Original article

Land cover effects on mesopredator abundance in the presence and absence of apex predators

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A B S T R A C T

Trophic downgrading due to loss of apex consumers has been detected in many ecosystems. Loss of larger predators implies that medium-sized mesopredators rise to the status of apex predators which are limited bottom-up rather than top-down. Hence the density of medium-sized predators should be more strongly related to land cover in absence of larger predators. We investigate this hypothesis at a continental scale (Eurasia) for a medium-sized predator, the red fox *Vulpes vulpes*, in presence and absence of an apex predator, the Eurasian lynx *Lynx lynx*. We predicted that in absence of lynx, fox density should be positively associated with open land covers, as these could favour foxes due to high prey availability. Our results showed that fox abundance was independent of land cover in presence of lynx. However, in absence of lynx, fox density was positively but asymptotically related to cropland, while negatively related to grassland. Fox density was highest when cropland constituted approximately 30% of the landscape, likely reflecting an optimal composition of foraging and breeding habitat. Grassland was associated with low productivity, likely reflecting low prey availability. Thus, cropland is favourable for red fox, but only in absence of top-down limitation by lynx. We suggest that there are two ecosystem states in Eurasia, one northern where lynx is present as an apex predator, and one south-eastern where red fox assumes the apex predator position and its abundance is subsidised by anthropogenic land cover.

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1. Introduction

Apex consumers can exert strong limitation of lower trophic levels, or on other species within the same trophic level, with cascading effects on lower trophic levels. Hence, loss of apex consumers implies trophic downgrading, where biotic interactions are lost or altered and ecosystems can transition to alternative states. Apex consumers therefore play an important role in the preservation of biodiversity, ecosystem function and regulation processes (Estes et al., 2011). Large predators typically function as apex consumers, which are limited by resource availability through bottom-up processes but also exert strong top-down control of the trophic level below (Estes et al., 2011; Fretwell, 1977; Oksanen et al., 1981; Oksanen and Oksanen, 2000). In ecosystems with long food chains, the lower level can consist of smaller predators which are suppressed through predation or interference competition (Berger et al., 2008; Carpenter et al., 1985; Elmhagen et al., 2010; Estes

et al., 2011, 1998; Fretwell, 1977; Levi and Wilmers, 2011; Ripple et al., 2014; Ritchie and Johnson, 2009). Hence, extirpation of large predators can cause mesopredator release, where smaller predators increase in abundance (Elmhagen et al., 2010; Estes et al., 2011; Soulé et al., 1988). Theory then predicts a shift from top-down to bottom-up control of mesopredators as they assume the apex position in the food chain. At the landscape scale, this entails that the abundance of smaller predators should become related to prey availability, and ultimately to bioclimatic factors such as productivity (Elmhagen et al., 2010). In addition, anthropogenic landscape changes can increase productivity (Haberl et al., 2007) and lead to fragmentation which alters the abundance and distribution of species (Fahrig, 2003). Habitat generalists may gain from fragmentation, and be more abundant in a fragmented landscape (Andrén, 1992; Andrén et al., 1997). Mesopredators are often generalists, and increased abundance of mesopredators can increase predation pressure and be detrimental for sensitive prey, for example some bird species (Crooks and Soule, 1999; Kurki et al., 2000; Soulé et al., 1988).

The red fox (*Vulpes vulpes*) is a mesopredator in large parts of its distribution range, where it is limited by the Eurasian lynx (*Lynx*

lynx), but it has been released from top-down limitation by Eurasian lynx in south-western Eurasia. In contrast, the grey wolf, which also co-occur with the red fox, does not seem to have a limiting effect on red fox abundance (Pasanen-Mortensen et al., 2013). The stronger interaction between red fox and lynx may be related to more intense interspecific competition, as the frequency of intraguild killing — the killing and sometimes also consumption of an individual that exploit the same resources, and the process that underlies limitation of mesopredators — is mainly observed when the dominant species is somewhat larger than the subordinate, but then decreases as the dietary overlap decreases at high body size differences (Donadio and Buskirk, 2006; Palomares and Caro, 1999). The Eurasian lynx generally weighs 2–3 times more than the red fox, and is known to kill foxes and limit their abundance (Elmhagen et al., 2010; Helldin et al., 2006; Matyushkin and Vaisfeld, 2003; Ritchie and Johnson, 2009). The lynx-induced mortality is additive, at least to some degree (Helldin et al., 2006). Interference competition is also evident, as foxes that have been killed by Eurasian lynx often are left uneaten (Helldin et al., 2006; Sunde et al., 1999). Such behaviour by apex predators can cause mesopredators to fear larger predators, leading them to avoid habitats with high risk of being killed, with a consequent additional negative effect on mesopredator population sizes (Ritchie and Johnson, 2009). In the case of the Eurasian lynx and red fox, lynx reduces fox abundance at local as well as regional and continental scales (Elmhagen et al., 2010; Helldin et al., 2006; Pasanen-Mortensen et al., 2013). Top-down effects of apex predators can be interrelated with other factors, such as primary productivity and anthropogenic activity (Elmhagen et al., 2010; Estes et al., 2011; Ritchie et al., 2012). In Sweden for instance, red fox abundance started to increase in the mid 19th century concurrent with a persecution-induced decline in apex predator populations. However, elimination of apex predators was faster in highly productive areas, where agriculture was expanding the most, and mesopredator release was most expressed in these areas (Elmhagen and Rushton, 2007). In absence of apex predators red fox abundance is limited bottom-up and positively related to summer temperature, productivity and human density (Pasanen-Mortensen et al., 2013).

