



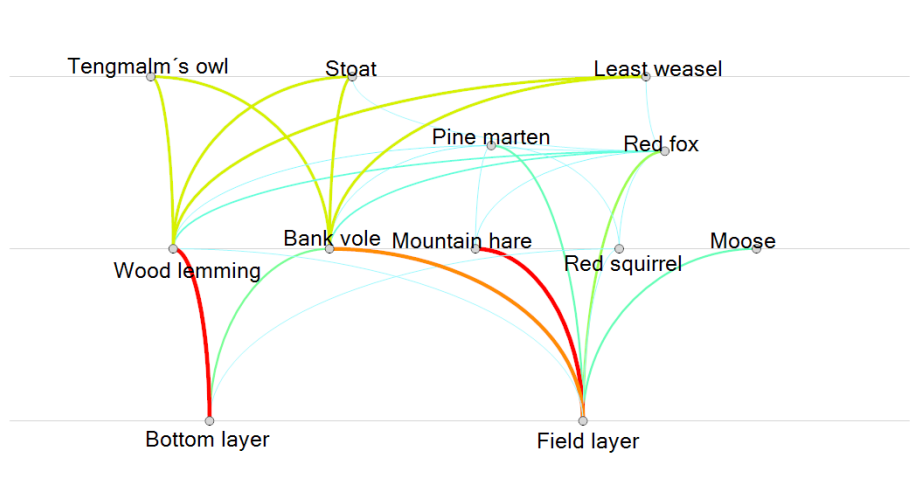
INLAND NORWAY
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Master thesis

To eat or to be eaten:
Modelling part of the vertebrate food web of the
boreal forest ecosystem in Fennoscandia



Master in Applied Ecology

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Abstract

Trophic relationships, amongst others, define the structure of an ecosystem. They are mostly simplified and described as plant-herbivore and predator-prey interactions. Modelling trophic interactions are one way to improve our understanding of the functioning, impact and management of ecosystems.

In this study, I explore how the cyclic vole and lemming populations affect the dynamics of the boreal forest in Fennoscandia. Specifically, I ask what mechanism controls the food web in years with peak and low densities of small rodents, the impact of small rodents on primary producers and how predator densities influence small rodents. To strengthen the conclusions, I test how robust the models are to $\pm 20\%$ changes in parameter values.

To answer these questions, I applied Ecopath, a mass-balance modelling approach, to explain trophic relationships in a system. The main output of the model is Ecotrophic Efficiency (EE), a measure to capture the consumed production of each trophic level. I modelled the vertebrate food web primarily connected to the cyclic voles and lemmings in the boreal forests, and built models according to their cycle phases. This is the first time this boreal forest community is modelled using Ecopath.

The models showed a top down control on the bottom layer (mosses, lichens and fungi) in peak rodent years. The densities of small rodents would need to increase 16 fold from observed densities to negatively affect the field layer (shrubs, herbs, grasses and grass-like species). Predator density would need to increase 4 times to be able to control their prey. In addition the model were robust to parameter changes up to 20%.

The system shows a strong herbivore-plant interaction in peak rodent years, but in low rodent years no control mechanism was apparent, indicating surplus resources for all components of the food web. Small rodents, specifically lemmings, deplete the bottom layer (mosses) in peak density years. Predators seem to only have a minor influence on the cycle dynamic. With this model approach a first systematic picture of the boreal forest community is captured, which to some extent coincides with hypothesis on small rodents population dynamics.

Key words: terrestrial food web, Ecopath, mass-balance model, population cycle, voles, lemmings

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1. Introduction

Ecosystems are communities of flora and fauna interacting with each other, and influenced by abiotic surroundings (Thompson et al., 2012). Communities are species in an ecosystem that get their energy from the same source (Trebilco, Baum, Salomon, & Dulvy, 2013). The interactions between species in a community can be described by trophic relationships (Levin, 1992; Thompson et al., 2012), often simplified to be linear, such as plant-herbivore or predator-prey interactions (Polis & Strong, 1996; Thompson et al., 2012). However, species interactions are in reality much more complex (Kefi et al., 2015; Polis & Strong, 1996), and can even be non-trophic, such as competition for space within a trophic level (Kefi et al., 2015). In contrast to trophic interactions, non-trophic interactions occur at the same trophic level and do not form vertical structures between trophic levels (Kefi et al., 2015).

Trophic interactions are best described in a food-web, in which the diet composition of species are mapped (Pimm, Lawton, & Cohen, 1991). A simple description of how energy passes from one organism to another, may be described in a food chain, which is a linear sequence with one organism in each trophic level. Multiple trophic interactions form a food web, which generally starts with plants (i.e. primary producers) that are eaten by herbivores (i.e. primary consumers), and herbivores that are consumed by predators (i.e. secondary consumers). In most ecosystems, secondary consumers are supported by a higher biomass of primary producers and consumers (although this may be reversed in some ecosystems; McCauley et al., 2018). Lastly, detritivores consume the dead material from plants, herbivores and predators, which circulates nutrients and make them available for plants again.

The state of an ecosystem is influenced by the type of control exerted on the communities (Ostfeld & Keesing, 2000). With bottom-up control, energy is passing upwards from primary producers to primary or secondary consumers, and primary producers control the abundance of consumers directly. In contrast, in top-down controlled communities, consumers directly or indirectly influence the abundance of the lower trophic levels. In a direct control, the secondary consumers control primary consumers, or primary consumers control primary producers. Alternately, in an indirect control the secondary consumers increase the abundance of primary producers through suppressing the trophic levels that which feed on them (Ostfeld & Keesing, 2000; Shurin, Gruner, & Hillebrand, 2006). In both cases, all trophic levels and

their biodiversity contribute to the function of the food web, and changes in the biomass in one trophic level can lead to major changes in the system (Neutel, Heesterbeek, & de Ruiter, 2002).

Overall, biodiversity loss results in a reduced efficiency (e.g. production of biomass, decomposition, recycling of nutrients) of ecosystems. This negatively influences the functioning of the ecosystem and the continuity of ecosystem services (Cardinale et al., 2012; Loreau et al., 2001). Human activities continuously change the composition of ecological communities through intense land use, habitat alteration, climate change and by promoting species invasion (Hooper et al., 2005). A change in biodiversity or the composition of species in the community, can change trophic interactions and influence the abundance of species that influence energy flows, or change energy flow directly. This may result in a trophic cascade: e.g. if a top predator is removed, a prey population may explode and deplete their food resources (Chapin III et al., 2000). This, in turn can cause complete shift in the abundance and composition of species – so called regime shifts (Scheffer & Carpenter, 2003), destabilizing the system until a new status quo has been established.

Boreal forests are distributed in the northern hemisphere and belong to one of the largest terrestrial ecosystems on earth (Aerts & Honnay, 2011; Gower et al., 2001). These forests are dominated by conifers, while the understory vegetation and species composition vary geographically (Boonstra et al., 2016). A major threat to boreal forests, next to exploitation is climate change. Climate change can change species distribution and community composition and therefore has the potential to change the ecosystem functioning (Chapin et al., 2004). Despite its lower biodiversity compared to other terrestrial ecosystems (e.g. temperate and tropical forests), the boreal forest ecosystem provides important ecosystem services, such as carbon storage, flood regulation, water filtration and timber provision (Schindler & Lee, 2010). In the present study, I concentrate on a part of the vertebrate food web in the boreal forest ecosystem of Fennoscandia.

One of the main food chains, and the focus in this thesis, that characterizes the boreal forest community in Fennoscandia, is the link between plants, small rodents and small-medium sized predators. The food web starts with a variety of plants consumed by small rodents, such as voles and lemmings. Small rodents in turn, are consumed by specialist-predators like least weasel (*Mustela nivalis*), stoat (*Mustela erminea*) and Tengmalm's owl (*Aegolius funereus*),

or generalist-predators like pine marten (*Martes martes*) and red fox (*Vulpes vulpes*; i.e. secondary consumers; Boonstra et al., 2016). The boreal forest communities show a high degree of complexity and dynamics and because of its lower biodiversity, interactions between species may be even more important for the function of the ecosystem (Paquette & Messier, 2011). Dynamics are assumed to be driven by small rodents, which exhibit regular multi-annual cycles in population abundance, as is characteristic of cyclic populations (Myers, 2018). These fluctuations in abundance play a major role in providing pulses of energy for all higher trophic levels (Ostfeld & Keesing, 2000) in the boreal forest (Andreassen, Glorvigen, Remy, & Ims, 2013; Boonstra et al., 2016).

