

# ECOGRAPHY

## Review and synthesis

### The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the Exploitation Ecosystem Hypothesis

Tarja Oksanen, Lauri Oksanen, Katariina E. M. Vuorinen, Christopher Wolf, Aurelia Mäkynen, Johan Olofsson, William J. Ripple, Risto Virtanen and Tove Aa. Utsi

T. Oksanen (<https://orcid.org/0000-0003-0531-5346>), L. Oksanen (<https://orcid.org/0000-0003-1006-1520>) ✉ ([lauoks@uit.no](mailto:lauoks@uit.no)) and T. Aa, Utsi, Dept of Arctic and Marine Biology, UiT – The Arctic Univ. of Norway, Alta, Norway. – K. E. M. Vuorinen (<https://orcid.org/0000-0002-4774-6796>), A. Mäkynen, TO and LO, Dept of Biology, Ecology Section, Univ. of Turku, Turku, Finland. KEMV also at: Dept of Natural History, NTNU Univ. Museum, Norwegian Univ. of Science and Technology, Trondheim, Norway. – C. Wolf and W. J. Ripple, Dept of Forest Ecosystems and Society, Oregon State Univ., Corvallis, OR, USA. – J. Olofsson, Dept of Ecology and Environmental Science, Umeå Univ., Umeå, Sweden. – R. Virtanen (<https://orcid.org/0000-0002-8295-8217>), Dept of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Leipzig, Germany, and German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany, and Dept of Ecology and Genetics, Univ. of Oulu, Oulu, Finland.

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Many terrestrial endotherm food webs constitute three trophic level cascades. Others have two trophic level dynamics (food limited herbivores; plants adapted to tackle intense herbivory) or one trophic level dynamic (herbivorous endotherms absent, thus plants compete for the few places where they can survive and grow). According to the Exploitation Ecosystems Hypothesis (EEH), these contrasting dynamics are consequences of differences in primary productivity. The productivity thresholds for changing food web dynamics were assumed to be global constants. We challenged this assumption and found that several model parameters are sensitive to the contrast between persistently warm and seasonally cold climates. In persistently warm environments, three trophic level dynamics can be expected to prevail almost everywhere, save the most extreme deserts. We revised EEH accordingly and tested it by compiling direct evidence of three and two trophic level dynamics and by studying the global distribution of felids. In seasonally cold environments, we found evidence for three trophic level dynamics only in productive ecosystems, while evidence for two trophic level dynamics appeared in ecosystems with low primary productivity. In persistently warm environments, we found evidence for three trophic level dynamics in all types of ecosystems. The distribution of felids corroborated these results. The empirical evidence thus indicates that two trophic level dynamics, as defined by EEH, are restricted to seasonally cold biomes with low primary productivity, such as the arctic–alpine tundra and the temperate steppe.

Keywords: arctic, arid, endotherms, terrestrial food webs, thermal seasonality, trophic exploitation



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## Introduction

Strong, exploitative food web interactions, and trophic cascades triggered by them, structure nature across the globe: in benthic marine and freshwater ecosystems, where community level trophic cascades were first documented (Estes and Palmisano 1974, Power and Matthews 1983, Power et al. 1985, 1989, Estes and Duggins 1995), in pelagic ecosystems (Carpenter et al. 1985, Daskalov 2002, Casini et al. 2008, Walsh et al. 2016, Batten et al. 2018), and also in terrestrial ones (Marquis and Whelan 1994, Terborgh et al. 2001, 2006, Beschta and Ripple 2009, 2019, Terborgh and Feeley 2010, Newsome and Ripple 2015, Ripple et al. 2015, Svenning et al. 2016, Morris and Letnic 2017, Beschta et al. 2018, Letnic et al. 2018), where the existence of strong, community level trophic cascades was initially regarded as unlikely (Strong 1992, Polis and Strong 1996, Shurin et al. 2006).

For terrestrial food webs, the conjecture of community level trophic cascades was pioneered by the Green World Hypothesis (GWH) of Hairston et al. (1960). Referring to the abundance of green plants and to the depletion of vegetation after predator extirpations, they proposed that the world remains 'green' (biomass rich) because the collective density of herbivores is regulated by the collective action of predatory animals. Predator and plant communities are thus structured by resource competition (Cajander 1909, Walter 1964, 1968, Rosenzweig 1966, MacArthur 1972, Tilman 1988, de Sàtge et al. 2017), whereas for herbivores, GWH implied that apparent competition rules (Holt 1977). Murdoch (1966) appreciated the broad scope of GWH, but criticized its reliance on the trophic level concept, foreshadowing the critique by Ehrlich and Birch (1967; for a response, see Slobodkin et al. 1967). Moreover, the top-down perspective of GWH was challenged by the bottom-up conjecture of Murdoch (1966) and White (1978, 2013), who proposed that the low nutritive value of plants limits the population growth of terrestrial herbivores. This plant quality hypothesis was re-enforced by the discovery of inducible plant defenses (Haukioja and Hakala 1975, Bryant and Kuropat 1980, Haukioja and Neuvonen 1985), providing a potential mechanism for density dependent regulation of herbivores.

Nevertheless, herbivores have recurrently devastated biomass rich plant communities in predator-free experimental and natural systems (Moen et al. 1993a, b, Rao et al. 2001, Terborgh et al. 2001, 2006, Hambäck et al. 2004, Ripple and Beschta 2004, 2005, 2006, 2007, 2008, 2012a, Rammul et al. 2007, Côté et al. 2008, Beschta and Ripple 2009, Dahlgren et al. 2009, Oksanen et al. 2010, Ripple et al. 2010, Terborgh and Feeley 2010, Tuomi et al. 2019, Supplementary material Appendices 1–3). When herbivores are not controlled by predators, they destroy even strongly defended shrubs and forbs (Moen et al. 1993a, Rammul et al. 2007, Dahlgren et al. 2009, Olofsson et al. 2012, 2014). Trees may seem invulnerable, but their Achilles' heel is in their browsing sensitive juvenile stages (Hansson 1985, Gill 1992, Ostfeld and Canham 1993,

Chouinard and Filion 2005, Nevalainen et al. 2016, Bognounou et al. 2018, Vuorinen et al. 2020). In the absence of predators, forest regeneration is therefore in peril (Beschta and Ripple 2009), and secondary succession may cease (Norrdahl et al. 2002, Supplementary material Appendix 4). The persistence of 'green worlds' thus requires predators, in accordance with GWH.

On the other hand, all worlds are not equally green. A large part of Planet Earth is covered by biomes with prostrate vegetation and low plant biomass (Walter 1964, 1968, Olson et al. 2001, Higgins et al. 2016). In his food chain hypothesis, Fretwell (1977) proposed that contrasting food chain dynamics contribute to these differences in plant biomass and vegetation characteristics among different ecosystems. The dynamic lengths of terrestrial food chains increase from one (plants only), to two (plants and herbivores), three (plants–herbivores–predators) and four trophic levels (plants–herbivores–predators–secondary predators), along gradients of increasing primary productivity, and the consequences of different food chain lengths cascade down the food web. Ecosystems with an even number of trophic levels are characterized by intense herbivory, low above ground plant biomass and predominance of grazing tolerant, prostrate plants; whereas ecosystems with an odd number of trophic levels are biomass rich and dominated by competitive plants. Fretwell (1977) thus used food web dynamics in explaining the characteristic traits of forest, steppe and tundra plants.

Oksanen et al. (1981) regarded Fretwell's (1977) energy-centered hypothesis as plausible for endotherms, given their high energy demands (see also Oksanen and Oksanen 2000). To control the logic of Fretwell's (1977) conjecture and to deduce testable predictions, Oksanen et al. (1981) modeled it, using Rosenzweig's (1973) three-dimensional exploitation models, which allow an explicit treatment of the dual role of herbivores as prey of carnivores and as predators of plants. Inspired by Rosenzweig's (1971) 'Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time', Oksanen et al. (1981) named the emerging conjecture the Exploitation Ecosystems Hypothesis (EEH). Along gradients of increasing primary productivity, EEH predicted that the dynamic food chain length increases from one to two and to three trophic levels, as proposed by Fretwell (1977). Conversely, EEH did not support Fretwell's (1977) arguments concerning four trophic level dynamics in endotherm food webs of maximally productive terrestrial ecosystems. Instead, it predicted that productive terrestrial ecosystems would be locked in three trophic level dynamics, because of the low eco-energetic efficiencies of endotherms and the biology-based assumption of saturating functional responses. The productivity thresholds for changing food web dynamics were inferred by matching predicted biomass patterns against arctic and boreal biomass data (Oksanen et al. 1981, Oksanen 1983).

As predicted by EEH, the strength of the top-down regulation of ungulates decreases and finally gives way to two trophic level dynamics along the gradient from productive forests to the less productive tundra (Crête and Manseau 1996,

Crête and Doucet 1998, Crête 1999, Ripple and Beschta 2012b). In Fennoscandia, the same pattern is seen in small rodents, too. They are regulated by predators in boreal ecosystems and in the most productive tundra habitats (Henttonen et al. 1987, Korpimäki and Norrdahl 1998, Klemola et al. 2000, Hanski et al. 2001, Ekerholm et al. 2004, Hambäck et al. 2004, Aunapuu et al. 2008, Hoset et al. 2014), whereas in less productive tundra ecosystems, the strong interaction is between rodents and plants (Moen et al. 1993b, Oksanen et al. 1997, Virtanen et al. 1997a, Virtanen 1998, 2000, Ravolainen et al. 2011, 2014, Olofsson et al. 2004a, 2009, 2012, 2014, Hoset et al. 2014, 2017, Saccone et al. 2014, Ruffino et al. 2016).

EEH is, however, supposed to apply globally, whereas the corroborating evidence, summarized in the previous paragraph, has been obtained from high-latitude ecosystems. Their endotherm food webs are simple (Mendoza and Araújo 2019) and a large fraction of the energy fixed by their plants is locked in the frozen soil in winter (Wielgolaski 1975, Turchin and Batzli 2001). Conceivably, these characteristics of northern ecosystems might influence the values of model parameters, and via them, the positions of the primary productivity thresholds separating one, two and three trophic level ecosystems from each other. In this contribution, we approach this issue by studying the consequences of contrasting thermal climates on food web dynamics. We will focus on the contrast between environments with and without real winters, with temperatures below 0°C, which can be regarded as an either-or issue in a global scale (Supplementary material Appendix 5).

To clarify our point of departure, we start by summarizing the EEH model. Thereafter, we study the expected impacts of contrasting thermal climates on parameter values and revise the EEH conjecture accordingly, considering both food web dynamics and their evolutionary implications. To test the revised EEH, we review the empirical evidence for three and two trophic level dynamics in terrestrial endotherm food webs. As an independent test, we use the geographical distributions of felids. Our choice of felids as indicators of three trophic level dynamics is based on their shared traits, indicating adaptations for killing healthy prey, and on their broad geographic distribution and varying habitat preferences, making it unlikely that their absence could depend on climate or habitat ‘per se’ (Supplementary material Appendix 6). In the final section, we explore the ramifications of our findings for nature protection and rewilding.

## Exploring the impact of thermal seasonality on terrestrial endotherm food web dynamics

### The structure of the model

Oksanen et al. (1981, p. 241) coped with the controversies concerning the importance of trophic exploitation by stating seven assumptions and exploring their logical consequences:

1) All plants are vulnerable to some herbivores, and each herbivore is vulnerable to at least one predator. This assumption can be regarded as the hard premise of EEH.

2) Herbivory-based food webs are dynamically independent from other food webs.

3) Trophic levels are discrete because ‘photosynthesis, utilization of vegetative plant organs, and predation require adaptations too different to allow an individual organism to be efficient in more than one of these modes of energy intake’.

4) For organisms with similar eco-energetic efficiency, trophic levels act as homogeneous blocks, because ‘competition within resource-limited trophic levels should make the sum of utilization curves match the distribution of resources so that rather homogeneous exploitation pressure should be exerted upon the populations on the trophic level below’.

5) Dynamics of consumers are determined by consumer–resource encounter rates, in accordance with the principle of mass action. Interference can act as a stabilizing factor (Oksanen et al. 1981, p. 250), but realistic levels of interference are insignificant for broad patterns of biomass and community structure (Rosenzweig 1977; see also Oksanen et al. 1995, 2001).

6) The maximum per biomass unit rate of plant biomass increase,  $r$  and the maximum sustainable above ground plant biomass,  $K$  (plant carrying capacity), are directly proportional to potential primary productivity,  $G$ , defined as the maximum primary productivity allowed by the physical environment (Oksanen et al. 1981, pp. 244–245). Thus  $r = \lambda_1 G$  and  $K = \lambda_2 G$ , where parameters  $\lambda_1$  and  $\lambda_2$  are positive constants;  $\lambda_1$  reflects the fraction of energy channeled into digestible tissues and  $\lambda_2$  is inversely proportional to the per biomass unit cost of maintenance of non-photosynthetic plant tissues.

7) All influences of climate on food web dynamics are mediated via the annual average value of  $G$ . Specifically, Oksanen et al. (1981, p. 246) assumed that ‘consumers are adapted to the climate in which they live and the costs of these adaptations are just a minor factor in the energy budgets of consumers’.