The red fox is a generalist that utilizes several habitats, although some seem to be more favourable. For example, red fox density in Finland increases when forests are fragmented by clear cuttings and agricultural land, and the highest fox density is reached in landscapes with 20–30 % agricultural land (Kurki et al., 1998). Likewise, red fox density in the taiga of north-western Russia is highest when the proportion of open habitat is 30–60 % (Kiener and Zaitsev, 2010). The threshold density reached at a certain proportion of open habitats is likely due to social regulation, where breeding territories become a limiting resource at high fox densities (Kiener and Zaitsev, 2010; Kurki et al., 1998). However, the relationships between red fox and open habitats have not been investigated in relation to presence or absence of apex predators.

Trophic processes and trophic downgrading often occur on large spatial scales (Estes et al., 2011). Here we investigate the relationship between red fox abundance and different types of open habitats at a continental scale, and if the associations differ in the presence and absence of Eurasian lynx. We therefore explore the relationships between red fox abundance and landscape composition with regard to the proportion of cropland (anthropogenic open habitats), grassland (semi-natural and natural open habitats) and a gradient of openness including all open habitats (anthropogenic, semi-natural and natural open habitats). Pasanen-Mortensen et al. (2013) showed that red fox abundance in Eurasia is limited by lynx presence and bioclimatic variables such as winter severity, summer temperature and productivity, but did not find any direct relationship with tree cover. However, tree cover only reflects the

percentage of open habitat in general, and we suggest that some open habitats, such as cropland, might be more important to red fox than others. In this study, we therefore investigate the effect on red fox of different types of open habitats separately, and we explore linear and non-linear relationships between these open habitats and red fox density. Our hypotheses are:

1) In the absence of lynx, red fox should be limited bottom-up. Hence red fox density should be related to land cover. Based on previous studies on smaller spatial scales, red fox should reach the highest density when the proportion of cropland is 20–30% (Kurki et al., 1998). The proportion of grassland and the gradient of openness should have a similar effect on red fox with high densities at 30–60% open areas (Kiener and Zaitsev, 2010).
2) In the presence of lynx, red fox should be limited top-down by lynx and hence not respond to variation in land cover.

2. Methods

2.1. Study sites: red fox density, lynx status and land cover data

In a previous study we compiled data on red fox density in natural, semi-natural and agricultural environments throughout Europe and northern Eurasia (Pasanen-Mortensen et al., 2013). In this study, we used the same data on red fox density to explore the potential effect of different land covers on fox abundance (Appendix A). We here summarize the methods used to retrieve those data, for details see Pasanen-Mortensen et al. (2013). Red fox data originated from reports and published studies from 1952 to 2010 (Pasanen-Mortensen et al., 2013). Data on red fox density were compiled by searching on Web of Science and Google scholar, and complemented with data collated by Bartoń and Zalewski (2007). We excluded one of the red fox locations in Barton and Zalewski, as non-conforming location and coordinates was discovered. The methods to survey foxes in the studies were mainly snow tracking, spotlight counts and den counts, but also camera trapping (cameras placed 20 cm above ground, taking photographs every 30:th second), means of juvenile population size (proportion of marked juvenile foxes not harvested), hunting bags, observations and track counts corrected with radio-tracking were used in one case each. When authors had not estimated densities (in six of the snow tracking studies and two of the den count studies), we used Priklonky's formula to estimate densities from snow tracking (Priklonsky, 1965), and assumed two adults per den (Panek and Bresiński, 2002) to estimate density from den counts in relation to the area given by the authors. For each location, presence-absence of lynx was assessed from descriptions in the reports and studies from which we compiled red fox data, or from publications on lynx distribution range (Pasanen-Mortensen et al., 2013).

The fox locations (n = 110) were distributed from 37.4°S to 68.8°N and from −7.69°W to 162.9°E (Fig. 1, Appendix A). Red fox reached the highest density outside the distribution range of lynx, with a maximum of 4.3 foxes/km^2 and a median of 0.73 foxes/km^2 (interquartile range 0.42–1.3, robust coefficient of variation (RCV) 123). Within the distribution range of lynx, the maximum density was 1.58 foxes/km^2 with a median of 0.073 foxes/km^2 (interquartile range 0.021–0.16, RCV 184). We applied the same buffer zone of 10 km (10 km radius, 314 km^2, hereafter red fox sites) as Pasanen-Mortensen et al. (2013) around each red fox location to assess the proportion of cropland, grassland and the degree of openness at each red fox site, as well as winter severity. A buffer zone of 10 km is expected to cover for variation in heterogeneity and uncertainty of the exact location (Bartoń and Zalewski, 2007). It should also be large enough to minimize effects of small scale changes in the