Population cycles can be observed in the Northern Hemisphere in several mammals, like the snowshoe hare (*Lepus americanus*), lemmings and voles (Korpimäki, Brown, Jacob, & Pech, 2004; Krebs, 1996). This phenomenon is widely studied and there are several hypotheses as to what drives these population fluctuations. Specialist predators are suggested to contribute to the multi-annual cycles of rodent populations (i.e. a top-down control); this is referred to as the predator hypothesis (Hanski, Henttonen, Korpimäki, Oksanen, & Turchin, 2001). The food-hypothesis (i.e. a bottom-up control) states that the quality or quantity of food resource or food habitat determines population growth (Andreassen et al., 2013; Johnsen et al., 2017), and the disease hypothesis suspects disease-outbreaks to decrease population densities (Krebs, 2013). Next to these extrinsic factors, there are also hypotheses describing how intrinsic factors such as maternal effects, genetic changes and behavioural changes can generate population cycles (Andreassen et al., 2013; Myers, 2018). However, there is an increasing interest in multi-factor hypotheses where extrinsic as well as intrinsic factors are included (Andreassen et al., 2013; Radchuk, Ims, & Andreassen, 2016).

To understand the ecosystem functioning, human impact on ecosystems and to manage them, modelling trophic interactions in the ecosystem's food web has proven to be a useful tool (Coll, Palomera, Tudela, & Sardà, 2006; Fetahi & Mengistou, 2007). Ecopath with Ecosim (EwE) is an ecosystem modelling software (Christensen & Pauly, 1992; Polovina, 1984) and currently most commonly used to model marine ecosystems (Gascuel, Morissette, Palomares, & Christensen, 2008). Ecopath provides a tool to set up a mass-balance model (i.e. biomass in the system, stays in the system) to explore biomass flows between trophic levels (Christensen, Walters, & Pauly, 2005). It can be used to e.g. evaluate harvest impacts (Coll et al., 2006),

find keystone species (Libralato, Christensen, & Pauly, 2006) or model the spread of contaminants in a system (Larsen, Sagerup, & Ramsvatn, 2016). This modelling approach has seldom been applied to terrestrial systems. Colléter et al. (2015) reported 365 studies which used Ecopath models in marine systems, 63 studies for freshwater systems and only 5 studies in terrestrial systems. In terrestrial systems, Ecopath has been used to model the snowshoe hare (*Lepus americanus*) – Canadian lynx (*Lynx canadensis*) cycle in the Kluane boreal forest, Canada (Ruesink, Hodges, & Krebs, 2002) and, trophic dynamics in the Canadian Arctic, with focus on primary production (Krebs et al., 2003). In addition, Legagneux et al. (2012) studied to what extent a tundra food web (in Canada) is dominated by plant-herbivore versus predator prey interactions. Recently, a study applied Ecopath for an environmental impact assessment in Natura 2000 areas in Germany (Fretzer, 2015, 2016).

To analyse how the cyclic vole and lemming populations in Fennoscandian boreal forests affect the dynamics of the ecosystem, I chose to model the food web primarily connected to the cyclic voles and lemmings in the boreal forests using Ecopath. This is an interesting system to study, due to its regular dynamics influencing the food web. My aim is to provide a better understanding of control mechanisms that influence community dynamics, and how resilient it is to changes in the abundance of species. More specifically I intended to find: 1) the food web control mechanisms in a year with a peak density of small rodents and in a year with a low density of small rodents; 2) at what small rodent density the primary producers experience detrimental effects; 3) at what predator density the primary consumers experience detrimental effects; and 4) how sensitive the model scenarios are to changes in parameter values and how robust the modelled scenarios are. I will discuss my results amongst other, by comparing with the Canadian boreal forest ecosystem. The Fennoscandian and Canadian boreal forest exhibit some interesting ecosystem differences, such as the 3-4 year population cycles, vegetation characterised by dwarf shrubs and the interaction between small rodents and small mustelid in Fennoscandia compared to the 10 year population cycles, vegetation characterised by tall shrubs and the interaction between snowshoe hare and lynx in Canada (Boonstra et al., 2016).

2. Methods

2.1 Study area

The boreal forest is a widespread region, ranging from 50°N to 70°N (Gower et al., 2001). In Fennoscandia it is dominated by conifers, with the main tree species being spruce (*Picea abies*) and pine (*Pinus sylvestris*) interspersed with birches (*Betula pubescens* and *Betula pendula*), and rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), willows (*Salix* sp.) and alder (*Alnus incana* and *Alnus glutinosa*). A layer of dwarf shrubs covers the ground, consisting of billberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*) and black crowberry (*Empetrum nigrum*), mosses (*Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castremsis*) and lichens (e.g. *Cladonia* spp.) covering the forest ground (Boonstra et al., 2016). The climate in the boreal forest region is defined by a continental climate. An exemplary average yearly temperature of the boreal forest of 0.6°C, with a monthly average of -9.9°C and 12.6°C in January and July respectively can be observed (Drevsjø, Norway, 61.15°N, 8.46°E). The forests are snow covered for 5-7 months a year with snow depths up to 1.35m (Johnsen et al., 2017), although a large variation may occur because of area-specific differences or due to latitudinal differences.

2.2 The food web

The food web primarily connected to the cyclic voles and lemmings and modelled here, is a subset of the vertebrate food web of the boreal forest ecosystem (Figure 1). I built models according to the cycle phases of voles and lemmings. The dominant vole species in the boreal forest of Fennoscandia is the bank vole (*Myodes glareolus*). It is a generalist herbivore and its preferred habitat consists of closed coniferous forests (Gorini et al., 2011). This is also the preferred habitat of the wood lemming (*Myopus schisticolor*; Stenseth & Ims, 1993), and included in the model. According to the food web presented in Boonstra et al. (2016) the specialist predators feeding on bank voles and wood lemmings in the forest are stoat, least weasel and the Tengmalm's owl. The generalists red fox and pine marten include small rodents in their diet, and also include mountain hare (*Lepus timidus*) and red squirrel (*Sciurus vulgaris*). In addition to voles and lemmings, the main herbivores in the system are mountain hare and moose (*Alces alces*). Voles and hares feed on shrubs, forbs and grasses, lemmings

utilize mostly mosses and red squirrel feeds mainly on conifer seeds. Moose browse on shrubs, deciduous trees and conifers, but include forbs in their summer diet (Wam & Hjeljord, 2010b).