Oksanen et al. (1981) technically assumed logistic growth of plant biomass and type II functional responses in consumers. However, all saturating functional responses yield convergent predictions for the impact of primary productivity on food chain length (Oksanen and Oksanen 2000). Given assumptions 1–7, and the above technical assumptions, the dynamics of state variables, i.e. the biomass of plants ( $P$ ), herbivorous endotherms ( $H$ ) and carnivores/predators ( $C$ ), are governed by the following three differential equations:

$$dP / dt = rP \left( \frac{K - P}{K} \right) - \frac{a}{1 + a\beta P} PH \quad (1)$$

$$dH / dt = -mH + \frac{ka}{1 + a\beta P} PH - \frac{\alpha}{1 + \alpha\eta H} HC \quad (2)$$

$$dC / dt = -\mu C + \frac{\kappa a}{1 + \alpha \eta H} HC \quad (3)$$

Plant biomass ( $P$ ) was operationally defined as the aboveground biomass of protoplasm-rich plant tissues (Oksanen et al. 1981, pp. 245–246), because respiratory costs are created by protoplasm, and protoplasm-rich tissues constitute the digestible part of plant biomass. For herbivores ( $H$ ), Oksanen et al. (1981) used the operational definition of Slobodkin et al. (1967), and defined herbivores as animals with the capacity ‘to consume the vegetation itself’. Carnivores/predators ( $C$ ) were defined as animals adapted to subdue and to kill healthy prey (Oksanen et al. 1981, p. 240).

### Definitions of state variables and parameters reconsidered

The operational definition of plant biomass by Oksanen et al. (1981) is problematic, as it embraces herbaceous and deciduous tissues that wither when conditions become unfavorable. Differential equation models can deal with production pulses by averaging over time (for stability issues, see Oksanen 1990a, Turchin and Batzli 2001 and Sauve et al. 2020), but resource pulses too short to be traced by consumers should not be included, as herbivore dynamics are not significantly influenced by the heights of short-lived peaks in plant biomass (Turchin and Batzli 2001, Humphries et al 2017). Therefore, we need to redefine the state variable  $P$  as the biomass of perennially available, protoplasm-rich plant tissues.

Our parameter definitions (1) converge to the parameter definitions of Turchin (2001, 2003), except for parameters  $a$  and  $\mu$ . Defining parameter  $a$  as the searching rate of herbivores would ignore the often large biomass losses inflicted mechanically or as consequences of partial consumption (Oksanen 1978, Hansson 1985, Åström et al. 1990, Gill 1992, Kobayashi et al. 1997), which characterize terrestrial herbivore–plant interactions and need to be embedded in the minus term of Eq. 1. Parameter  $a$  must therefore be defined

as the attack rate experienced by plants (Box 1). Moreover, defining parameter  $\mu$  as the energetic costs of maintenance of predators and their per capita rate of decline in the absence of resources (Oksanen and Oksanen 2000, Turchin 2001, 2003) presupposes that predators are entirely dependent on herbivorous prey. However, predators may be ‘subsidized’ by donor-controlled energy flows (Polis and Strong 1996). To embrace these additional resources, we need to redefine parameter  $\mu$  as the rate of energy gain from herbivores required for zero population growth of predators.

### Anticipated impact of seasonally cold climate on parameter values

In thermally seasonal environments, temperature differences among the three coldest months are small (Walter et al. 1967). Thus there is a natural dichotomy between seasonally cold environments, where the thermal winter (a period with weekly mean temperatures below 0°C) lasts for at least three months, and environments where thermal winters do not exist at all (Supplementary material Appendix 5). Environments of the latter type will be referred to as persistently warm (including coastal regions with cool climate and tropical mountains with regular night frosts). Comparing the climate charts of Walter et al. (1967) to the boundaries of the seasonally cold biomes of Higgins et al. (2016), we found that their boundaries by and large converge with the limits of areas with thermal winters.

Seasonally cold climate reduces the useful part of primary productivity, because in fall, soluble organic compounds are translocated from withering herbaceous shoots and deciduous leaves to roots and rhizomes, to be locked into the frozen soil, which reduces the value of parameter  $\lambda_1$ . Moreover, the maintenance costs of herbaceous and deciduous tissues and the energetic costs of translocating organic compounds reduce the amount of energy available for the maintenance of perennial tissues and, therefore, the value of  $\lambda_2$ . Seasonally cold climate thus reduces the values of parameters  $r (= \lambda_1 G)$  and  $K (= \lambda_2 G)$ .

#### Box 1. Parameter definitions

$G$  = potential primary productivity

$\lambda_1$  = the fraction of primary production channeled to perennial, protoplasm-rich aboveground plant biomass.

$\lambda_2$  = the energy available for maintenance of perennial aboveground tissues.

$r = \lambda_1 G$  = maximum per biomass unit rate of plant biomass increase

$K = \lambda_2 G$  = maximum sustainable above ground plant biomass

$a$  = the probability that a given plant biomass unit is ingested, mechanically destroyed or lethally damaged by a given, actively foraging herbivore in a unit time.

$\beta$  = the average time used by herbivores when inflicting a loss of plant biomass unit.

$k$  = herbivores’ constant of proportionality, relating their energy gain to all biomass losses inflicted upon plants.

$m$  = the per capita energy gain rate of herbivores, required to maintain zero rate of population growth.

$\alpha$  = the searching efficiency of predators.

$\kappa$  = predators’ constant of proportionality, relating their energy gains to losses inflicted on herbivores.

$\eta$  = the average per prey handling time of predators.

$\mu$  = the per capita energy gain rate from herbivores, required for zero rate of population growth of predators.

In addition, seasonally cold climate influences the values of the herbivory-related parameters  $a$ ,  $\beta$ ,  $k$  and  $m$ . To tackle these impacts, let us break parameter  $a$  into the forage searching rate,  $a_1$ , and the rate at which an herbivore inflicts collateral biomass losses,  $a_2$ ; and let  $c$  be the assimilation efficiency of herbivores. As inflicting collateral damages gives nothing to the herbivore and does not include handling time, the coefficient of proportionality,  $k$ , relating energy gains to inflicted losses, is obtained as  $k = ca_1/(a_1 + a_2)$ , and the overall handling time,  $\beta$ , as  $\beta = a_1h/(a_1 + a_2)$ , where  $h$  is handling time per biomass unit of ingested forage.

Winter conditions profoundly increase the value of  $a_2$ , whereas the value of  $a_1$  is reduced. When plants are embedded in snowpack, accessing them is difficult and inflicts collateral damages (Virtanen et al. 2002a, Dahlgren et al. 2009, Olofsson et al. 2014, Supplementary material Appendix 1). Moreover, utilization of phloem and cambium (girdling) destroys vital transport systems, thus inflicting large secondary biomass losses (Hansson 1985, Gill 1992, Supplementary material Appendices 1–2). The forage handling time,  $h$ , should be independent of seasonality, whereas the low digestibility of winter forage decreases the value of  $c$  (assimilation efficiency). The rate of energy acquisition,  $ca_1P/(1 + a_1hP)$  is thus reduced by seasonally cold climate, while the energetically demanding winter foraging (removing the hard tundra snow or wading in the deep and soft taiga snow) increases the value of parameter  $m$ . In addition, the high value of  $a_2$  and the consequently low value of  $\beta$  increase the biomass losses experienced by plants. Winter foraging by herbivorous endotherms thus inflicts large biomass losses on plants, but little energy is gained from this energetically costly foraging effort.

By increasing the energetic costs of mobility, snow cover also increases the foraging costs of predators, thus increasing the value of parameter  $\mu$ . Moreover in seasonally cold environments, endotherm food webs are simple, and dependable connections between endotherm and ectotherm webs are lacking (Mendoza and Araújo 2019). Predatory endotherms of northern ecosystems are therefore dependent on herbivores as prey (Erlinge 1974, 1977, Erlinge et al. 1983, Messier and Crête 1985, Krebs et al. 1995, Crête and Manseau 1996,

Helldin 1999, Peterson 2007, Ripple and Beschta 2012b, Boonstra et al. 2016, Humphries et al. 2017). Conversely, in persistently warm environments, a large number of mammals feed on ectotherms. Energy is channeled from the detritus-based food web to predatory endotherms. Additional resources are provided by high-quality plant products, such as fruits and tubers (Emmons 1987, Polis 1991, Doolan and MacDonald 1996, Polis and Strong 1996, Vernes et al. 2001, Lynch and McCann 2007, Ayal 2007, Basuony et al. 2013, Rocha-Mendes et al. 2010, Nakabayashi et al. 2016, Mendoza and Araújo 2019). These additional energy flows reduce the dependency of predators on herbivorous prey, thus reducing the value of parameter  $\mu$ . The above consequences of thermal seasonality on model parameters are summarized in Box 2.

### Exploring patterns of food web dynamics predicted for seasonally cold and for persistently warm environments

Using the information summarized in the previous section, we can now explore the predicted relationship between potential primary productivity and endotherm food web dynamics in seasonally cold and in persistently warm environments. As we focus on cascading impacts of predation, we can simplify the graphics by operating in the  $C=0$  phase plane. Technically, we assume that predators are absent from the focal ecosystem but present in its surroundings, thus being able to invade the focal ecosystem. The zero isoclines for plants (4), herbivores (5) and carnivores/predators (6), respectively, can be then be solved by setting the left hand sides of Eq. 1–3 equal to zero and substituting  $C=0$  in the resulting equations, which yields:

$$H = \frac{r(1 + a\beta P)(K - P)}{aK} \text{ for the plant isocline} \quad (4)$$

$$P^* = \frac{m}{a(k - m\beta)} \text{ for the herbivore isocline} \quad (5)$$

#### Box 2. Anticipated impact of thermal seasonality on values of model parameters

The product  $ka$  decreases, because the increase in  $a$  is entirely due to collateral damage that does not yield energy to the herbivore.

|                        |                                      |
|------------------------|--------------------------------------|
| $r \downarrow$         | $\downarrow$ negative                |
| $K \downarrow$         | = no obvious impact                  |
| $a \uparrow$           | $\uparrow$ positive                  |
| $\beta \downarrow$     | $\uparrow\uparrow$ strongly positive |
| $k \downarrow$         |                                      |
| $m \uparrow$           |                                      |
| $\alpha \downarrow$    |                                      |
| $\kappa =$             |                                      |
| $\eta =$               |                                      |
| $\mu \uparrow\uparrow$ |                                      |

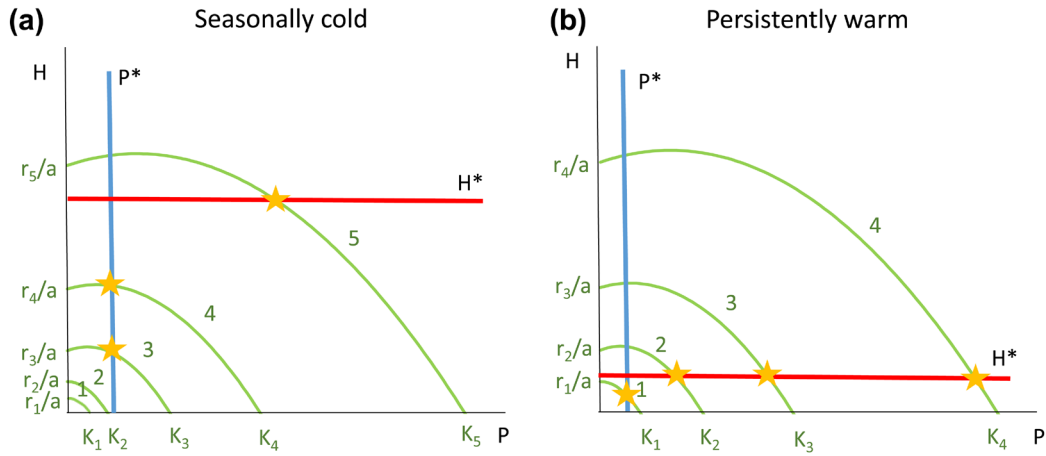


Figure 1. Plant isoclines (green curved lines) for five ecosystems differing in primary productivity, and their shared herbivore ( $P=P^*$ ) and predator ( $H=H^*$ ) isoclines in the  $C=0$  phase plane. Non-trivial equilibrium points with  $H>0$  are denoted by a yellow star. For three trophic level ecosystems, equilibrium points have been projected to the  $C=0$  phase plane. The green numbers refer to potential primary productivity. (a) Refers to seasonally cold environments, (b) refers to persistently warm ones. For persistently warm environments, the plant isocline for ecosystem 5 lies outside the area shown in (b).

$$H^* = \frac{\mu}{\alpha(\kappa - \mu\eta)} \text{ for the carnivore/predator isocline} \quad (6)$$

Equation 4 implies that the plant isocline has the characteristic parabola shape, meeting the herbivore axis at  $H=r/a$  and the plant axis at  $P=K$ . As interference between herbivores and between predators was assumed to be too weak to have an impact on biomass patterns (assumption 5, see also Rosenzweig 1977), the herbivore isocline (Eq. 5) is a vertical line in the  $C=0$  phase plane. For the same reason, the predator isocline (Eq. 6) is a horizontal line perpendicular to the herbivore axis (Fig. 1).

