-Effects Models in S and S-plus*. Springer Verlag, New York.
- Post, E., Peterson, R.O., Stenseth, N.C. & McLaren, B.E. (1999). Ecosystem consequences of wolf behavioural response to climate. *Nature*, 401, 905-907.
- Rueness, E.K., Jorde, P.E., Hellborg, L., Stenseth, N.C., Ellegren, H. & Jakobsen, K.S. (2003). Cryptic population structure in a large, mobile mammalian predator: the Scandinavian lynx. *Mol. Ecol.*, 12, 2623-2633.
- Sæther, B.E. (1999). Top dogs maintain diversity. *Nature*, 400, 510-511.
- Schmidt, K.A. (2003). Nest predation and population declines in Illinois songbirds: a case for mesopredator effects. *Conserv. Biol.*, 17, 1141-1150.
- Schmitz, O.J., Hambäck, P.A. & Beckerman, A.P. (2000). Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.*, 155, 141-153.
- Schmitz, O.J., Kalies, E.L. & Booth, M.G. (2006). Alternative dynamic regimes and trophic control of plant succession. *Ecosystems*, 9, 659-672.
- Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B. *et al.* (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.*, 5, 785-791.
- Sinclair, A.R.E., Mduma, S. & Brashares, J.S. (2003). Patterns of predation in a diverse predator-prey system. *Nature*, 425, 288-290.
- Slotte, H. (2001). Harvesting of leaf-hay shaped the Swedish landscape. *Landscape Ecol.*, 16, 691-702.
- SMHI, Swedish Meteorological and Hydrological Institute. (1961-1990). Average length of the growing season in Sweden 1961-1990. <http://www.smhi.se> (accessed on 29 September 2006)
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, M. & Hill, S. (1988). Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.*, 2, 75-92.
- Sveriges Officiella Statistik. (1827-1860). *Kungl. Maj:ts Befallningshafvandes Femårsberättelser*. [Sweden's Official Statistics. *The Five-year Reports of the Royal Majesty's Officials*. In Swedish.]
- Sveriges Officiella Statistik. (1866-1917). *Jordbruk och Boskapsskötsel - Hushållningssällskapens Berättelser. Årsrapporter*. [Sweden's Official Statistics. *Agriculture and Stock-farming. Yearly reports*. In Swedish.] Norstedt & Söner, Stockholm.
- Sveriges Officiella Statistik. (1870-1917). *Skogsväsendet. Årsberättelser*. [Sweden's Official Statistics. *Forestry. Yearly reports*. In Swedish.] Norstedt & Söner, Stockholm.
- Sveriges Officiella Statistik. (1879). *Skogsstyrelsen Underdåniga Berättelse angående Skogs- och Jaktväsendet i Sverige intill år 1870*. [Sweden's Official Statistics. *The National Board of Forestry's Humble Report on Forestry and Hunting in Sweden up until 1870*. In Swedish.] Norstedt & Söner, Stockholm.
- Tannerfeldt, M., Elmhagen, B. & Angerbjörn, A. (2002). Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, 132, 213-220.
- Terborgh, J., Estes, J.A., Paquet, P., Ralls, K., Boyd-Heger, D., Miller, B.J. *et al.* (1999). The role of top carnivores in regulating terrestrial ecosystems. In: *Continental conservation: design and management principles for long-term, regional conservation networks*. (eds. Soulé, M. & Terborgh, J.). Island Press, Covelo, CA and Washington DC. pp. 39-64.
- Terborgh, J., Lopez, L., Nuñez, P.V., Rao, M., Shahabuddin, G., Orihuela, G. *et al.* (2001). Ecological meltdown in predator-free forest fragments. *Science*, 294, 1923-1926.

This manuscript was accepted by Ecology Letters on November 27 (2006) and published in March 2007.

It should be cited as:

Elmhagen, B. and Rushton, S. P. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters* **10**: 197-206.