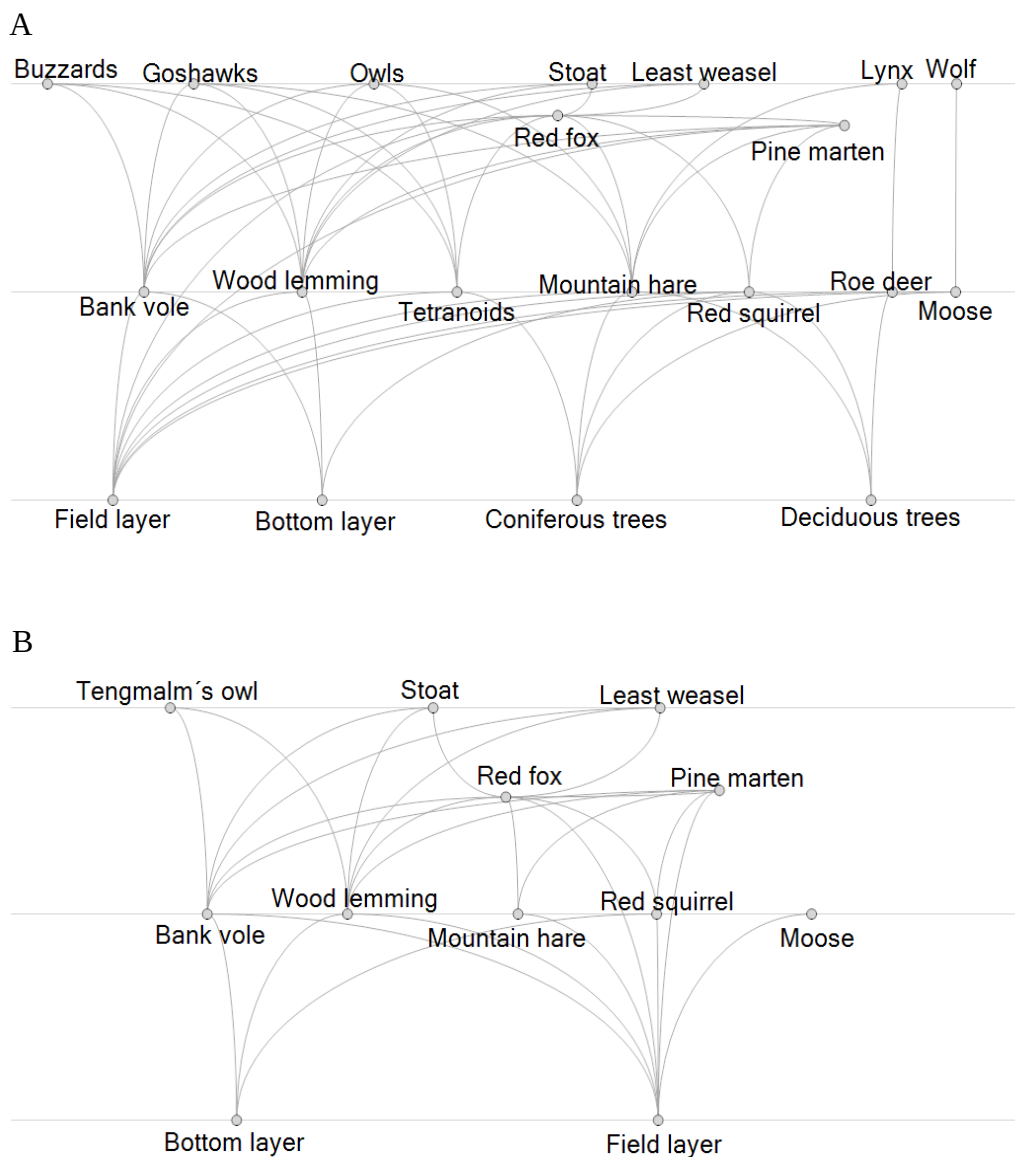


Figure 1: An example of the vertebrate food web for the boreal forest ecosystem (A) and the selected food web for this study (B). The lines represent the trophic levels calculated by Ecopath.

This is the first time this boreal forest community is modelled using Ecopath. To avoid complexity of the model I grouped the first producers into: the vegetation from the field layer and the bottom layer. I excluded most of the species not directly linked to voles and lemmings such as trees, grouse (*Tetrao* spp.) and their predators (Goshawk *Accipiter gentillis* and

buzzards *Buteo spp.*). I also excluded apex predators (wolf *Canis lupus*, lynx *Lynx lynx* and brown bear *Ursus arctos*) as well as wolverine (*Gulo gulo*), because their densities are low and their diets do not include rodents (Boonstra et al., 2016; Tovmo, Mattisson, & Brøseth, 2017). The roe deer (*Capreolus capreolus*) was excluded because of its low densities (Odden, Linnell, & Andersen, 2006).

With the described species the boreal forest community includes all trophic levels with producers (plants), primary consumers (voles, lemming, red squirrel, mountain hare and moose) and secondary consumers (stoat, least weasel, Tengmalm's owl and red fox; Figure 1B).

2.3 Mass-balance modelling approach

To analyse the food web I applied Ecopath, which provides a static picture of a food web in a mass balance modelling approach, with the main equation (Ruesink et al., 2002):

$$B_r \left(\frac{P_r}{B_r} \right) E E_r + I_r = \sum_c \left[B_c \frac{Q_r}{B_c} d_{rc} \right] + \Delta B_r + E_r \quad (1)$$

The model is based on estimates of biomass (B), production (P), ecotrophic efficiency (EE), immigration (I), consumption (Q), diet composition (d) and emigration (E). The index r stands for the parameter belonging to the resource, while the index c stands for parameters belonging to the consumer. The first parameter needed is the biomass of a species in an area (B). The production per unit biomass (P/B) is the biomass one unit of biomass (kg) produces over a time period (per year). The rate of consumption per unit biomass (Q/B) is the intake rate of one unit biomass (kg) over a time period (per year). The diet composition (d) is entered as the fraction of the resource (r) in the diet of the consumer (c). EE is the ecotrophic efficiency and represents the fraction of production of a species consumed in the system. EE can thus be estimated for primary producers and primary consumers (herbivores), but not for predators. In a system where the current state can be preserve (i.e. balanced system), EE is between 0 and 1. A value close to 1 is an indicator that almost all of the production of a species is consumed and a value > 1 shows overconsumption and is an indicator of an unbalanced system and top-down control.

Here, I assumed a closed system (i.e. immigration and emigration are 0) and no change in biomass (ΔB). Thus, the equation simplifies to:

$$B_r \left(\frac{P_r}{B_r} \right) E E_r = \sum_c \left[B_c \frac{Q_r}{B_c} d_{rc} \right] \quad (2)$$

Four of the parameters in equation 2 must be provided for each species: B , P/B , Q/B . EE is calculated by Ecopath. Trophic levels in Ecopath are calculated according to the diet composition (Christensen & Pauly, 1992), so a generalist predator which feeds on several different species including producers, has a lower trophic level than a specialised predator who feeds only on the consumer level.

2.4 Model parameters

The parameters introduced to Ecopath were calculated for a constant year without any dynamics. Table 1 shows the parameters used in the base model for the average model scenario (see Table A1 for the other model scenarios) and in the following I describe the estimation of the various parameters.

Table 1: Parameters Biomass (B), Production/biomass (P/B) and Consumption/biomass (Q/B) calculated for a year with mean densities for all species (see text for references on how the parameters were obtained).

Species	Biomass (B) kg/km ²	P/B	Q/B
Tengmalm's owl	0.0057	0.750	43.260
Red fox	0.538	0.905	18.600
Pine marten	0.068	1.439	23.900
Stoat	0.054	2.874	34.800
Least weasel	0.009	3.972	41.400
Moose	146.300	0.223	8.750
Mountain hare	4.320	1.048	20.200
Red squirrel	2.240	2.124	29.500
Bank vole	9.400	5.302	48.400
Wood lemming	9.100	5.234	48.030
Field layer	17 090	0.770	
Bottom layer	23 420	0.030	

2.4.1 Biomass (B)

Biomass was estimated as kg of a species per km² for the peak and low years of vole and lemming density (Table 2). The estimation of biomass was based on body mass per individual (kg) and the density of the population (individuals/100 km²) in years with high vole and lemming abundance and in years with low vole and lemming abundance, which were obtained from Boonstra et al. (2016) and for bank voles from Korpimaki & Norrdahl (1991). The population density of wood lemmings is hard to estimate, as they are difficult to trap (Stenseth & Ims, 1993), and they are known to have large amplitudes in their fluctuations. I therefore used expected population densities in low and peak years (H.P. Andreassen, pers. comm.). Biomass was transferred from fresh weight to dry weight. For birds I used a fresh weight/dry weight ratio of 0.4 and for mammals I used a fresh weight/dry weight ratio of 0.35 (Horn & de la Vega, 2016; Pace & Rathbun, 1945; Table 1).

The vegetation data used in this study was collected from 2011-2015 as part of the Becodyn project (Schrijvers-Gonlag et al., 2018), in two study areas (near Rena and near Evenstad,

Hedmark county, Norway), using the same sampling plots each year. I used data from the field layer (dwarf shrubs, grasses and grass-like species, forbs) and the bottom layer (mosses, lichens, fungi), which was recorded in percentages per quadrat for different habitat types (pine forest, spruce forest, deciduous forest). I grouped the plant data into peak vole/lemming years (2011, 2013 and 2014) and low vole/lemming year (2012 and 2015) according to Johnsen et al. (2017). The bottom and field layer were selected, since these include the vegetation utilized by higher trophic levels of my food web. I combined the percentage vegetation cover for the species into the two groups, field layer and bottom layer, and calculated the average biomass (dry weight) with the study from Muukkonen et al. (2006). The equation for the field layer in pine forests: $y = 0.919 * x + 18.755$ (y being the dry biomass in g/m^2 and x the cover in percentage) and spruce forests: $y = 0.983 * x + 2.959$ and for the bottom layer in pine forests: $y = 0.994 * x + 1.540$ and spruce forests: $y = 0.885 * x + 21.072$ was used for pine and spruce forests. The mean of these were applied as a measure of biomass for the boreal forest ecosystem. Since the data in deciduous forest habitat was lacking input, it was neglected.

2.4.2 Production per Biomass (P/B)

Production per Biomass was assessed using the equation from Banse & Mosher (1980) who investigated the production rate (per unit biomass) of populations (Table 1 and 2). The equation used was: $P/B = aM^b$; with the coefficients $a = 1.11$ and $b = -0.33$ for mammals and M for adult weight in kg. The production/biomass is scaled by species size measured as weight and the coefficients were calculated with: $\log(P/B) = a + b * \log M$ in a linear regression. The equation does not take into account extreme habitats, temperatures or an increased production due to favourable environmental conditions, but gives the expected production/biomass for a unit biomass of an animal.

For the P/B of the Tengmalm's owl I used their productivity (survival * mean number of fledglings/100) to calculate a mean P/B (Korpimäki & Lagerström, 1988). The Production of plants is hard to estimate without extensive field sampling (Persson, 1975; Pouliot, Marchand-Roy, Rochefort, & Gauthier, 2010). Therefore, I used estimates Krebs et al. (2003) used in their Ecopath model of a Canadian Arctic system. Legagneux et al. (2012) reported similar values for plants in a High Arctic Tundra system. In all my models I assumed a constant production, because I used empirical relationships and not separately calculated ratios.