On the basis of Eq. 4–6, we can now construct sets of isocline graphs for ecosystems differing in potential primary productivity, for seasonally cold (Fig. 1a) and for persistently warm (Fig. 1b) environments. As the productivity dependent parameters  $r (= \lambda_1 G)$  and  $K (= \lambda_2 G)$  do not appear in the equations for herbivore (5) and predator (6) isoclines, their positions in the plant–herbivore phase plane are fixed. Thus we can illustrate the impact of primary productivity on food web dynamics by superimposing plant isoclines, representing ecosystems with five different primary productivity values, on these fixed herbivore and predator isoclines. Seasonally cold climate reduces the values of  $r/a$  and  $K$  (see previous section), reducing the height of the plant isocline along the herbivore axis and its extent along the plant axis. We illustrate this by letting each plant isocline for seasonally cold environments (Fig. 1a) match the plant isocline in persistently warm environments with one step lower primary productivity (Fig. 1b). In Fig. 2, we summarize the predictions of the revised EEH on equilibrium plant biomass (the width of the green field) and on the intensity of endotherm herbivory (the width of the yellow field) for seasonally cold (Fig. 2a) and persistently warm (Fig. 2b) environments in relation to potential primary productivity.

In seasonally cold environments, challenges of winter conditions (see above) result in a high value of  $P^*$ . In the low end of the primary productivity axis, there is thus a substantial interval, where plant and herbivore isoclines do not cross (plant isoclines 1 and 2 in Fig. 1a, interval 1 in Fig. 2a). These ecosystems display one trophic level dynamics: herbivorous endotherms are absent and plants compete for the few sites where they can grow (Oksanen 1980, 1990b, Olofsson et al. 1999, Supplementary material Appendix 7 Fig. A27).

Advancing along the gradient of increasing primary productivity, we pass a threshold where herbivore and plant isoclines cross, but predator and plant isoclines do not. This isocline constellation generates two trophic level dynamics (plant isoclines 3 and 4 in Fig. 1a, interval 2 in Fig. 2a). Due to the high value of parameter  $\mu$ , resulting in a high value of  $H^*$ , the potential primary productivity interval with two trophic level dynamics is wide. Within this productivity interval, Rosenzweig’s (1971) Paradox of enrichment rules: increasing potential primary productivity results in intensification of herbivory pressure, favoring grazing tolerant plants (Oksanen 1990b, Oksanen and Virtanen 1997). Among herbivores, the ability to exploit a depleted forage base is favored even at the cost of reduced agility (Oksanen 1992, Oksanen et al. 2008). With increasing potential primary productivity, the system meets a bifurcation point (orange arrow in Fig. 2a), where stable dynamics are replaced by violent oscillations (Rosenzweig 1971, Turchin et al. 2000, Turchin and Batzli 2001), creating niches for outbreak croppers (Ruffino and Oksanen 2014).

With further increase in potential primary productivity, we meet the next threshold, where plant and predator isoclines cross (plant isocline 5 in Fig. 1a, interval 3 in Fig. 2a). Predators can now persist, if they invade in numbers high enough to prevent critical forage depletion by herbivores (Abrams and Roth 1994, Oksanen et al. 2013). A three

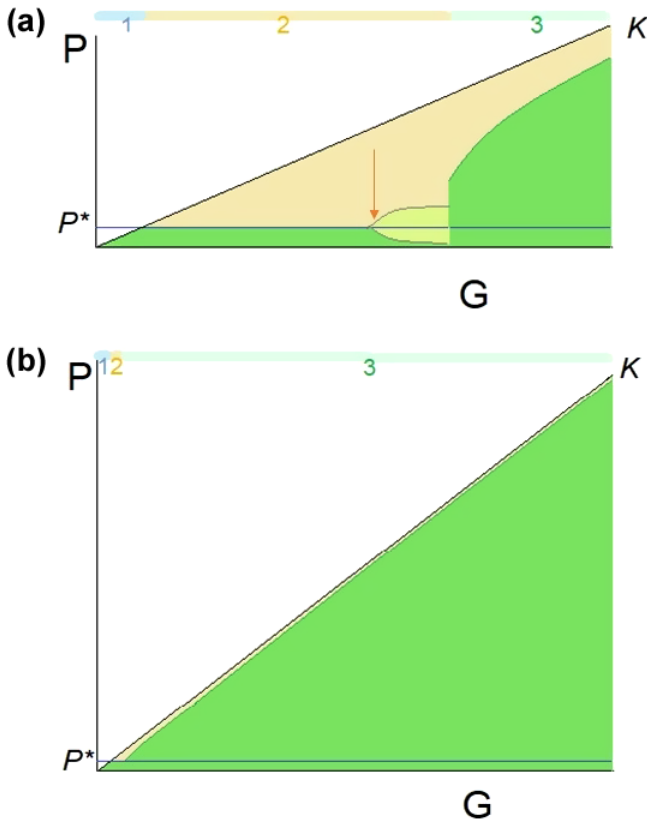


Figure 2. Predicted relation of plant carrying capacity ( $K$ , black oblique line), above ground plant biomass at the herbivore isocline ( $P^*$ , horizontal blue line), equilibrium above ground plant biomass (the width of the green field) and the predicted impact of natural herbivory on above ground plant biomass (the width of the yellow field) to potential primary productivity ( $G$ ) in a seasonally cold environment (a) and in a persistently warm environment (b). The broad lines on the top of each figure illustrate the widths of productivity intervals with one (blue) two (yellow) and three (green) trophic level dynamics. The yellow arrow represents the bifurcation point; the width of the light green field in illustrates the variation in above ground plant biomass during different phases of herbivore oscillations.

trophic level equilibrium emerges and is likely to be the only locally stable one (see Fig. 2c in Oksanen et al. 1981). Projected to the  $C=0$  phase plane, this equilibrium lies at the intersection of plant and predator isoclines. Herbivory pressure is reduced, aboveground plant biomass increases sharply, and grazing tolerant plants are replaced by more competitive species (Oksanen 1980, 1990b). Among herbivores, apparent competition starts to favor agile and fertile species (Holt 1977, Oksanen 1992, 1993) and create tradeoffs between foraging, reproduction and predator avoidance (Oksanen and Lundberg 1995). As the value of  $H^*$  is high, the intensity of herbivory is nevertheless substantial (Fig. 2a, see also Ericson 1977), but herbivores are not starving. Hence their impacts on plants are selective, favoring plants with permanent or inducible defenses (Pastor and Naiman 1992, Bryant et al. 1994).

In persistently warm environments, forage plants can be detected, accessed and consumed without inflicting large collateral damages and without spending much energy. Hence the value of  $a_1$  (actual searching efficiency) is high and the value of parameter  $m$  is low, resulting in a low value of  $P^*$ . Ecosystems with one trophic level dynamics (interval 1 in Fig. 2b) are therefore restricted to almost sterile areas. Moreover, the value of  $H^*$  is low, as foraging costs are low and predators have alternative resources. In arid environments, the searching efficiency of predators can be further increased by the need of herbivores to search waterholes (Oksanen and Oksanen 2000). Consequently, the primary productivity range of two trophic level ecosystems (plant isocline 1 in Fig. 1b, interval 2 in Fig. 2b) is narrow. Within this interval, the intensity of herbivory is moderate at its most (Fig. 2b), possibly accounting for some plant traits, such as the frequent occurrence of spines in desert plants, but not for major patterns in plant strategies.

When the threshold for three trophic level dynamics is passed, increasing primary productivity is predicted to rapidly reduce the intensity of herbivory (plant isoclines 2–4 in Fig. 1b, interval 3 in Fig. 2b). For persistently warm environments, the dynamics generated by the revised EEH thus by and large converge to GWH, but with the additional prediction that increasing primary productivity increases the strength of the trophic cascade (the distance between  $P^*$  and the upper end of the green field in Fig. 2b).

## Testing the revised EEH

### Preface

To test the revised EEH summarized in the previous section, we examined evidence for three and two trophic level dynamics in terrestrial endotherm food webs and related it to the biome system of Higgins et al. (2016) and to landscape level primary productivity, as ‘spillover predation’ from productive habitats can override local dynamics in landscapes where productive habitats abound (Oksanen 1990c, Oksanen et al. 1992a, b; see also Holt 1984). To ensure that our results reflect local food web dynamics, we focused on resident herbivores and on short-range migrants. Moreover, we mapped the collective distribution of felids, whose shared traits imply adaptations for killing healthy prey and which are present in cold and hot climates and in open and densely vegetated habitats (Supplementary material Appendix 6).

We obtained our primary productivity estimates from NASA’s satellite-based data. NASA’s values are consistently only about half of the IBP estimates used by Oksanen et al. (1981). For example, the IBP (International Biological Program) estimate for the lowland tundra at Barrow, Alaska, was  $230 \text{ g m}^{-2} \text{ yr}^{-1}$ , (Miller et al. 1980), whereas NASA’s dataset yielded  $102 \text{ g m}^{-2} \text{ yr}^{-1}$ . As primary productivity of the tundra has increased in response to global warming (Mekonnen et al. 2018), methodological issues probably account for this difference. EEH’s primary productivity thresholds were

therefore reduced from the 35 and 700  $\text{g m}^{-2}\text{yr}^{-1}$ , to 20 and 400  $\text{g m}^{-2}\text{yr}^{-1}$ .

### Predictions to be tested

1) For all ecosystems with primary productivity  $> 400 \text{ g m}^{-2}\text{yr}^{-1}$  and, in persistently warm environments, for all ecosystems with primary production  $> 20 \text{ g m}^{-2}\text{yr}^{-1}$ , exclusion, extirpation or decimation of predators or their spontaneous absence results in at least a 30% reduction in community level plant biomass, vegetation cover and NDVI (normalized difference vegetation index), and in large changes in the composition of the vegetation. The return or recovery of predators reverses these changes.

2) For all ecosystems in seasonally cold environments with landscape level primary productivity between 20 and 400  $\text{g m}^{-2}\text{yr}^{-1}$ , exclusion of herbivorous endotherms or their absence increases the community-level plant biomass and its proxies by at least 30% and results in replacement of low growing, grazing-tolerant plants by taller and more competitive ones. Return, recovery or re-introduction of herbivorous endotherms reverses these changes.

3) Excluding physically inaccessible areas (islands, Australia), felids are present in all ecosystems with primary productivity  $> 400 \text{ g m}^{-2}\text{yr}^{-1}$ . In persistently warm environments, felids are present everywhere, except for extreme deserts, with primary production  $< 20 \text{ g m}^{-2}\text{yr}^{-1}$ .

4) In seasonally cold environments, felids are restricted to ecosystems with primary productivity  $> 400 \text{ g m}^{-2}\text{yr}^{-1}$ .

We chose the 30% impact threshold in order to exclude minor top-down impacts (Polis et al. 2000, Ripple et al. 2016), but to ensure the inclusion of large impacts, which do not necessarily fully unfold during the short time horizon typical for ecological experiments (Oksanen and Moen 1994, Johnson et al. 2011, Saccone et al. 2014).

## Methods

### *Literature review of evidence for three and two trophic level dynamics*

To identify ecosystems with documented three or two trophic level dynamics, we conducted a literature search for enclosure experiments, extirpations, re-introductions and island-mainland comparisons with the potential to refute or to corroborate predictions 1–4. For each test site thus found, we assessed the primary productivity and identified the biome according to Higgins et al. (2016, Supplementary material Appendix 6 Fig. A22).

We conducted the search primarily in the ISI (Institute for Scientific Information) Web of Science, using keywords ‘trophic cascade’, ‘herbivory’, ‘grazing’, ‘browsing’ and ‘exclosure’, along with names of common herbivore species and terms connected to theories on food web dynamics. We also searched corresponding evidence from government reports and popular science journals. To avoid pseudoreplication, we pooled all cases in which the herbivores or their predators

could belong to the same population and all repeated studies. We excluded Africa, because it harbors megaherbivores, which are today resistant to non-human predators (Owen Smith 1988, Bond 2005, Van Valkenburgh et al. 2016).

To assess the landscape-level primary productivities of these ecosystems, we used the 30-second resolution 2015 NASA MOD17A3 net primary productivity (NPP) dataset (Running and Zhao 2015), averaging the NPP over pixels within 4 km of the target location. The logic and details of island-mainland comparisons are explained in Supplementary material Appendices 2–3.

In our statistical analyses, we divided the documented cases of two and three trophic level dynamics into two groups: 1) studies from seasonally cold environments with  $\text{NPP} < 400 \text{ g m}^{-2}\text{yr}^{-1}$ , predicted to have two trophic level dynamics, and 2) studies from persistently warm environments with  $\text{NPP} > 20 \text{ g m}^{-2}\text{yr}^{-1}$  and from seasonally cold ones with  $\text{NPP} > 400 \text{ g m}^{-2}\text{yr}^{-1}$ , where the revised EEH predicts three trophic level dynamics. We tested the correspondence between observations and predictions using a chi-square test.