2.4.3 Consumption per Biomass (Q/B)

Consumption per biomass was assessed using the equation from Nagy (1987), for estimating intake rate for mammals and birds per day: $y = ax^b$ (y = intake rate in g/d; x = body mass in g). The coefficients for mammals were $a = 0.235$ and $b = 0.822$ (see equation 19 in Nagy, 1987) and for birds: $a = 0.648$ and $b = 0.651$ (see equation 31 in Nagy, 1987). The coefficients were derived from the regression in the form: $\log y = \log a + b \log x$.

The intake rate is the amount needed for an animal to preserve their steady state, it does not take into account an elevated energy requirement during e.g. reproduction (Table 2). Because intake rate per year was needed, the intake rate/biomass was multiplied by 365 to get the consumption per biomass over a year (Table 1). I took a constant consumption in all my models regardless of food availability. For wood lemmings I tested the impact of a doubled intake rate of wood lemmings in my models, because they eat mosses with a low nutritious value (Stenseth & Ims, 1993).

Ecopath uses a value of 0.2 to account for unassimilated consumption (i.e. food not converted into nourishment), I used this default value in all my models, as has been done for other terrestrial models (Legagneux et al., 2012; Ruesink et al., 2002).

Table 2: Summary of parameter explanation

Parameter	Explanation
Biomass (B)	Based on body mass per individual (kg) and the density of the population (km^2)
Production/biomass (P/B)	Production rate (per unit biomass) over a time period (year)
Consumption/biomass (Q/B)	Intake rate (per unit biomass) over a time period (year)
Diet composition (d)	Fraction of the resource in the diet of the consumer
Ecotrophic efficiency (EE)	Fraction of production of a species consumed in the system

2.4.4 Diet composition (d)

Boonstra et al. (2016) compiled the diet for species inhabiting the Scandinavian boreal forests. The diet compositions was provided as proportions, which I could directly apply in the Ecopath model (Table 2 and 3; Table A2 and A3). I used only summer diets as there is a

lack of knowledge on the variation in diet between seasons. For red fox, pine marten, moose, mountain hare, red squirrel, bank vole and wood lemmings I reviewed literature for more details (Dell'Arte, Laaksonen, Norrdahl, & Korpimaki, 2007; Eskelinen, 2002; Hansson, 1979; Hansson & Larsson, 1978; Helldin, 1999, 2000; Johannessen & Samset, 1994; Moller, 1983; Needham, Odden, Lundstadsveen, & Wegge, 2014; Storch, Lindstrom, & Dejoune, 1990; Wam & Hjeljord, 2010a, 2010b). For the specialist predators, Tengmalm's owl, least weasel and stoat, I assumed that they prey only on bank voles and wood lemmings in equal proportion.

Table 3: Diet composition in proportions for a year with average densities for all species and species groups. "Import" indicates food items eaten from outside the presented food web (see text for references).

Prey/Consumer	1	2	3	4	5	6	7	8	9	10
1 Tengmalm's owl	█									
2 Red fox		█								
3 Pine marten		0.001	█							
4 Stoat		0.001		█						
5 Least weasel		0.001			█					
6 Moose						█				
7 Mountain hare		0.100	0.050				█			
8 Red squirrel		0.050	0.050					█		
9 Bank vole	0.500	0.150	0.100	0.500	0.500				█	
10 Wood lemming	0.500	0.150	0.100	0.500	0.500					█
11 Field layer		0.350	0.200			0.200	1.000	0.050	0.800	0.010
12 Bottom layer								0.020	0.100	0.990
Import		0.197	0.500			0.800		0.930	0.100	

2.4.5 Detritus

A detritus group had to be implemented in the model. Since this was not a group of interest, I chose a value and tested if that value changed estimates for other groups. I tested different values for detritus biomass from 1 to 100 kg/km² and did not notice any change in the outcome.

2.5 Model analysis

I built five different base models for the different phases of a population cycle, with the corresponding plant biomass:

- 1) An *average model* where I took the average biomass estimates of all species from all data.
- 2) An *increase phase model* simulating the increase phase of a population cycle, with high vole and lemming densities, high plant biomass and low predator densities.
- 3) A *peak phase model* simulating the peak phase of a population cycle, with high vole and lemming densities, high plant biomass and high predator densities.
- 4) A *decrease phase model* simulating the decrease phase of a population cycle, with low vole and lemming densities, low plant biomass and high predator densities.
- 5) A *low phase model* simulating the low phase of a population cycle, with low vole and lemming densities, low plant biomass and a low predator density.

2.6 Uncertainty and sensitivity

Because the model estimates are based on studies with different temporal and spatial scales (B and d) and empirical relationships (P/B and Q/B), I tested how sensitive my parameters and estimates react to changes.

To test the sensitivity and the robustness of the parameter values and estimates, I chose to change each parameter separately per species $\pm 20\%$. For the diet composition d , I tested different compositions with help of the before mentioned literature (see Table A4, A5 and A6 for tested diet compositions). To plot and compare the resulting variation in EEs , I calculated

the absolute deviation of the median: $\frac{1}{n} \sum_{i=1}^n |x_i - m(x)|$ where x_i is the a value of a variable, and $m(x)$ the chosen measure of central tendency, here the median, because EE is right skewed.

To evaluate if changes in parameter values change my base model estimates, I performed a generalized linear model (GLM) with a Gamma distribution in R 3.4.3 (RStudio Team, 2016), I used *EE* as the response variable, and included model scenarios, changes in parameters (sensitivity) and species as predictors. I excluded Tengmalm's owl, red fox and moose in the analysis, because in this food web no species predate on them and therefore their *EE* is zero. I also tried models with an inverse Gaussian distribution, because it deals with a right skewed continuous positive data. The model estimates showed similar values, and I only present the model results with a Gamma distribution. I used the MuMIn package (Bartoń, 2018) for selecting models. Models were selected with Akaike's Information Criteria (AIC), candidate models within $\Delta AIC \leq 2$ were assumed to be equally supported by the data (Burnham & Anderson, 2002). I evaluated assumptions using the DHARMA package (Hartig, 2018) and used the ggplot2 package (Wickham, 2009) and the cowplot package (Wilke, 2017) to visualize. Initially, I included interactions, but because assumptions were not met for interaction models I excluded those models.

3. Results

All five model scenarios built in this study, showed the highest biomass at the producer level of the food web (Figure 2). The bottom and the field layer of the plants had in all scenarios over 99.4% of the biomass. The predator biomass, with red fox, pine marten, stoat, Tengmalm's owl and least weasel, constitute the lowest biomass with less than 0.01% of all the biomass in the system. Because all model scenarios were based on the summer diet, the trophic interactions between species and trophic levels are in the same directions.

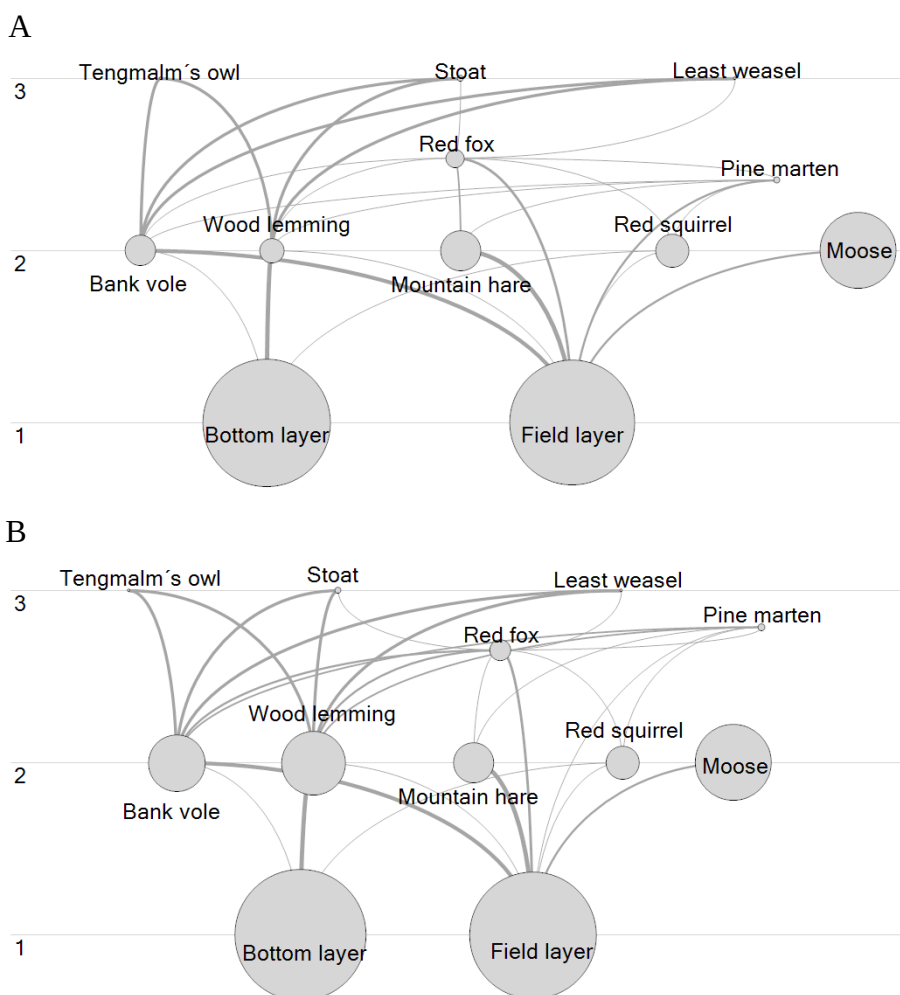


Figure 2: A flow-diagram of the food web and the flows in the system. The size of the nodes represents the biomass in the system and the size of the lines depicts how much is consumed. The horizontal lines are the trophic level (1) producer level, 2) consumer, 3) secondary consumer). The flow diagrams show a crash phase (A) and a peak phase (B) of the vole and lemming population.

3.1 Control mechanism

The ecotrophic efficiency (EE), which describes the fraction of production consumed by higher trophic levels, is presented for all model scenarios in table 4. The model scenarios for the average, decrease and low phase showed a balanced system with all EE s below one, which suggests that the current state of the system can be preserved and is not under a top down or bottom up control. The model scenarios for the increase and peak phases however, had EE values for the bottom layer of 2.94. This indicates an overconsumption and a top down control on the bottom layer, which is mainly due to wood lemming consumption of the bottom layer. In the average year the highest EE value can also be found in the bottom layer with almost 80% of the production being consumed by higher trophic levels, which indicates that only 20% contributes to the population growth.

The field layer shows in all model scenarios an EE value close to zero. The fraction of production consumed by predators of mountain hares is in the average, increase and peak phase scenarios between 20% – 27%, and in the decrease and low phases at 40% and 31% respectively. A high fraction of production removed from the population can also be observed for the least weasel, with 25% - 28% in the average, decrease and low phase scenarios and with 49% and 62% in the increase and peak phase model scenarios respectively.

In the decrease and crash phase scenarios, the highest fraction of removed production can be found in wood lemmings (around half of the population). In the same scenarios, a quarter of the production is consumed of the bank vole population. For the other scenarios (average, increase and peak phase) the wood lemming and bank vole EE are close to zero, which indicates that nearly all production contributes to population growth. The EE s of the other species are in all scenarios under 0.15, and only have small differences between scenarios, which indicates that the species do not undergo big changes in predation pressure.

Table 4: *EE* estimates for the different base model scenarios for each species.

Species	EE				
	Average	Increase phase	Peak phase	Decrease phase	Low phase
Tengmalm's owl	0	0	0	0	0
Red fox	0	0	0	0	0
Pine marten	0.10	0.11	0.10	0.10	0.11
Stoat	0.06	0.11	0.14	0.07	0.06
Least weasel	0.28	0.49	0.62	0.31	0.25
Moose	0	0	0	0	0
Mountain hare	0.24	0.21	0.27	0.40	0.31
Red squirrel	0.12	0.10	0.13	0.13	0.10
Bank vole	0.06	0.03	0.03	0.27	0.23
Wood lemming	0.06	0.01	0.02	0.52	0.45
Field layer	0.05	0.09	0.09	0.04	0.04
Bottom layer	0.78	2.94	2.94	0.09	0.09

3.2 Effect of small rodent densities on primary producers

The bottom layer is overconsumed in the increase and peak phase scenarios (Table 4), while in the decrease and low phase scenarios only 9% of the production is consumed by higher trophic levels. With a doubled intake rate of wood lemmings, the *EE* of the bottom layer also doubles in all scenarios. The field layer in the increase and peak phase scenarios also shows that 9%, and in the decrease and low phase scenarios 4%, of production is consumed by higher trophic levels, which indicates a low predation pressure. In the increase and peak phase scenarios, the bottom layer biomass has to be 3 times higher for the *EE* to drop below one, no overconsumption is observed.

Another possibility to reduce the fraction of production consumed of the bottom layer is if the biomass of wood lemmings reduces from 5 000 to 880 ind/km² to achieve no overconsumption in the increase and peak phase scenarios. In the decrease and low phase scenarios instead, the bottom layer has to be 11 times smaller, for the *EE* to rise above one and thus for overconsumption to occur.

The fraction of consumed production of the field layer is in all scenarios close to zero. To observe an EE above one, the biomass of the field layer has to decrease in the increase and peak phase scenarios 12 fold, and in the decrease and low scenarios 30 fold. If the bank vole biomass would increase from 2 500 to 40 000 ind/km² in the increase and peak phase scenarios, the field layer EE would rise over one.

Table 5: Summary of results for the effect of small rodents on producer and the effect of predation on small rodents.

	Peak density scenarios	Low density scenarios
Effect on producer: bottom layer	Biomass increase of bottom layer threefold for an $EE < 1$ Density increase of lemmings from 5 000 to 880 ind/km ² for an $EE < 1$	Biomass decrease of bottom layer 11 fold for an $EE > 1$
Effect on producer: field layer	Biomass decrease of bottom layer 12 fold for an $EE > 1$ Density increase of bank voles from 2 500 to 40 000 ind/km ² for an $EE > 1$	Biomass decrease of field layer 30 fold for an $EE > 1$
Effect on small rodents: generalist predators	Generalist predators function as specialist predators: EE of wood lemmings > 1	Generalist predators function as specialist predators: EE of wood lemmings > 1 Density increase of specialist
Effect on small rodents: specialist predators	Density increase of specialist predators from 1 to 95 ind/km ² for an $EE > 1$	predators: from 1 to 4 ind/km ² (increase phase) or to 5 ind/km ² (low phase) for $EE > 1$

3.3 Effect of predator densities on small rodents

In the increase and peak phase scenarios, the predation pressure on the wood lemming and bank vole populations is minimal, between 1% and 3% of the production consumed by predators. In the decrease and low phase scenarios, the predation pressure rises for wood lemmings to 52% and 45% and for bank voles to 27% and 23% of production consumed by predators. If generalist predators would switch their diet to solely bank voles and wood lemmings, the *EE* in the increase and peak phase scenarios would double and in the decrease and low phase scenarios it would triple. This means that wood lemmings are overconsumed in the decrease and low phase scenarios with an *EE* of 1.65 and 1.32 respectively.

If generalist predators exclude wood lemmings and bank voles in their diet or are entirely excluded in the system, the *EEs* of wood lemmings and bank voles are three times smaller in the increase and peak phase scenarios and halved in the decrease and low phase scenarios. On the other hand, if specialist predators are missing in the system, the *EE* shifts downward and is 1.6 times smaller for wood lemmings and 1.5 times smaller for bank voles than with specialist predators. In the decrease phase and low phase scenarios the *EEs* for wood lemmings and voles is 2.0 and 2.3 times lower than with specialist predators. For an increase in *EE* to above one, the biomass of specialist predators would need to increase from a maximum of 1 to a density of 95 ind/km² in the increase and peak phase scenarios. In the decrease phase the biomass would need to increase to 4 ind/km² and in the low phase to 5 ind/km².

3.4 Sensitivity and robustness of the model scenarios

Manipulating the biomass parameters $\pm 20\%$ for all species of the average scenario had only a slight influence on the *EE* (ΔEE between 0.001 and 0.05). Increases of biomass values resulted in a downwards shift of *EEs* of least weasel (from 0.280 to 0.275), while *EEs* of bank voles increased by 0.001 (from 0.058 to 0.059). When biomass values decreased by 20%, *EEs* increased. For the least weasel that resulted in a shift of *EE* from 0.280 to 0.288, and for the pine marten and stoat from 0.102 to 0.103 and from 0.064 to 0.065, respectively.

Changes in P/B influenced EEs of all levels. A 20% reduction of P/B increased EEs by up to 0.008 and a 20% increase in P/B resulted in a decrease of EEs by up to 0.06. The bottom layer, had a higher response by shifting downwards by 0.134 when increasing P/B by 20%, and an upwards shift by 0.195 when decreasing P/B by 20%. The opposite can be observed with changes in Q/B . A 20% decrease of Q/B decreased all EEs by 0.054, while a 20% increase of Q/B increased all EEs by up to 0.009. The bottom layer EE has the biggest shift with a decrease and increase of 0.156.