### *Felid distribution*

We mapped the collective geographical range of felids, using species range maps of the IUCN (International Union for Conservation of Nature) Red List ([www.iucnredlist.org/resources/spatial-data-download](http://www.iucnredlist.org/resources/spatial-data-download)). For each species’ range map, we used only polygons where the species was classified as ‘extant’ or ‘probably extant’. We converted range maps to a 100-km grid system by treating a species as present in a grid cell if at least half of its range overlapped it. To ensure accessibility for felids, we excluded Australia and all islands, except for ones where the isolating strait is less than 50 km wide and freezes predictably in winter. The 50-km value was based on the re-invasion of the Eurasian lynx to Åland (Andersson 2013, Supplementary material Appendix 6). For determining the marine areas with ice cover, we used the National Snow & Ice Data Center (NSIDC) MASIE-NH 4-km resolution sea ice map for 7 March 2017 (<https://nsidc.org/data/G02186>). This is a conservative estimate of past ice cover, as the distribution of winter ice has been more extensive in the past.

To take into account the strong preference of predators for the most productive habitats (Oksanen et al. 1992b, Aunapuu and Oksanen 2003, Aunapuu et al. 2008), we re-projected the foregoing described dataset to 1-km resolution in Mollweide equal-area projection and then re-projected the result to 100-km grids (in Mollweide projection), using the average of the top 10% NPP 1-km raster grid cells within each 100-km cell. We refer to the result as ‘predator NPP’. As an index of thermal climate, we used the latitudinal position of the area. We chose the breakpoints (latitude  $> 45^\circ\text{N}$  or  $45^\circ\text{S}$ ) because the 45th latitudes are halfway between the equator and the poles and because most ecosystems on poleward sides of these latitudes are characterized by seasonally cold climates, whereas on the equatorial sides of 45th latitudes, most unproductive areas are non-seasonal or show



only hydric seasonality (Walter et al. 1967, Higgins et al. 2016, Supplementary material Appendix 5).

We overlaid species-specific felid range maps over the ‘predator NPP’ map described in the previous paragraphs to obtain predator NPP values for areas with and without felids. Observations were weighted by the proportion of land contained within each grid. In addition, resampling to predator NPP pixels (100-km resolution) helped to ensure that the spatial scale of analysis was appropriate, given the uncertainty in the range maps (Hurlbert and Jetz 2007). Logistic regression was performed with the logarithm of the predator NPP and latitudinal position as the independent variables and the cumulative distribution of felids (i.e. whether or not at least one felid species was present) as the dependent variable,

$$\log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \log_{10} \text{NPP} + \beta_2 \text{HighLat} + \beta_3 \log_{10} \text{NPP} \times \text{HighLat}$$

where  $p$  is the probability of felid presence in a grid cell and HighLat is a binary variable indicating whether the grid cell has latitude  $\geq 45^\circ$  or not. The estimates for the four parameters  $\beta_0, \dots, \beta_3$  are shown in the rows of Table 2. The model was fit to a total of 12 642 observations (8171 with latitude  $< 45^\circ$  and 4471 with absolute latitude  $\geq 45^\circ$ ). Moreover, we tested whether the regression differs between high ( $\geq 45$ ) and low ( $< 45$ ) latitude areas. We also overlaid the IUCN felid map over the biome map of Higgins et al. (2016) and computed the percentages of felid-free areas in each biome (Supplementary material Appendix 6 Fig. A22).

## Results

In our global search, we found 34 terrestrial ecosystems, for which 3 or 2 trophic level dynamics in endotherm food webs had been unambiguously demonstrated (Table 1). All ecosystems with documented two trophic level dynamics were in seasonally cold environments with  $\text{NPP} < 400 \text{ g m}^2 \text{ yr}^{-1}$  (the SLB and SLC biomes of Higgins et al. 2016). In seasonally cold environments, evidence for three trophic level dynamics had been obtained from productive landscapes and from an exceptionally productive habitat within an unproductive tundra landscape (Aunapuu et al. 2008, Supplementary material Appendix 2). In persistently warm environments, three trophic level dynamics prevailed from tropical forests to deserts (Fig. 3). The match between the observed and predicted distribution of these cases was statistically significant ( $\chi^2 = 30.147$ ,  $df = 1$ ,  $p = 4.006 \cdot 10^{-8}$ ).

According to the IUCN distribution maps, felids are present in most ecosystems with primary productivity exceeding  $400 \text{ g m}^2 \text{ yr}^{-1}$  (Fig. 4). A doubling in NPP is associated with an estimated 45.8% (95% C.I.: [40.4%, 51.4%]) increase in the odds of felid presence at low latitudes (absolute latitude

$< 45^\circ$ ) and a 250.7% (218.3%, 287.5%) increase at high latitudes (absolute latitude  $\geq 45^\circ$ ) (Table 2, Fig. 4). There is strong ( $p < 0.001$ ) evidence that the effect of NPP differs between low and high latitudes: the increase in the odds of felid presence per doubling of NPP was estimated to be 140.6% (116.8%, 167.7%) greater at high latitudes than at low latitudes (Table 2, Fig. 4). The felid free areas of the Holarctic region show a relatively good match with the SLB biome of Higgins et al (2016) (Table 3, Supplementary material Appendix 6 Fig. A22). Also, a large fraction of the SLC biome was felid free (Table 3). In persistently warm environments, felid-free areas were found only in the most barren deserts (the SLN biome of Higgins et al. 2016).

## Discussion

The ambition of Oksanen et al. (1981) was to open a quest for understanding natural food web dynamics by modelling Fretwell’s (1977) ideas as simply as possible. The resulting EEH model has performed quite well. In accordance to its predictions, the strength of the top–down regulation of herbivores by predators increases with increasing primary productivity (Crête 1999, Ripple and Beschta 2012b, Letnic and Ripple 2017). Whether the shallow, positive relationship between herbivore biomass and primary productivity in three trophic level ecosystems is due to predator interference, in contrast to assumption 5), or caused by evolutionary responses of herbivores to intense predation (Oksanen 1992) remains to be investigated.

On the other hand, the existence of a thermal winter has a profound impact on model parameters and, via them, on dynamics of endotherm food webs, contradicting assumption 7). Seasonally cold climate reduces the fraction of primary productivity available for herbivores and increases the costs of foraging and maintenance of herbivores and predators, thus increasing the values of  $P^*$  and  $H^*$ . The value of  $H^*$  is further increased by the simplicity of the endotherm communities in seasonally cold environments (Mendoza and Araújo 2019) and the consequent lack of dependable alternative resources. The foregoing reasoning is corroborated by the results of our meta-analysis. All cases of documented two trophic level dynamics came from unproductive ecosystems, located in seasonally cold environments.

In persistently warm environments, foraging is less costly and the intertwining of different food web branches increases the resource basis of predators, in contrast to assumption 2) (Polis 1991, Polis and Strong 1996, Mendoza and Araújo 2019). In the context of persistently warm environments, our revised EEH thus by and large converges with GWH, but with the additional prediction that strength of the three trophic level cascade is re-enforced by increased primary productivity. In accordance with this prediction, exclusion of predators from a hot desert has resulted only in a moderate decline in grass cover (Morris and Letnic 2017, Letnic et al. 2018). In the highly productive tropical forests of Venezuela,

Table 1. Cases with documented two or three trophic level dynamics. ‘Herbivore size’ refers to the truncated 10-based logarithm of body weight in grams. The biome acronyms are based on Higgins et al. (2016). The first letter refers to vegetation height (S=small, T=tall), the next to primary productivity (L=low, M=moderate H=high) and the third one to the existence and characteristics of the non-growing season (C=cold, D=dry, B=both cold and dry, N=non-seasonal). Details of cases denoted by an asterisk are provided in Supplementary material Appendices 2–4.

| Site                                | Biome   | NPP  | Seasonality  | Trop. levels | Herbiv. size | Reference   |
|-------------------------------------|---------|------|--------------|--------------|--------------|---|
| Western Olympic Peninsula           | TMN     | 904  | Non-seasonal | 3            | 4            | Beschta and Ripple 2009   |
| Yosemite Valley                     | TMN     | 490  | Non-seasonal | 3            | 4            | Beschta and Ripple 2009   |
| Zion Canyon                         | TMN     | 204  | Non-seasonal | 3            | 4            | Beschta and Ripple 2009   |
| Haida Gwai vs Prince Rupert’s Land* | TMN     | 747  | Non-seasonal | 3            | 4            | Pojar 2008, Stroh et al. 2008   |
| Lago Guri*                          | THN     | 1253 | Non-seasonal | 3            | 4            | Terborgh et al. 2001, 2006  |
| Channel Country                     | SLN     | 39   | Non-seasonal | 3            | 4            | Letnic et al. 2018  |
| Sturt and Strzelecki                | SLN     | 86   | Non-seasonal | 3            | 4            | Morris and Letnic 2017  |
| Sturt and Strzelecki                | SLN     | 89   | Non-seasonal | 3            | 4            | Morris and Letnic 2017  |
| Lamar Valley, Yellowstone           | TMB     | 418  | Seasonal     | 3            | 5            | Beschta and Ripple 2009   |
| Wind Cave                           | TMB     | 529  | Seasonal     | 3            | 4            | Beschta and Ripple 2009   |
| Anticosti versus Mingan*            | TMB     | 513  | Seasonal     | 3            | 4            | Anouk Simard et al. 2008, Côté et al. 2008  |
| Skye versus Rùm*                    | TMC-SMN | 472  | Seasonal     | 3            | 5            | Watson 1983, Ball 1987, Clutton-Brock and Guinness 1987, Yalden 1999, Rixson 2001, Virtanen et al. 2002b, Manning et al. 2009, Vuorinen et al. 2020 |
| Alajoki*                            | TMC     | 469  | Seasonal     | 3            | 1            | Norrdahl et al. 2002  |
| Blå Jungfrun versus Oskarshamn*     | TMC     | 645  | Seasonal     | 3            | 3            | Ottoson 1971.   |
| Barrow                              | SLB     | 102  | Seasonal     | 2            | 1            | Johnson et al. 2011, Lara et al. 2017   |
| Pen Island                          | SLB     | 91   | Seasonal     | 2            | 4            | Newton et al. 2014.   |
| Deception Bay, Nunavik              | SLB     | 95   | Seasonal     | 2            | 4            | Morrisette-Boileau et al. 2018  |
| Riviere George                      | SLB     | 144  | Seasonal     | 2            | 4            | Manseau et al. 1996, Crête and Doucet 1998, Campeau et al. 2019   |
| Zackenbergl                         | SLB     | 19   | Seasonal     | 2            | 5            | Mosbacher et al. 2019   |
| Brøggerhalvøya                      | SLB     | 32   | Seasonal     | 2            | 4            | Hansen et al. 2007  |
| Čoalbma-Likčájávri                  | SLB     | 172  | Seasonal     | 2            | 1            | Oksanen and Oksanen 1981, Oksanen 1988, Oksanen and Moen 1994   |
| Čearro                              | SLB     | 179  | Seasonal     | 2            | 1            | Oksanen and Oksanen 1981, Oksanen and Moen 1994   |
| Ceavdni (Joatka Highland)           | SLB     | 174  | Seasonal     | 2            | 1            | Grellmann 2002, Moen and Oksanen 1998, Aunapuu et al. 2008, Olofsson et al. 2014, Ruffino et al. 2016, Hoset et al. 2017                            |
| Lássijunjavri (Joatka Lowland)      | SLB     | 162  | Seasonal     | 2            | 1            | Olofsson et al. 2004b, 2009, Kaarlejärvi et al. 2015  |
| Skirvinjarga (Skillefjordnes)       | SLC     | 188  | Seasonal     | 2            | 1            | Ruffino et al. 2016   |
| Komagelv                            | SLB     | 237  | Seasonal     | 2            | 1            | Ravolainen et al. 2011, 2014  |
| Vestre Jakobselv                    | SLB     | 277  | Seasonal     | 2            | 1            | Ravolainen et al. 2011, 2014  |
| Jeahkaš, Kilpisjärvi                | SLB     | 136  | Seasonal     | 2            | 1            | Oksanen 1983, Virtanen 1998, 2000, Saccone et al. 2014  |
| Vássijávri                          | SLC     | 132  | Seasonal     | 2            | 1            | Olofsson et al. 2004a, 2009, 2012   |
| Baddus, Abisko                      | SLB     | 198  | Seasonal     | 2            | 1            | Olofsson et al. 2004a, 2009, 2012   |
| Dawu                                | SLB     | 192  | Seasonal     | 2            | 2            | Qu et al. 2016, Pang and Guo 2018   |
| Maqin                               | SLB     | 102  | Seasonal     | 2            | 2            | Sun et al. 2015   |
| Gurvan Saykhan Mt.s                 | SLB     | 117  | Seasonal     | 2            | 2            | Retzer 2007   |
| leávri*                             | SLB     | 149  | Seasonal     | 3            | 1            | Hambäck et al. 2004, Aunapuu et al. 2008, Dahlgren et al. 2009, Tuomi et al. 2019   |

loss of predators has resulted in massive habitat destruction (Rao et al. 2001, Terborgh et al. 2001, 2006, Supplementary material Appendix 3 Fig. A13–A15). In the evolutionary time scale, absence of predators from productive and persistently warm environments seems to result in the development of closely clipped grazing lawns, dominated by genetically dwarfed plants (Hnatiuk et al. 1976, Merton et al. 1976, see also Oksanen et al. 2010).