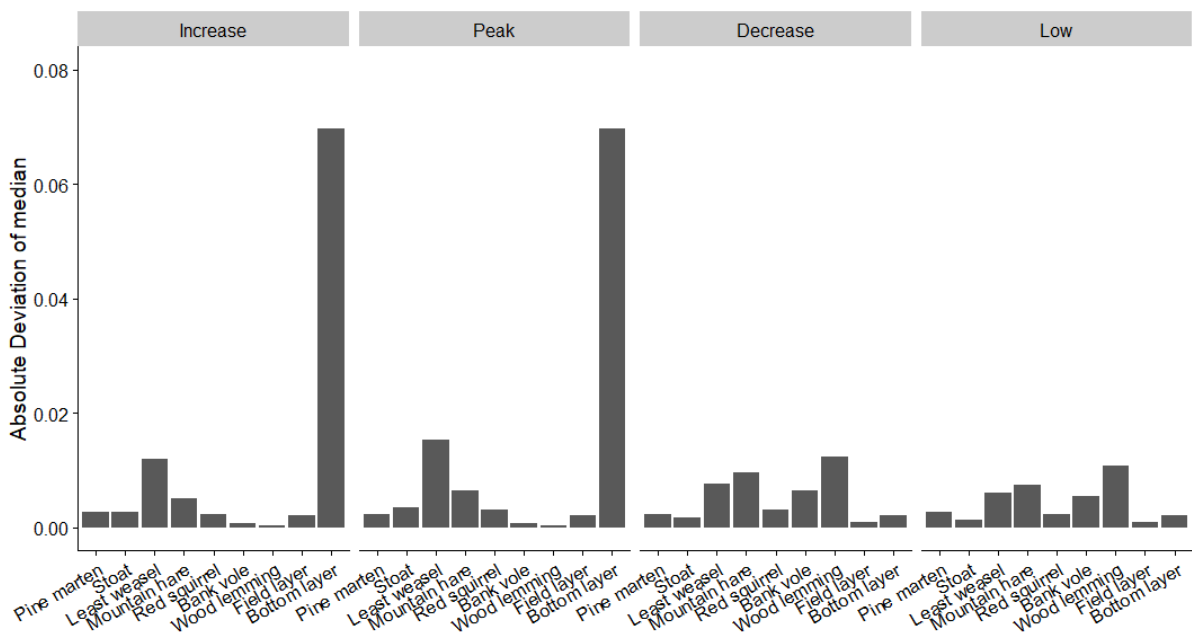


Figure 3: The absolute deviation from the median for the EEs resulting from changing the parameter (B , P/B and Q/B) values $\pm 20\%$ in the different cycle scenarios.

Changing the parameters separately per species, resulted in the changes of EEs , figure 3 shows the absolute deviation from the median. The EE of the bottom layer showed the highest variation, particularly in the increase and peak phase scenarios. There was also some variation in EEs of least weasel and mountain hare, and for wood lemming in the decrease and crash phase scenarios, although as the scale indicates, variations tend to be minor (Figure 3 and 4, Figure A1). All other species showed small shifts of EEs with changes of the parameters.

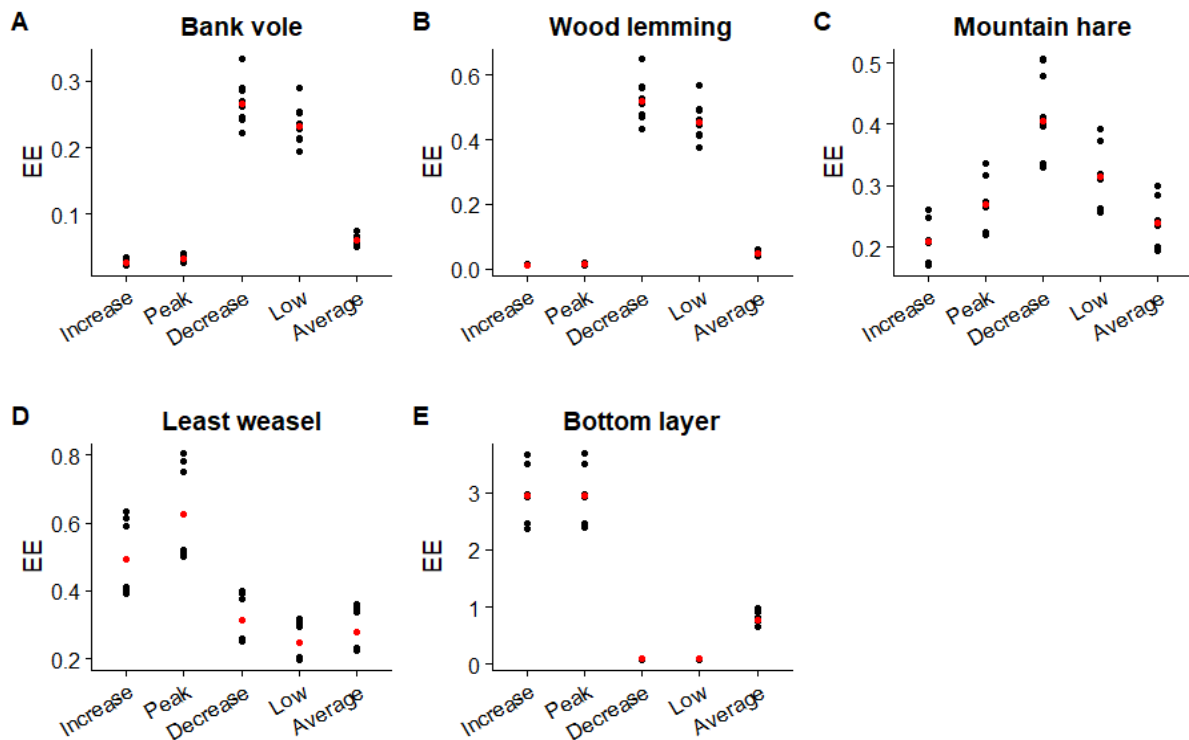


Figure 4: The EEs for bank voles (A), wood lemmings (B), mountain hares (C), least weasel (D) and the bottom layer (E) for the different cycle phases. The red dot is the base model, while the black dots are the resulting EEs of changes in the parameters B , P/B and Q/B .

Changing the parameters by 20% did result in minor shifts of EEs for wood lemming and bank vole in the increase and peak phase scenarios (Figure 4). In the decrease and low phase scenarios the variation in EEs is higher. Even though the bottom layer shows highest variation in EEs in the increase and peak phase scenarios, in the decrease and low phase scenarios shifts in EEs are minor. The mountain hare shows in all scenarios the some variation in EEs . The least weasel also showed a noticeable variation in all years, which was higher particular in the increase and peak phase scenarios (Figure 4).

The AIC model selection revealed EE to be robust to parameter changes $\pm 20\%$ (Table A7). I selected the best model, which included species and model scenario (Table 6). The next model with ΔAIC 2.02 difference, included sensitivity. The AIC did not improve with this additional variable. If EEs would not be robust to changes, sensitivity would have added to the variation explained in the model.

Table 6: Estimates from the with AIC selection selected Gamma distributed GLM (CI = Confidence interval)

	Estimate	95% CI
Intercept ⁽¹⁾	7.316	6.820 / 7.832
Peak phase	-0.034	-0.109 / 0.040
Decrease phase	1.093	0.919 / 1.276
Low phase	1.590	1.377 / 1.814
Average	1.368	1.172 / 1.574
Bottom layer	-6.901	-7.423 / -6.413
Field layer	8.668	7.525 / 9.842
Leas weasel	-5.382	-5.916 / -4.867
Mountain hare	-4.503	-5.056 / -3.967
Pine marten	1.562	0.784 / 2.347
Red squirrel	0.701	-0.038 / 1.442
Stoat	3.001	2.154 / 3.860
Wood lemming	-3.259	-3.846 / -2.685

⁽¹⁾ The intercept represents the *EE* for the increase phase scenario, for the bank vole

4. Discussion

The focus of this study has been to explore control mechanisms in the boreal forest food web (1), the effect of small rodents on primary producers (2), the effect of predators on small rodents (3), and to study the sensitivity and robustness of the model scenarios (4). The vertebrate community in the Fennoscandian boreal forest experiences strong herbivore-plant interactions during peak rodent years, while the system is only under a minor predator control. The various model scenarios showed to have outputs robust to changes in parameter estimates.

The trophic interactions during different phases of the rodent cycle are simple in all cycle phases. This could be expected as northern ecosystems have fewer trophic interactions than ecosystems in lower latitudes (Willig, Kaufman, & Stevens, 2003). The modelled community of the boreal forest ecosystem has, like most ecosystems, most biomass in the producer level (i.e. a bottom-heavy system). The estimates of the ecotrophic efficiency (*EE*) in two of the four cycle phases (decrease and crash phase) are close to zero, indicating a system with no excessive overconsumption of any species in the system. This means that there is sufficient energy in the system to be maintained for a long time. However, Ecopath shows a snapshot of the system at one point in time. For instance, the scenarios for the decrease and crash phase do not capture the growing vole populations. Because the natural system is constantly changing due to its fluctuations in the abundance of species, e.g. vole population cycles, I modelled various scenarios in various phases of the cycle.

In the increase and peak phase, the bottom layer is overconsumed by higher trophic levels, mostly by wood lemmings. This indicates a top-down control, caused by the high number of small rodents, especially by the high abundance of wood lemming. This top-down control of the bottom layer can lead to a bottom-up regulated system where the producer level will be depleted and cannot sustain the current state of the system in the long run. Hence, a decline and crash in the population of wood lemmings can be expected to follow. This strong lemming-bottom layer interaction, backs up the food hypothesis (Turchin & Batzli, 2001) for lemming population cycles, and is additionally supported by other studies (Moen, Lundberg,

& Oksanen, 1993; Turchin, Oksanen, Ekerholm, Oksanen, & Henttonen, 2000). The strong effect between wood lemmings and the bottom layer may be explained by the large amplitude in the wood lemming population cycle and their specialisation on low productivity mosses (Andreassen & Bondrupnielsen, 1991; Prins, 1982; Stenseth & Ims, 1993). In years with a small wood lemming population, the bottom layer gets the opportunity to recover, and thus restart the cycle. It is unlikely that this is the only factor influencing the wood lemming population. However, my results suggest that this mechanism has a strong influence on both the crash and recovery of the wood lemming population. For vole populations, Johnsen et al. (2017 and 2018) show that food during winter can be a limiting factor as well. Similar results have also been suggested from the analyses of time series of vole populations (Hansen, Stenseth, Henttonen, & Tast, 1999).

It has been suggested that vegetation with low productivity is under a higher pressure from herbivores and that the role of predation on herbivores is less important, than in systems where the vegetation is highly productive (Oksanen, Fretwell, Arruda, & Niemela, 1981; Turchin et al., 2000). My results reinforce this suggestion and show the same pattern. In the increase and peak phase the bottom layer with a low productivity was being depleted by the wood lemming, while the wood lemming was not under predation pressure. The ecosystem modelled would require a threefold increase in the biomass of the bottom layer to avoid being depleted by herbivores in the increase and peak phase. The field layer on the other hand can support the system as indicated by the low *EEs* in all scenarios. The consumed proportion of the production of the field layer is close to zero. It is unlikely that herbivores that were excluded from the models, would cause an overconsumption of the field layer, as their densities are generally low (e.g. Odden et al., 2006; Solvang, Pedersen, Storaas, & Hagen, 2009)

Red foxes consume minor proportions of pine marten, stoat and least weasel (Dell'Arte et al., 2007; Storch et al., 1990). Interestingly, the results for all phases suggest that a large proportion of the production of the least weasel population is consumed by the red fox. Mustelids do not represent a regular part in the diet of red foxes. But because mustelids cover long distances in search for prey, the encounter rate between red fox and mustelids is high, which increases the predation risk (Dell'Arte et al., 2007). The observed proportion in the diet of red fox, could also be an effect of the low densities of least weasel, so even small

proportions in the diet can have a large influence on the population. An alternative explanation would be that I underestimated the biomass of the least weasel or overestimated the fraction consumed in the diet.

Predators respond to the prey densities in numbers and in behaviour (Gilg et al., 2006; Jaksíé, Jiménez, Castro, & Feinsinger, 1992; Korpimäki, Norrdahl, & Rinta-Jaskari, 1991). This influences the flows in the food web. A strong numerical response towards early decreasing prey densities, could lead to a top-down control of rodents. In my system this effect could be underestimated. Also, an increasing intake rate (functional response) can influence how much of the production from the prey populations are taken and can therefore result in a predator-control (Gilg et al., 2006). Although I tested for changes in intake rate as well as changes in biomass, an increase of more than 20% for predator's biomass or intake rate could possibly have an effect on the cycle dynamics and they might be responsible for a longer crash phase (Jaksíé et al., 1992; Korpimäki et al., 1991).

In the increase and peak phases the predator densities would need to increase 95 fold if we should observe a predator control from specialist predators. In the decrease and crash phases a top-down control on small rodents might be possible if the biomass of the specialist predators is underestimated or if the biomass of wood lemmings and bank voles are overestimated. Generalist predators have the potential to regulate wood lemmings and bank voles, under the condition that they undergo a diet shift to solely wood lemming and bank voles. Generalist predators functioning as small rodent specialists could regulate the small rodent populations. Such a specific diet shift seems unlikely for predators like red fox and pine marten, who are known for being highly opportunistic species (Dell'Arte et al., 2007; Storch et al., 1990). I accounted for opportunistic behaviour using different proportions in the diet composition for the different model scenarios. These findings support minor roles of predators in my study system.

Even though, I have simplified the system for modelling, my results give an overall picture of the actual system, as I modelled the main contributors to the Fennoscandian boreal forest ecosystem. I did not include all vertebrate species, hence I see implications for part of the system, but cannot draw conclusions for the whole system. Assumptions like a closed system, no migration, constant production and consumption and no seasonality limit the conclusiveness of my results as it does for all Ecopath models. The model also assumes that

all species are available everywhere which is quite unlikely in today's fragmented systems (Andrén, 1994; Wiens, Stenseth, Vanhorne, & Ims, 1993). This assumption could lead to an overestimation of consumption by predators if species are less available or an underestimation of consumption by predators, if more is available. However, these effects should cancel each other out and the model scenarios do not look at a local scale. Uncertainty at the producer level comes especially from recording of vegetation coverage, as this method is likely to contain observer errors. However, my results show that the biomass for the producer has to change drastically for *EEs* to shift. (Ruesink et al., 2002) state that the error around the values does not appear to influence the overall picture, and my study supports a similar conclusion. It is likely, however that large changes, over 20%, would influence the *EEs*. Especially large changes in the consumption by predators can lead to higher *EEs* of lower trophic levels. On the other hand, a higher production among the prey species would reduce *EEs* of prey again. I also observed that minor changes to the diet do not change the food web interactions. The proportion of bank voles and wood lemmings in the diet of predators were set to be equal in the different model scenarios, a preference for one of the small rodent species could change this outcome (Koivunen, Korpimäki, Hakkarainen, & Norrdahl, 1996). Certainly, the proportion of production of consumed voles and lemmings is quite low, especially in peak years, so a preference alone would unlikely result in a predator control. Most likely all of the above mentioned limitations contribute to errors in my models. Nevertheless, my models give a first systematic picture of the ecosystem in Fennoscandia and do to a large extent support empirical studies performed at the population level (e.g. with regard to small rodent dynamics).

The boreal forest of Fennoscandia and in North-America differ in vegetation, temperature, species composition and population cycles (Boonstra et al., 2016). In the system in North-America, unlike the Fennoscandian system, a pronounced hare-lynx cycle can be observed. Ruesink et al. (2002) studied the Canadian system with Ecopath (Kluane National park). Unlike in my study they found indications that predation is the initiating factor for a decline in the mountain hare population, Ruesink et al. (2002) argued that when the predator densities increased, the impact on the producer decreased. Because I did not separate biomass for each cycle phase it was not possible to link a numerical response of predators and the impact on plants. However, I detected strong impacts on producers in peak cycle years, showing that herbivores control the bottom layer. In the cycle phases I assumed a constant production.

Hence, I cannot infer to a change in production. However, my study suggests a stronger herbivore-plant control than a predator-control unlike what controls the boreal forest system in Canada (Ruesink et al., 2002). Another interesting aspect I observed in the system is a stronger predation pressure on mountain hares in low vole and lemming years in Fennoscandia. This corresponds to the Canadian system, where ground squirrels experience a stronger predation pressure in low snowshoe-hare years (Ruesink et al., 2002). Both systems experience a non-equilibrium state in the short term. The regular population cycle leads the system smoothly from one state into another. Therefore, we do not observe trophic cascades or a regime shift to a different state (Scheffer & Carpenter, 2003).

It is important to understand the energy flow in a system, especially to anticipate and predict how an ecosystem will change with increasing anthropogenic pressure and climate change. Therefore, it is important to understand influences on the system, especially in respect to climate change, which is suggested to have a high influence on the dampening of vole and lemming cycle amplitudes (Cornulier et al., 2013). Yet, the returning cycle in the recent years suggests that climate change is not proven to be the answer for the observed changes in small rodent dynamics (Myers, 2018). Climate change dampening cycles for lemmings can be a result of thinner snow covers or the influence on mosses, which have generally a higher net primary production with colder climate (Ims & Fuglei, 2005; Turetsky et al., 2012). Generally, a dampening or change in the cycle influences the dynamic boreal forest system, and the consequences are still unclear.