The revised EEH thus restricts the high values of  $P^*$  and  $H^*$ , required for the emergence of one trophic level and two trophic level ecosystems, to seasonally cold environments, i.e. to the SLB–SLC biome complex of Higgins et al. (2016), combining the arctic and the alpine tundra with the temperate steppe (Fig. 3). For the arctic and alpine tundra, the importance of herbivorous endotherms is further supported by landscape level remote sensing data (Olofsson et al. 2012,

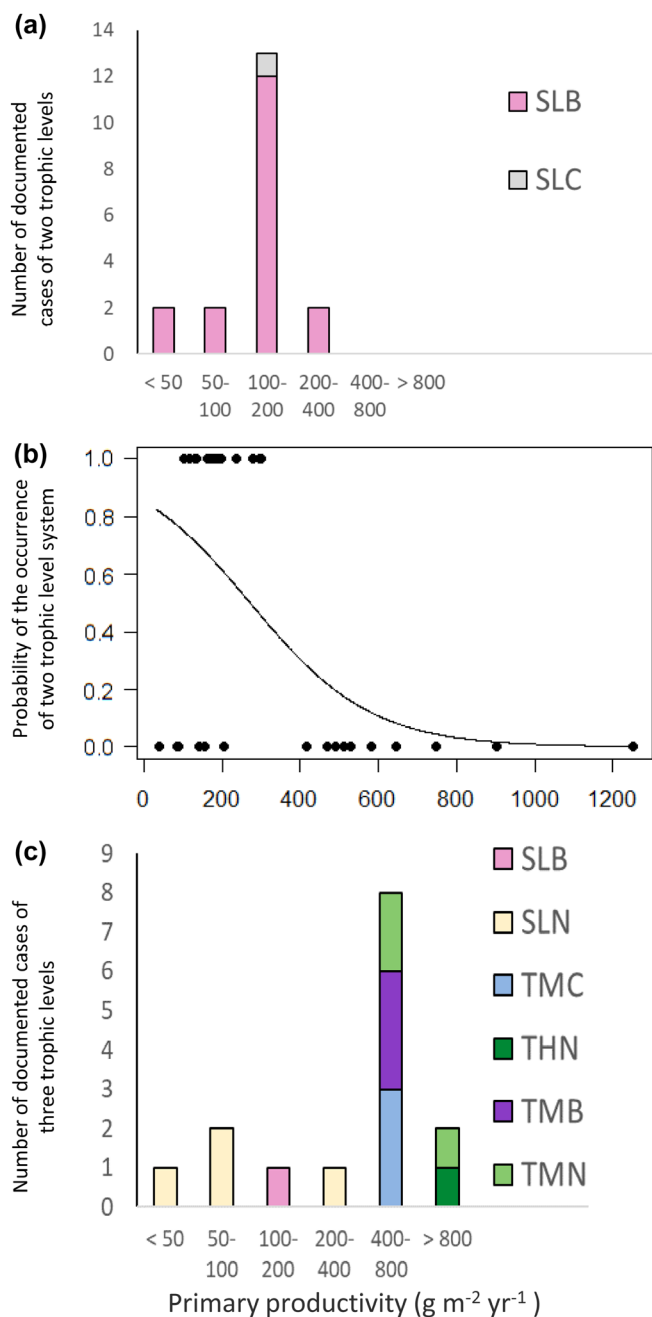


Figure 3. Numbers of documented cases of two (a) and three (c) trophic level trophic dynamics along terrestrial primary productivity gradients. The (b)-panel shows the locations of the site on the primary productivity axis and also displays the cumulative probability of two trophic level dynamics in relation to decreasing primary productivity (high probability for two-level dynamics corresponding to low probability of three-level dynamics, and vice versa). The colors represent the biomes to which each documented case belongs in the biome system of Higgins et al. (2016). For Abbreviations, see Table 1. For detailed definitions, see Higgins et al. (2016), their Eq. 1–4.

Newton et al. 2014, Qin et al. 2020), by the striking spatial and temporal differences in aboveground plant biomass in response to the presence versus absence of pivotal herbivores

(Oksanen 1983), and by the aberrant vegetation patterns of herbivore-free islands with maritime tundra climate (Werth 1928, Virtanen et al. 1997b, Supplementary material Appendix 7 Fig. A29–A36).

The dynamics of small arctic herbivores (lemmings and voles) still contain unresolved riddles. The evidence for strong lemming–vegetation interactions (Fig. 3, see also Supplementary material Appendix 7 Fig. A23, A28) comes from Fennoscandia and Alaska (Table 1). As the gap between these areas is bridged by observations of heavy lemming impacts on the Siberian tundra (Tihomirov 1959, Virtanen et al. 2006), the case for two trophic level dynamics appears to be strong for the Eurasian–Beringian tundra. In the Canadian–Greenlandic sector, however, lemmings are heavily exploited by marine-subsidized avian predators (Krebs et al. 2003, Gilg et al. 2006, Gauthier et al. 2011, Legagneux et al. 2012, 2014, Fauteux et al. 2016, but see Fuller et al. 1977), and impacts of lemmings on the vegetation can be weak (Bilodeau et al. 2014). Differences in physical geography might account for this contrast. In Fennoscandia, Russia and Alaska, tundra habitats suitable for lemmings cover vast expanses of land (Walker et al. 2005, Virtanen et al. 2016). Hence, marine-based avian predators can freely spread and their impact is therefore diluted (Ruffino et al. 2016). In High Arctic Canada and Greenland, in turn, coasts are steep and inland areas are occupied by glaciers or polar deserts, forcing avian predators to aggregate to the coastal tundra pockets.

The foregoing inferences are supported by the global distribution of felids. On the equatorial sides of the 45th latitudes, felids are present everywhere but the most extreme deserts. On the polar sides of these latitudes, only ecosystems with primary productivity exceeding  $400 \text{ g m}^{-2} \text{yr}^{-1}$  are likely to harbor felids (Fig. 4b). The presence of felids in the mountainous steppe landscapes of central Asia (Supplementary material Appendix 6 Fig. A22) probably reflects the heterogeneity of mountainous areas and the inclusions of areas where felids are restricted to the deepest valleys in the IUCN range maps (Supplementary material Appendix 6 Fig. A21). The absence of native felids from the productive landscapes of western and central Europe (Supplementary material Appendix 6 Fig. A22) has doubtlessly been caused by humans. Moreover, IUCN maps do not include feral domestic cats, which are important predators in western Europe (Erlinge et al. 1983).

With a vegetation dominated by grazing tolerant plants, two trophic level ecosystems are natural rangelands. Moreover, herbivores of two trophic level ecosystems have apparently been easier to domesticate than the alert and agile herbivores of three trophic level ecosystems (Oksanen 1992). In Eurasia, the SLB biome of Higgins et al. (2016), dominated by two trophic level ecosystems, covers most of the inland, including the vicinities of the cradles of agriculture (Supplementary material Appendix 6 Fig. A22), which probably contributed to the early start of the Eurasian domestication process (Zeder and Hesse 2000). In most Eurasian steppe, mountain and tundra landscapes, wild ungulates were long ago replaced by their domesticated descendants. The intense grazing pressure

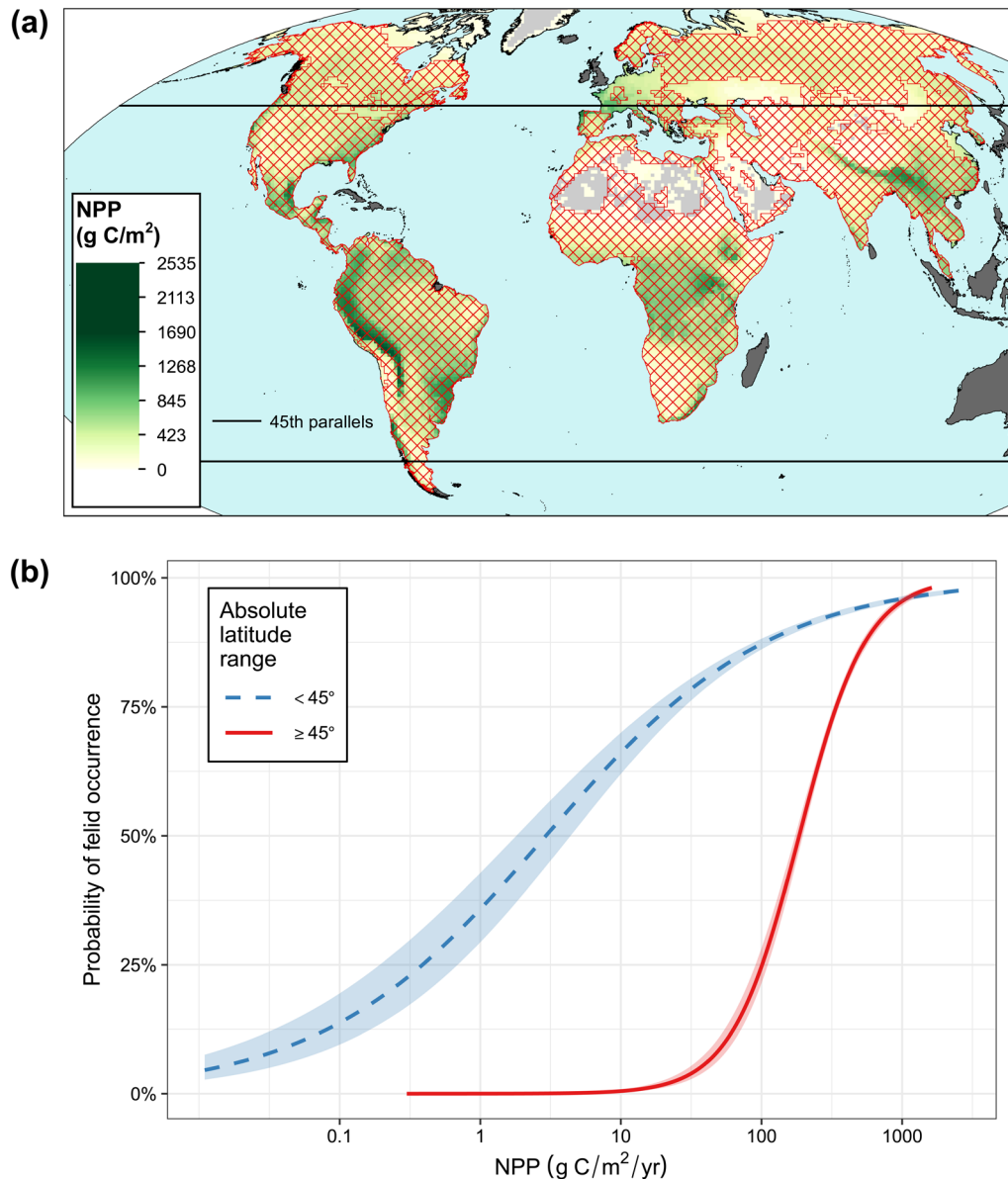


Figure 4. (a) Areas within the collective distribution of felids (cross raster), superimposed on a global primary productivity map. Islands not reachable by ice bridge (shown in dark gray) have been excluded from the analysis. (b) Logistic regression with 95% confidence intervals describing the relationship between log primary productivity and the presence of felids on equatorial and poleward sides of the 45th latitude.

exerted by these ungulates maintains the natural state of these ecosystems and is vital for the persistence of their species-rich vegetation (Miller et al. 1999, 2010, Olofsson and Oksanen 2005, Geddes and Miller 2010, Pajunen et al.

2011, 2012, Harris et al. 2015, Kaarlejärvi et al. 2015, 2017, Eskelinen et al. 2016).

During the development of large-scale pastoralism in Eurasia, an increasing fraction of the herbivore community

Table 2. Logistic regression model results for the probability of felid occurrence as a function of NPP and whether or not absolute latitude is  $\geq 45^\circ$  (abs. lat.  $\geq 45^\circ$ ). The columns indicate the predictor variable (or intercept) and the associated model parameter's estimate, 95% confidence interval lower and upper bounds, standard error, Z statistic and p-value.

| Term                              | Estimate | Lower  | Upper | SE    | Z-value | p-value |
|-----------------------------------|----------|--------|-------|-------|---------|---------|
| Intercept                         | 3.171    | 3.045  | 3.301 | 0.065 | 48.592  | < 0.001 |
| log NPP                           | 1.251    | 1.127  | 1.377 | 0.064 | 19.658  | < 0.001 |
| Abs. lat. $\geq 45^\circ$         | -0.118   | -0.341 | 0.107 | 0.114 | -1.034  | 0.301   |
| log NPP:abs. lat. $\geq 45^\circ$ | 2.916    | 2.571  | 3.271 | 0.178 | 16.341  | < 0.001 |

Table 3. Biomes of Higgins et al. (2016) where at least 30% of the area was found to be felid free according to our method, based on the IUCN maps, presented in the Supplementary material Appendix 6 Fig. A22. Areas potentially inaccessible for felids have been excluded.

| Biome | Total area (10 <sup>6</sup> km <sup>2</sup> ) | Area without felids (%) |
|-------|---|-------------------------|
| SLB   | 18.7  | 41.4                    |
| SLN   | 18.9  | 35.7                    |
| SLC   | 0.8   | 32.6                    |

was associated with armed herders, thus increasing the mortality of predators (parameter  $\mu$ ). The need to avoid herders reduced searching efficiency (parameter  $\alpha$ ). Recall that  $H^* = \mu / (\alpha(\kappa - \mu\eta))$ . Hence, these parameter changes lifted the predator isocline to successively higher herbivore densities, widening the primary productivity range and the geographical extent of two trophic level ecosystems (Walter 1968, Gimingham 1972, Ellenberg 1996, Oksanen and Olofsson 2018). During this gradual process, plants adapted to two trophic level dynamics could spread in pace with ‘trophic downgrading’ (Estes et al. 2011), creating grazing dependent semi-natural ecosystems with high biodiversity (Virtanen et al. 2002b, Butaye et al. 2005, Rosén 2006, Helm et al. 2007, see also Grime 1973).