The food web studied here gives insight on how the boreal forest ecosystem might function. It gives a simplified picture of the trophic relationships between vertebrates in the boreal forest of Fennoscandia. I found evidence of strong herbivore-plant relationships, and minor support for the role of predators. For a future scenario it would be interesting to see if adding variation in production and consumption reveals bottom-up mechanisms. However, to minimise uncertainty in the model, extensive fieldwork over several complete cycles is required. Including the whole vertebrate food web, could add to the insights provided by this study and might improve our evidence and understanding of the driving mechanisms in the boreal forest vertebrate community.

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Appendix

Table A1: The Biomass (B in kg/km²) for the different model scenarios.

Species	increase phase	peak phase	decrease phase	crash phase
Tengmalm's owl	0.0046	0.0069	0.0069	0.0046
Red fox	0.473	0.600	0.600	0.473
Pine marten	0.054	0.082	0.082	0.054
Stoat	0.054	0.054	0.054	0.054
Least weasel	0.009	0.009	0.009	0.009
Moose	146.300	146.300	146.300	146.300
Mountain hare	4.320	4.320	4.320	4.320
Red squirrel	2.240	2.240	2.240	2.240
Bank vole	21.880	21.880	1.750	1.750
Wood lemming	45.500	45.500	0.910	0.910
Field layer	18 030	18 030	15 570	15 570
Bottom layer	25 750	25 750	19 930	19 930

Table A2: Diet composition in proportions for the increase and peak scenarios. "Import" indicates food items eaten from outside the presented food web.











Prey/Consumer	1	2	3	4	5	6	7	8	9	10
1 Tengmalm's owl										
2 Red fox										
3 Pine marten		0.001								
4 Stoat		0.002								
5 Least weasel		0.002								
6 Moose										
7 Mountain hare		0.100	0.050							
8 Red squirrel		0.050	0.020							
9 Bank vole	0.500	0.200	0.150	0.500	0.500					
10 Wood lemming	0.500	0.200	0.150	0.500	0.500					
11 Field layer		0.300	0.100			0.200	1.000	0.050	0.800	0.010
12 Bottom layer								0.020	0.100	0.990
Import		0.145	0.530			0.800		0.930	0.100	

Table A3: Diet composition in proportions for decrease and crash scenarios. “Import” indicates food items eaten from outside the presented food web.

Prey/Consumer	1	2	3	4	5	6	7	8	9	10
1 Tengmalm’s owl	█									
2 Red fox		█								
3 Pine marten		0.001	█							
4 Stoat		0.001		█						
5 Least weasel		0.001			█					
6 Moose						█				
7 Mountain hare		0.150	0.080				█			
8 Red squirrel		0.050	0.020					█		
9 Bank vole	0.500	0.100	0.040	0.500	0.500				█	
10 Wood lemming	0.500	0.100	0.040	0.500	0.500					█
11 Field layer		0.350	0.260			0.200	1.000	0.050	0.800	0.010
12 Bottom layer								0.020	0.100	0.990
Import		0.247	0.560			0.800		0.930	0.100	

Table A4: Diet compositions for herbivores tested to test changes in the model scenarios. “Import” indicates food items eaten from outside the presented food web.

Prey/Consumer	6	8	9	10
1 Tengmalm’s owl				
2 Red fox				
3 Pine marten				
4 Stoat				
5 Least weasel				
6 Moose	█	█		
7 Mountain hare				
8 Red squirrel		█	█	
9 Bank vole			█	
10 Wood lemming				█
11 Field layer		1	1	1
12 Bottom layer				1
Import	1	1		

Table A5: Diet compositions of generalist predators tested for peak density rodent scenarios. “Import” indicates food items eaten from outside the presented food web.

Prey/consumer	Red fox				Pine marten			
1 Tengmalm’s owl								
2 Red fox	■	■	■	■				
3 Pine marten		0.002			■	■	■	■
4 Stoat		0.003						
5 Least weasel		0.003						
6 Moose								
7 Mountain hare	0.050	0.050	0.150		0.005	0.100	0.020	
8 Red squirrel		0.100	0.050		0.005	0.050	0.020	
9 Bank vole	0.250	0.300	0.150	0.500	0.200	0.250	0.100	0.500
10 Wood lemming	0.250	0.300	0.150	0.500	0.200	0.250	0.100	0.500
11 Field layer	0.300	0.200	0.400		0.050	0.150	0.200	
12 Bottom layer								
Import	0.150	0.142	0.100		0.540	0.200	0.56	

Table A6: Diet compositions of generalist predators tested for low density rodent scenarios. “Import” indicates food items eaten from outside the presented food web.

Prey/Consumer	Red fox				Pine marten			
1 Tengmalm’s owl								
2 Red fox	■	■	■	■				
3 Pine marten		0.002			■	■	■	■
4 Stoat		0.002						
5 Least weasel		0.002						
6 Moose								
7 Mountain hare	0.180	0.200	0.100		0.100	0.150	0.050	
8 Red squirrel	0.080	0.100	0.100		0.050	0.100	0.020	
9 Bank vole	0.050		0.150	0.500	0.020		0.080	0.500
10 Wood lemming	0.050		0.150	0.500	0.020		0.080	0.500
11 Field layer	0.300	0.400	0.250		0.300	0.350	0.200	
12 Bottom layer								
Import	0.340	0.294	0.250		0.510	0.400	0.570	

Table A7: AIC selection of the generalized linear models used to analyse the effect of scenario, species and sensitivity on the ecotrophic efficiency (EE). All models are displayed with the number of parameters in the model (K) and the Akaike weight ($AICc\omega$).

Model	K	$AICc$	$\Delta AICc$	$AICc\omega$
Scenario + species	13	-5300.8	0.00	0.733
Scenario + species + sensitivity	14	-5298.8	2.02	0.267
Species	9	-4821.2	479.55	0.00
Species + sensitivity	10	-4819.2	481.56	0.00
Scenario	5	-1731.1	3569.65	0.00
Scenario + sensitivity	6	-1729.1	3571.66	0.00
Null model	1	-1260.2	4040.56	0.00
Sensitivity	2	-1258.2	4042.56	0.00

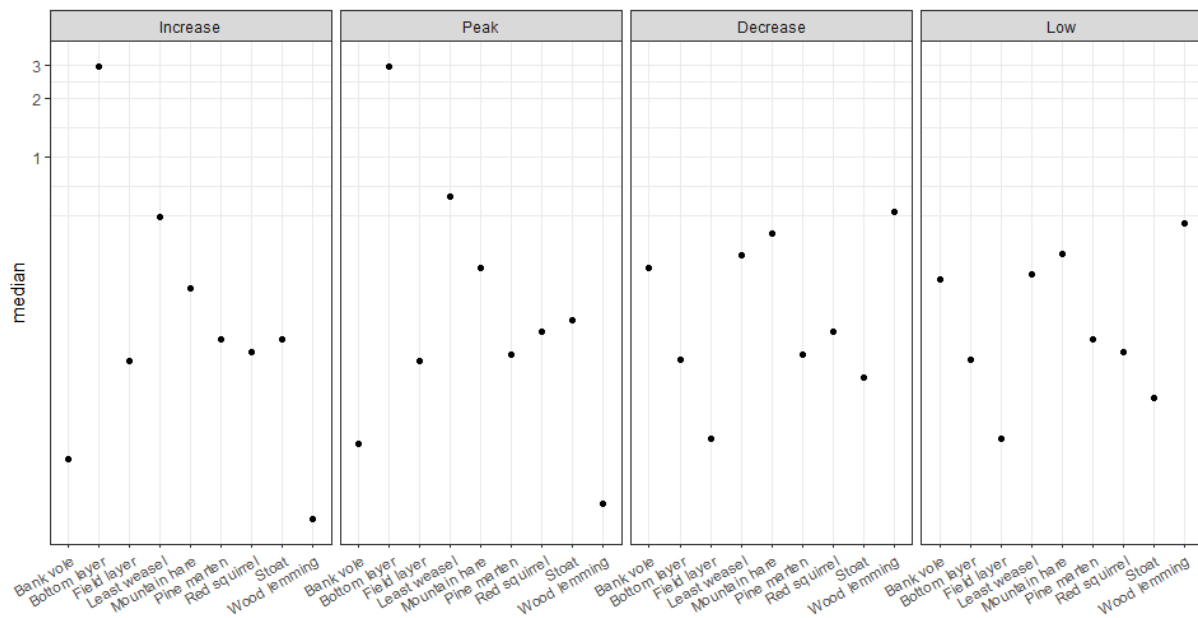


Figure A1: The median of the EE from all parameter changes.