In North America, two trophic level ecosystems have more restricted distribution (Supplementary material Appendix 6 Fig. A22) and indigenous pastoralism never developed. Instead, Eurasian cattle were introduced in the recent past, causing invasions of woody plants unpalatable for cattle (Walter 1968, Brown and Archer 1989). Moreover, large predators were extirpated, which triggered an eruption of cervids, which in turn exposed plant communities, dominated by competition adapted, grazing sensitive species, to intense herbivory. The consequent ecosystem collapses call for restoration of three trophic level dynamics (Ripple and Beschta 2006, Ripple et al. 2010, Beschta and Ripple 2009, 2019, Beschta et al. 2018).

Three and two trophic level dynamics favor different plants and create environments suitable for different animals. Rapid changes in food web dynamics result in disequilibria, where plants and animals are exposed to dynamics that they have not evolved to cope with. Gradual changes need not be detrimental as they replace one ecosystem type with another. Moreover, three and two trophic level ecosystems provide different ecosystem services, and the values of these services depend on the physical environment. Three trophic level dynamics are vital for the carbon sequestration capacity of productive forests, as dense browser populations prevent the replacement of old trees by young and rapidly growing ones (Beschta and Ripple 2009, Vuorinen et al. 2020). At high latitudes, however, most of the ecosystem carbon is in the soil. By increasing the rate of decomposition, forest expansion causes net release of carbon from the ecosystem to the atmosphere (Zimov et al. 2009, Hartley et al. 2012). Mammalian herbivory prevents forest expansion (Olofsson et al. 2009, Aune et al. 2011, Olofsson and Post 2018), protects permafrost against melting, which

could release large amounts of carbon to atmosphere (Beer et al. 2020) and can increase the capacity of ecosystems to sequester carbon (Zimov et al. 2009, Väisänen et al. 2014). Moreover, the high surface albedo of the tundra cools down the planet (Cohen et al. 2013, Cromsigt et al. 2018), providing an appreciable ecosystem service.

Compared to the original EEH, our revision reduces the predicted geographical extent of two trophic level and one trophic level ecosystems to areas with low primary productivity and seasonally cold climate. On the other hand, this combination characterizes the SLB biome of Higgins et al. (2016), i.e. the tundra and the cool temperate steppe, which is the world’s most widespread biome, covering the Arctic, the Eurasian inland and the northwestern highlands and plains of North America (Supplementary material Appendix 6 Fig. A22). Also, EEH as we have revised it predicts that Planet Earth harbors three widespread ecosystem categories with fundamentally different food web dynamics. Each of them has its unique organisms, evolved to different intensities of resource competition and apparent competition. Understanding these patterns, their evolutionary consequences, and different human impacts on them in different regions could help us in preserving global biodiversity and in maintaining important ecosystem services.

#### Data availability statement

The empirical part of the paper is exclusively based on published data. Much of the procedure has been explained in the methods section and in the Supplementary material. The raw felid and primary productivity data are available in Figshare: <<https://ndownloader.figshare.com/articles/12649193/versions/1>>.

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## References

- Abrams, P. and Roth, J. 1994. The response of unstable food chains to enrichment. – *Evol. Ecol.* 8: 150–171.
- Andersson, R. 2013. Ekosystemeffekter av lodjur, *Lynx lynx*: hur kan återkoloniseringen av lodjur påverka Ålands ekosystem? – Dept Basic Biology, Uppsala Univ., Uppsala, Sweden, <<http://files.webb.uu.se/uploader/858/BIOKand-13-023-Andersson-Rebecka-Uppsats.pdf>>.
- Anouk Simard, M. et al. 2008. On being the right size: food-limited feedback on optimal body size. – *J. Anim. Ecol.* 77: 635–637.
- Åström, M. et al. 1990. Partial prey consumption by browsers: tree as patches. – *J. Anim. Ecol.* 59: 287–300.
- Aunapuu, M. and Oksanen, T. 2003. Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. – *Evol. Ecol.* 17: 371–392.
- Aunapuu, M. et al. 2008. Spatial patterns and dynamic responses of arctic foodwebs corroborate the exploitation ecosystems hypothesis (EEH). – *Am. Nat.* 171: 249–262.
- Aune, S. et al. 2011. Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. – *Can. J. For. Res.* 41: 437–449.
- Ayal, Y. 2007. Trophic structure and the role of predation in shaping hot desert communities. – *J. Arid Environ.* 68: 171–187.
- Ball, M. E. 1987. Botany, woodland and forestry. – In: Clutton-Brock, T. H. and Ball, M. E. (eds), *Rhum: the natural history of an island*. Edinburgh Univ. Press, pp. 43–62.
- Basuony, M et al. 2013. Food and feeding ecology of the Egyptian mongoose, *Herpestes ichneumon* (Linnaeus, 1758) in Egypt. – *J. Appl. Sci. Res.* 9: 5811–5816.
- Batten, S. D. et al. 2018. Pink salmon induce a trophic cascade in plankton populations in the southern Bering Sea and around the Aleutian Islands. – *J. Fish. Oceanogr.* 27: 548–559.
- Beer, C. et al. 2020. Protection of permafrost soils from thawing by increasing herbivore density. – *Sci. Rep.* 10: 4170.
- Beschta, R. L. and Ripple, W. J. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. – *Biol. Conserv.* 11: 2401–2414.
- Beschta, R. L. and Ripple, W. J. 2019. Can large carnivores change streams via a trophic cascade? – *J. Ecohydrol.* 12: e2048.
- Beschta, R. L. et al. 2018. Trophic cascades at multiple spatial scales shape recovery of young aspen in Yellowstone. – *J. For. Ecol. Manage.* 413: 62–69.
- Bilodeau, F. et al. 2014. Does lemming winter grazing impact vegetation in the Canadian Arctic? – *Polar Biol.* 37: 845–857.
- Bognounou, F. et al. 2018. Role of climate and herbivory on native and alien conifer seedling recruitment at and above the Fennoscandian tree line. – *J. Veg. Sci.* 29: 573–584.
- Bond, W. J. 2005. Large parts of the world are brown or black: a different view on the ‘Gree World’ hypothesis. – *J. Veg. Sci.* 16: 261–266.
- Boonstra, R. et al. 2016. Why do the boreal forest ecosystems of northwestern Europe differ from those of western North America? – *BioScience* 66: 722–734.
- Brown, J. R. and Archer, S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history – *Oecologia* 80: 19–26.
- Bryant, J. P. and Kuropat, P. J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. – *Annu. Rev. Ecol. Syst.* 11: 261–285.
- Bryant, J. P. et al. 1994. Biogeography of woody plant chemical defense against snowshoe hare browsing: comparison of Alaska and eastern North America. – *Oikos* 70: 385–395.
- Butaye, J. et al. 2005. Conservation and restoration of calcareous grasslands: a concise review of the effects of fragmentation and management on plant species. – *Biotechnol. Agron. Soc. Environ.* 9: 111–118.
- Cajander, A. K. 1909. Über die Waldtypen. – *Fennia* 28: 1–175.
- Campeau, A. B. et al. 2019. Long-term changes in the primary productivity of migratory caribou (*Rangifer tarandus*) calving grounds and summer pasture on the Quebec-Labrador Peninsula (northeastern Canada): the mixed influences of climate change and caribou herbivory. – *Polar Biol.* 42: 1005–1023.
- Casini, M. et al. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. – *Proc. R. Soc. B* 1644: 1793–1801.
- Carpenter, S. R. et al. 1985. Cascading trophic interactions and lake productivity. – *BioScience* 35: 634–649.
- Chouinard, A. and Filion, L. 2005. Impact of introduced white-tailed deer and native insect defoliators on the density and growth of conifer saplings on Anticosti Island, Quebec. – *Écoscience* 12: 506–518.
- Clutton-Brock, T. H. and Guinness, F. E. 1987. Red deer. – In: Clutton-Brock, T. H. and Ball, M. E. (eds), *Rhum: the natural history of an island*. Edinburgh Univ. Press, pp. 95–109.
- Cohen, J. et al. 2013. Effect of summer reindeer grazing on spring snowmelt, albedo and energy balance. – *Remote Sens. Environ.* 135: 107–117.
- Côté, S. D. et al. 2008. High herbivore density and boreal forest ecology: white-tailed deer on Anticosti Island. – In: Gaston, A. J. et al. (eds), *Lessons from the islands: introduced species and what they tell us about how ecosystems work*. Can. Wildl. Serv. Environment Canada, Ottawa, ON, pp. 154–161.
- Crête, M. 1999. The distribution of deer biomass supports the hypothesis of exploitation ecosystems. – *Ecol. Lett.* 2: 223–227.
- Crête, M. and Manseau, M. 1996. Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. – *Evol. Ecol.* 10: 51–62.
- Crête, M. and Doucet, G. J. 1998. Persistent suppression in dwarf birch after release from heavy summer browsing by caribou. – *Arct. Alpine Res.* 30: 126–132.
- Cromsigt, J. P. et al. 2018. Trophic rewilding as a climate change mitigation strategy? – *Phil. Trans. R. Soc. B* 373: 20170440.
- Dahlgren, J. et al. 2009. Plant defenses to no avail? Responses of plants with varying edibility to food web manipulations in a low arctic scrubland. – *Evol. Ecol. Res.* 11: 1189–1203.
- Daskalov, G. M. 2002. Overfishing drives a trophic cascade in the Black Sea. – *Mar. Ecol. Prog. Ser.* 225: 53–63.
- de Satgé, J. et al. 2017. Competition and coexistence in a small carnivore guild. – *Oecologia* 184: 873–884.

- Doolan, S. P. and Macdonald, D. W. 1996. Diet and foraging behaviour of group-living meerkats, *Suricata suricata*, in the southern Kalahari. – *J. Zool.* 239: 697–716.
- Ehrlich, P. R. and Birch, L. C. 1967. The 'balance of nature' and 'population control'. – *Am. Nat.* 101: 97–107.
- Ekerholm, P. et al. 2004. The impact of short term predator removal on vole dynamics in a subarctic–alpine habitat complex. – *Oikos* 106: 457–468.
- Ellenberg, H. 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. – Ulmer.
- Emmons, L. 1987. Comparative feeding ecology of felids in a Neotropical rain-forest. – *Behav. Ecol. Sociobiol.* 20: 271–283.
- Ericson, L. 1977. Influence of voles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. – *Wahlenbergia* 4: 1–115.
- Erlinge, S. 1974. Distribution, territoriality and numbers of the weasel (*Mustela nivalis*) in relation to prey abundance. – *Oikos* 25: 308–314.
- Erlinge, S. 1977. Spacing strategies in the stoat, *Mustela erminea*. – *Oikos* 28: 32–42.
- Erlinge, S. et al. 1983. Predation as regulating factor on small rodent populations in southernmost Sweden. – *Oikos* 40: 36–52.
- Eskelinen, A. et al. 2016. Herbivory mediates the long-term shift in the relative importance of microsite and propagule limitation. – *J. Ecol.* 104: 1326–1334.
- Estes, J. A. and Palmisano, J. F. 1974. Sea otters, their role in structuring near shore communities. – *Science* 185: 1058–1060.
- Estes, J. A. and Duggins, D. O. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. – *Ecol. Monogr.* 65: 75–100.
- Estes, J. A. et al. 2011. Trophic downgrading of Planet Earth. – *Science* 333: 301–306.
- Fauteux, D. et al. 2016. Top-down limitation of lemmings revealed by experimental reduction of predators. – *Ecology* 97: 3231–3241.
- Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. – *Perspect. Biol. Med.* 20: 169–185.
- Fuller, W. A. et al. 1977. Biology and secondary production of *Dicrostonyx groenlandicus* on Truelove Lowland. – In: Bliss, L. C. (ed.), Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. Univ. Alberta Press, pp. 437–459.
- Gauthier, G. et al. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. – *Écoscience* 18: 223–235.
- Geddes, C. and Miller, C. R. 2010. Long-term changes in the size of an Alpine gentian, *Gentiana nivalis* L., population in Scotland. – *Watsonia* 28: 65–73.
- Gilg, O. et al. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. – *Oikos* 113: 193–216.
- Gill, R. M. A. 1992. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. – *Forestry* 65: 363–388.
- Gimingham, C. H. 1972. Ecology of heathlands. – Springer.
- Grellmann, D. 2002. Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. – *Oikos* 98: 190–204.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. – *Nature* 242: 344–347.
- Hairston, N. G. et al. 1960. Community structure, population control and competition. – *Am. Nat.* 94: 421–425.
- Hambäck, P. A. et al. 2004. Predators indirectly protect tundra plants by reducing herbivore abundance. – *Oikos* 106: 85–92.
- Hansen, B. B. et al. 2007. Ungulate impact on vegetation in a two trophic level system. – *Polar Biol.* 30: 549–558.
- Hanski, I. et al. 2001. Small rodent dynamics and predation. – *Ecology* 82: 1505–1520.
- Hansson, L. 1985. Damage by wildlife, especially small rodents, to North American *Pinus contorta* provenances introduced into Sweden. – *Can. J. For. Res.* 15: 1167–1171.
- Harris, R. B. et al. 2015. Herbivory and competition of Tibetan steppe vegetation in winter pasture: effects of livestock enclosure and plateau pika reduction. – *PLoS One* 10: e0132897.
- Hartley, I. P. et al. 2012. A potential loss of carbon associated with greater plant growth in the European Arctic. – *Nat. Clim. Change* 2: 875–879.
- Haukioja, E. and Hakala, T. 1975. Herbivore cycles and periodic outbreaks: formulation of a general hypothesis. – *Rep. Kevo Subarctic Res. Stat.* 12: 1–9.
- Haukioja, E. and Neuvonen, S. 1985. Induced long-term resistance of birch leaves against defoliators: defensive or accidental? – *Ecology* 66: 1303–1308.
- Helldin, J.-O. 1999. Diet, body condition and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. – *Ecography* 22: 324–336.
- Helm, A. et al. 2007. Plant diversity and species characteristics of alvar grasslands in Estonia and Sweden. – *Acta Phytogeogr. Suec.* 88: 33–42.
- Henttonen, H. et al. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? – *Oikos* 50: 353–365.
- Higgins, S. I. et al. 2016. Defining functional biomes and monitoring their change globally. – *Global Change Biol.* 22: 3583–3593.
- Hnatiuk, S. et al. 1976. Giant tortoise and vegetation interaction on Aldabra atoll. II. Coastal. – *Biol. Conserv.* 9: 305–316.
- Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. – *Theor. Popul. Biol.* 12: 276–290.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions and the coexistence of prey species. – *Am. Nat.* 124: 377–406.
- Hoset, K. S. et al. 2014. Spatial variation in vegetation damage relative to primary productivity, small rodent abundance and predation. – *Ecography* 37: 894–891.
- Hoset, K. H. et al. 2017. Changes in the spatial configuration and strength of trophic control across a productivity gradient during a massive rodent outbreak. – *Ecosystems* 20: 1421–1435.
- Humphries, M. M. et al. 2017. To everything there is a season: summer-to winter food webs and the functional traits of keystone species. – *Integr. Comp. Biol.* 57: 961–976.
- Hurlbert, A. H. and Jetz, W. 2007. Species richness, hotspots and the scale dependence of range maps in ecology and conservation. – *Proc. Natl Acad. Sci. USA* 104: 13384–13389.
- Johnson, D. R. et al. 2011. Exclusion of brown lemmings reduces vascular plant cover and biomass in Arctic coastal tundra: resampling of a 50+ year herbivore enclosure experiment near Barrow, Alaska. – *Environ. Res. Lett.* 6: 045507.
- Kaarlejärvi E. et al. 2015. Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. – *Global Change Biol.* 21: 3379–3388.
- Kaarlejärvi, E. et al. 2017. Herbivores rescue diversity in warming tundra by modulating trait dependent species losses and gains. – *Nat. Commun.* 8: 419.

- Klemola, T. et al. 2000. Experimental tests of predation and food hypotheses for population cycles of voles. – *Proc. R. Soc. B* 267: 351–356.
- Kobayashi, T. et al. 1997. Effects of trampling and vegetation removal on species diversity and micro-environment under different shade condition. – *J. Veg. Sci.* 8: 873–880.
- Korpimäki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small mammal cycles. – *Ecology* 79: 2448–2455.
- Krebs, C. J. et al. 1995. Impact of food and predation on snowshoe hare cycle. – *Science* 269: 1112–1115.
- Krebs, C. J. et al. 2003. Terrestrial trophic dynamics in the Canadian Arctic. – *Can. J. Zool.* 81: 827–843.
- Lara, M. J. et al. 2017. Peak season carbon exchange shifts from a sink to a source following 50+ years of herbivore exclusion in an Arctic tundra ecosystem. – *J. Ecol.* 105: 122–131.
- Legagneux, P. et al. 2012. Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. – *Ecology* 93: 1707–1716.
- Legagneux, P. et al. 2014. Arctic ecosystem structure and functioning shaped by climate and herbivore body size. – *Nat. Clim. Change* 4: 379–383.
- Letnic, M. and Ripple, W. J. 2017. Large-scale responses of herbivore prey to canid predators and primary productivity. – *Global Ecol. Biogeogr.* 26: 860–866.
- Letnic, M. et al. 2018. Strength of a trophic cascade between an apex predator, mammalian herbivore and grasses in a desert ecosystem does not vary with temporal fluctuations in primary productivity. – *Ecosystems* 21: 153–165.
- Lynch, A. B. and McCann, Y. 2007. The diet of the pine marten (*Martes martes*) in Killarney National Park. – *Proc. R. Irish Acad.* 107B: 67–76.
- MacArthur, R. H. 1972. Geographical ecology. – Harper and Row.
- Manning, A. D. et al. 2009. Restoring landscapes of fear with wolves in the Scottish Highlands. – *Biol. Conserv.* 142: 2314–2321.
- Manseau, M. et al. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community structure and landscape level. – *J. Ecol.* 84: 503–513.
- Marquis, R. J. and Whelan, C. J. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. – *Ecology* 75: 2007–2014.
- Mekonnen, Z. A. et al. 2018. 21st century tundra shrubification could enhance carbon uptake of North America Arctic tundra under an RCP8.5 climate trajectory. – *Environ. Res. Lett.* 13: 054029.
- Mendoza, M. and Araújo, M. B. 2019. Climate shapes mammal community trophic structures and humans simplify them. – *Nat. Commun.* 10: 5197.
- Messier, F. and Crête, M. 1985. Moose–wolf dynamics and the natural regulation of moose populations. – *Oecologia* 65: 503–512.
- Merton, L. F. et al. 1976. Giant tortoise and vegetation interaction on Aldabra atoll. I. Inland. – *Biol. Conserv.* 9: 293–304.
- Miller, P. C. et al. 1980. Biophysical processes and primary production. – In: Brown, J. et al. (eds), *An Arctic ecosystem: the coastal tundra at Barrow, Alaska*. Dowden, Hutchinson and Ross, pp. 66–101.
- Miller, G. R. et al. 1999. Response of the alpine gentian *Gentiana nivalis* L. to protection from grazing by sheep. – *Biol. Conserv.* 87: 311–318.
- Miller, G. R. et al. 2010. Effects of excluding sheep from an alpine dwarf-herb community. – *Plant Ecol. Divers.* 3: 87–93.
- Moen, J. and Oksanen, L. 1998. Long-term exclusion of folivorous mammals in two arctic–alpine plant communities: a test of the hypothesis of exploitation ecosystems. – *Oikos* 82: 333–346.
- Moen, J. et al. 1993a. Grazing by food-limited microtine rodents on a productive, experimental plant community: does the green desert exist? – *Oikos* 68: 401–413.
- Moen, J. et al. 1993b. Lemming grazing on snowbed vegetation during a population peak, northern Norway. – *Arct. Alpine Res.* 25: 130–135.
- Morris, T. and Letnic, M. 2017. Removal of an apex predator initiates a trophic cascade that extends from herbivores to vegetation and the soil nutrient pool. – *Proc. R. Soc. B* 284: 20170111.
- Morrisette-Boileau, C. et al. 2018. Revisiting the role of migratory caribou in the control of shrub expansion in northern Nunavik (Québec, Canada). – *Polar Biol.* 41: 1845–1853.
- Mosbacher, J. B. et al. 2019. Muskoxen modify plant abundance, phenology and nitrogen dynamics in a High Arctic fen. – *Ecosystems* 22: 1095–1107.
- Murdoch, W. W. 1966. Community structure, population control and competition: a critique. – *Am. Nat.* 100: 219–226.
- Nakabayashi, M. et al. 2016. Behavioral feeding strategy of frugivorous civets in a Bornean rainforest. – *J. Mammal.* 97: 798–805.
- Nevalainen, S. et al. 2016. Moose damage in National Forest Inventories (1986–2008) in Finland. – *Silva Fennica* 50: article id 1410.
- Newsome, T. M. and Ripple, W. J. 2015. A continental scale trophic cascade from wolves through coyotes to foxes. – *J. Anim. Ecol.* 84: 49–59.
- Newton, E. J. et al. 2014. Remote sensing reveals long-term effects of caribou on tundra vegetation. – *Polar Biol.* 37: 715–725.
- Norrdahl, K. et al. 2002. Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. – *Oikos* 99: 419–430.
- Oksanen, L. 1978. Lichen grounds of Finnmarksvidda, northern Norway, in relation to summer and winter grazing by reindeer. – *Rep. Kevo Subarctic Res. Stat.* 14: 64–71.
- Oksanen, L. 1980. Abundance relationships between competitive and grazing-tolerant plants in productivity gradients of Fennoscandian mountains. – *Ann. Bot. Fenn.* 17: 410–429.
- Oksanen, L. 1983. Trophic exploitation and arctic phytomass patterns. – *Am. Nat.* 122: 45–52.
- Oksanen, L. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence. – *Am. Nat.* 131: 424–444.
- Oksanen, L. 1990a. Exploitation ecosystems in seasonal environments. – *Oikos* 57: 14–24.
- Oksanen, L. 1990b. Predation, herbivory and plant strategies along gradients of primary productivity. – In: Tilman, D. and Grace, J. (eds), *Perspectives on plant competition*. Academic Press, pp. 445–473.
- Oksanen, L. 1992. Evolution of exploitation ecosystems I. Predation, foraging ecology and population dynamics in herbivores. – *Evol. Ecol.* 6: 15–33.
- Oksanen, L. and Oksanen, T. 1981. Lemmings (*Lemmus lemmus*) and grey-sided voles (*Clethrionomys rufocanus*) in interaction with their resources and predators on Finnmarksvidda, northern Norway. – *Rep. Kevo Subarctic Res. Stat.* 17: 7–31.
- Oksanen, L. and Moen, J. 1994. Predictability of plant responses to the exclusion of grazers in three Fennoscandian tundra habitats. – *Écoscience* 1: 31–39.



- Oksanen, L. and Lundberg, P. 1995. Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk. – *Evol. Ecol.* 9: 45–56.
- Oksanen, L. and Virtanen, R. 1997. Adaptation to disturbance as a part of the strategy of arctic and alpine plants: perspectives for management and restoration. – In: Crawford, R. M. M. (ed.), *Disturbance and recovery in arctic lands*. Kluwer Academic Publishers, pp. 91–113.
- Oksanen, L. and Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. – *Am. Nat.* 155: 703–723.
- Oksanen, L. and Olofsson, J. 2018. Vertebrate herbivory and its ecosystem consequences, 2nd ed. *Encyclopedia of life sciences*. – Wiley.
- Oksanen, L. et al. 1981. Exploitation ecosystems in gradients of primary productivity. – *Am. Nat.* 118: 240–261.
- Oksanen, L. et al. 1997. Outlines of food webs in a low arctic tundra landscape in relation to three theories of trophic dynamics. – In: Gange, A. C. and Brown, V. K. (eds), *Multitrophic interactions in terrestrial systems*. Blackwell, pp. 351–373.
- Oksanen, L. et al. 2010. Islands as tests of the green world hypothesis. – In: Terborgh, J. and Estes, J. A. (eds), *Trophic cascades: predators, prey and the changing dynamics of nature*. Island Press, pp. 163–177.
- Oksanen, T. 1990c. Exploitation ecosystems in heterogeneous habitat complexes. – *Evol. Ecol.* 4: 220–234.
- Oksanen, T. 1993. Does predation prevent Norwegian lemmings from establishing permanent populations in lowland forests? – In: Stenseth, N. C. and Ims, R. A. (eds), *The biology of lemmings*. Linnaean Soc. Symp. Series 15. Academic Press, pp. 425–437.
- Oksanen, T. et al. 1992a. Exploitation ecosystems in heterogeneous habitat complexes II: impact of small-scale heterogeneity on predator–prey dynamics. – *Evol. Ecol.* 6: 383–398.
- Oksanen, T. et al. 1992b. Habitat use of small mustelids on north Fennoscandian tundra: a test of the hypothesis of patchy exploitation systems. – *Ecography* 15: 237–244.
- Oksanen, T. et al. 1995. Ideal free habitat selection and consumer–resource dynamics. – *Am. Nat.* 146: 565–583.
- Oksanen, T. et al. 2001. Regulation, cycles and stability in northern carnivore–herbivore systems: back to first principles – *Oikos* 94: 101–117.
- Oksanen, T. et al. 2008. Arctic lemmings, *Lemmus* spp. and *Dicrostonyx* spp.: integrating ecological and evolutionary perspectives. – *Evol. Ecol. Res.* 10: 415–434.
- Oksanen, T. et al. 2013. Impact of marine-subsidized predators on lemming–plant oscillations. – *Evol. Ecol. Res.* 15: 1–24.
- Olofsson, J. and Oksanen, L. 2005. Effects of reindeer density on plant diversity in the Fennoscandian mountain chain. – *Rangifer* 25: 5–18.
- Olofsson, J. and Post, E. 2018. Effects of large herbivores on tundra vegetation in a changing climate and implications for rewilding. – *Phil. Trans. R. Soc. B* 373: 20170437.
- Olofsson, J. et al. 1999. On the balance between positive and negative plant interactions in harsh environments. – *Oikos* 86: 539–543.
- Olofsson, J. et al. 2004a. Reindeer influence ecosystem processes on the tundra. – *Oikos* 105: 386–396.
- Olofsson, J. et al. 2004b. Importance of large and small herbivores for the plant community structure in the forest–tundra ecotone. – *Oikos* 106: 324–334.
- Olofsson, J. et al. 2009. Herbivores inhibit climate driven shrub expansion on the tundra. – *Global Change Biol.* 15: 2681–2693.
- Olofsson, J. et al. 2012. Vole and lemming activity observed from space. – *Nat. Clim. Change* 2: 880–883.
- Olofsson, J. et al. 2014. Long-term experiments reveal strong interactions between lemmings and plants in the Fennoscandian highland tundra. – *Ecosystems* 17: 606–615.
- Olson, D. M. et al. 2001. Terrestrial ecoregions of the world: a new map of life on earth. – *BioScience* 51: 933–938.
- Ostfeld, R. S. and Canham, C. D. 1993. Effects of meadow vole population density on tree seedling survival on an old field. – *Ecology* 74: 179–801.
- Ottoson, I. 1971. Något om skogshararnas inverkan på ön Jungfrun i Kalmarsund. – *Fauna Flora* 66: 229–240.
- Owen-Smith, R. N. 1988. Megaherbivores. The influence of very large body size on ecology. Cambridge Univ. Press.
- Pajunen, A. M. et al. 2011. Impact of shrub canopies on understorey vegetation in western Eurasian tundra. – *J. Veg. Sci.* 22: 837–846.
- Pajunen, A. et al. 2012. Browsing-mediated shrub canopy changes drive composition and species richness in forest–tundra ecosystems. – *Oikos* 121: 1544–1552.
- Pang, X. P. and Guo, Z. G. 2018. Plateau pika disturbances alter plant productivity and soil nutrients in alpine meadows of the Qinghai-Tibetan Plateau, China. – *Rangeland J.* 39: 133–144.
- Pastor, J. B. and Naiman, R. J. 1992. Selective foraging and ecosystem processes in boreal forests. – *Am. Nat.* 139: 690–705.
- Peterson, R. O. 2007. *The wolves of Isle Royale: a broken balance*. – Univ. Michigan Press.
- Pojar, J. 2008. Changes in vegetation of Haida Gwaii in historical time. – In: Gaston, A. J. et al. (eds), *Lessons from the islands: introduced species and what they tell us about how ecosystems work*. Can. Wildl. Serv. Environment Canada, Ottawa, ON, pp. 32–38.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. – *Am. Nat.* 138: 123–155.
- Polis, G. A. and Strong, D. R. 1996. Food web complexity and community dynamics. – *Am. Nat.* 147: 813–846.
- Polis, G. A. et al. 2000. When is a trophic cascade a trophic cascade? – *Trends Ecol. Evol.* 15: 473–475.
- Power, M. E. and Matthews, W. J. 1983. Algae-grazing minnows (*Campostoma anomalum*), piscivorous bass (*Micropterus* spp.) and the distribution of attached algae in a small prairie-margin stream. – *Oecologia* 60: 328–332.
- Power, M. E. et al. 1985. Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. – *Ecology* 69: 1448–1456.
- Power, M. E. et al. 1989. Grazing catfish, fishing birds and attached algae in a Panamanian stream. – *Environ. Biol. Fish.* 26: 285–295.
- Qin, Y. et al. 2020. Species monitoring using unmanned aerial vehicle to reveal the ecological role of Plateau Pika in maintaining vegetation diversity on the northeastern Qinghai-Tibetan Plateau. – *Rem. Sens.* 12: 2480.
- Qu, J. et al. 2016. The more the merrier? Multi-species grazing of small herbivores mediates plant community impacts. – *Biodivers. Conserv.* 25: 2055–2069.
- Rammul, Ü et al. 2007. Vole–vegetation interactions in an experimental, enemy free taiga floor system. – *Oikos* 116: 1501–1513.

- Rao, M. et al. 2001. Increased herbivory in forest isolates: implications for plant community structure and composition. – *Conserv. Biol.* 15: 624–633.
- Ravolainen, V. T. et al. 2011. Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. – *Basic Appl. Ecol.* 12: 643–653.
- Ravolainen, V. T. et al. 2014. Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. – *J. Appl. Ecol.* 51: 234–241.
- Retzer, V. 2007. Forage competition between livestock and Mongolian pika (*Ochotona pallasi*) in southern Mongolian mountain steppes. – *Basic Appl. Ecol.* 8: 147–157.
- Ripple, W. J. and Beschta, R. L. 2004. Wolves, elk, willows and trophic cascades in the upper Gallatin range of southwestern Montana, USA. – *For. Ecol. Manage.* 200: 161–181.
- Ripple, W. J. and Beschta, R. L. 2005. Linking wolves and plants. Aldo Leopold on trophic cascades. – *BioScience* 55: 613–621.
- Ripple, W. J. and Beschta, R. L. 2006. Linking a cougar decline, trophic cascade and catastrophic regime shift in Zion National Park. – *Biol. Conserv.* 133: 397–408.
- Ripple, W. J. and Beschta, R. L. 2007. Restoring Yellowstone's aspen with wolves. – *Biol. Conserv.* 138: 514–519.
- Ripple, W. J. and Beschta, R. L. 2008. Trophic cascades involving cougar, mule deer and black oaks in Yosemite National Park. – *Biol. Conserv.* 141: 1249–1256.
- Ripple, W. J. and Beschta, R. L. 2012a. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. – *Biol. Conserv.* 145: 205–213.
- Ripple, W. J. and Beschta, R. L. 2012b. Large predators limit herbivore densities in northern forest ecosystems. – *Eur. J. Wildl. Res.* 58: 733–742.
- Ripple, W. J. et al. 2010. Large predators, deer and trophic cascades in boreal and temperate ecosystems. – In: Terborgh, J. and Estes, J. A. (eds), *Trophic cascades*. Island Press, pp. 141–161.
- Ripple, W. J. et al. 2015. Wolves trigger a trophic cascade to berries as alternative food for grizzly bears. – *J. Anim. Ecol.* 84: 652–654.
- Ripple, W. J. et al. 2016. What is a trophic cascade? – *Trends Ecol. Evol.* 31: 842–849.
- Rixson, D. 2001. The small isles: canna, rum, egg and muck. – *Birlinn*.
- Rocha-Mendes, F. et al. 2010. Feeding ecology of carnivores (Mammalia, Carnivora) in Atlantic Forest remnants, southern Brazil. – *Biota Neotrop.* 10: 21–30.
- Rosén, E. 2006. Alvar vegetation of Öland – changes, monitoring and restoration. – *Proc. R. Irish Acad.* 106B: 387–399.
- Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. – *J. Mammal.* 47: 602–612.
- Rosenzweig, M. L. 1971. Paradox of enrichment: the destabilization of exploitation ecosystems in ecological time. – *Science* 171: 385–387.
- Rosenzweig, M. L. 1973. Exploitation in three trophic levels. – *Am. Nat.* 107: 275–294.
- Rosenzweig, M. L. 1977. Aspects of biological exploitation. – *Quart. Rev. Biol.* 52: 371–380.
- Ruffino, L. and Oksanen, T. 2014. Co-evolution of jaegers (*Stercorarius* spp.) and arctic lemmings (*Dicrostonyx* spp. and *Lemmus* spp.) and the formation of the jaeger guild: a hypothesis. – *Evol. Ecol. Res.* 16: 121–132.
- Ruffino, L. et al. 2016. Predator–rodent–plant interactions along a coast-inland gradient in Fennoscandian tundra. – *Ecography* 39: 871–883.
- Running, S. W. and Zhao, M. 2015. User's guide daily GPP and annual NPP (MOD17A2/A3). NASA Earth Observing System MODIS Land Algorithm, Ver. 3.0 for collection 6. – NASA, Washington DC.
- Saccone, P. et al. 2014. Environmental perturbation, grazing pressure and soil wetness jointly drive mountain tundra toward divergent alternative states. – *J. Ecol.* 102: 1661–1672.
- Sauve, A. M. C. et al. 2020. The effect of seasonal strength and abruptness on predator–prey dynamics. – *J. Theor. Biol.* 491: 110175.
- Shurin, J. B. et al. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. – *Proc. R. Soc. B* 273: 1–9.
- Slobodkin, L. B. et al. 1967. Regulation in terrestrial ecosystems and the implied balance of nature. – *Am. Nat.* 101: 109–124.
- Stroh, N. et al. 2008. Deer prevent western red cedar (*Thuja plicata*) regeneration in old-growth forests of Haida Gwaii: is there a potential for recovery? – *For. Ecol. Manage.* 12: 3973–3979.
- Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. – *Ecology* 73: 747–754.
- Sun, F. et al. 2015. Effects of plateau pika activities on seasonal plant biomass and soil properties in the alpine meadow ecosystems of the Tibetan Plateau. – *Grassland Sci.* 61: 195–203.
- Svenning, J.-C. et al. 2016. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. – *Proc. Natl Acad. Sci. USA* 113: 898–906.
- Terborgh, J. and Feeley, K. 2010. High redundancy and diffuse vertical links create multiple pathways for the trophic cascade in tropical forests. – In: Terborgh, J. and Estes, J. A. (eds), *Trophic cascades*. Island Press, pp. 125–140.
- Terborgh, J. et al. 2001. Ecological meltdown in predator-free forest fragments. – *Science* 294: 1923–1926.
- Terborgh, J. et al. 2006. Vegetation dynamics on predator-free land bridge islands. – *J. Ecol.* 94: 253–263.
- Tihomirov, B. A. 1959. Vzájmosvázi životnogo mira i rastitel' nogo pokrova tundry. – *Botaničeskij Inst. Komarova, Akademiá Nauk SSSR, Moscow, Russia*.
- Tilman, D. 1988. Plant strategies and the dynamic structure of plant communities. – *Princeton Univ. Press*.
- Tuomi, M. et al. 2019. Herbivore effects on ecosystem process rates in a low-productive system. – *Ecosystems* 22: 827–843.
- Turchin, P. 2001. Does population ecology have general laws? – *Oikos* 94: 17–26.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. – *Princeton Univ. Press*.
- Turchin, P. and Batzli, G. O. 2001. Availability of food and the population dynamics of arvicoline rodents. – *Ecology* 82: 1521–1534.
- Turchin, P. et al. 2000. Lemmings: prey or predators. – *Nature* 405: 562–564.
- Väisänen, M. et al. 2014. Consequences of warming on tundra carbon balance determined by reindeer grazing history. – *Nat. Clim. Change* 4: 1–5.
- Van Valkenburgh, B. et al. 2016. The impact of large terrestrial carnivores on Pleistocene ecosystems. – *Proc. Natl Acad. Sci. USA* 113: 862–867.
- Vernes, K. et al. 2001. Mammalian diet and broad hunting strategy of the dingo (*Canis familiaris dingo*) in the wet tropical rain forests of northeastern Australia. – *Biotropica* 33: 339–345.
- Virtanen, R. J. 1998. Impact of grazing and neighbour removal on a heath plant community transplanted onto a snowbed site, NW Finnish Lapland. – *Oikos* 81: 359–367.

- Virtanen, R. 2000. Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland. – *Oikos* 90: 295–300.
- Virtanen, R. J. et al. 1997a. Lemming grazing and structure of a snowbed plant community – a long-term experiment at Kilpisjärvi, Finnish Lapland. – *Oikos* 79: 155–166.
- Virtanen, R. et al. 1997b. Topographic and altitudinal patterns in plant communities on European arctic islands. – *Polar Biol.* 17: 95–113
- Virtanen, R. et al. 2002a. Winter grazing by the Norwegian lemming *Lemmus lemmus* at Kilpisjärvi (NW Finnish Lapland) during a moderate population peak. – *Ann. Zool. Fenn.* 39: 335–341.
- Virtanen, R. et al. 2002b. Red deer management and vegetation on the Isle of Rum. – *J. Appl. Ecol.* 39: 572– 583.
- Virtanen, R. et al. 2006. Broad-scale vegetation–environment relationships in Eurasian high-latitude areas. – *J. Veg. Sci.* 17: 519–528.
- Virtanen, R. et al. 2016. Where do the treeless tundra areas of northern highlands fit in the global biome system: toward an ecologically natural subdivision of the tundra biome. – *Ecol. Evol.* 6: 143–158.
- Vuorinen, K. E. M. et al. 2020. Do deer decrease impacts of warming? Herbivory and climate as drivers of woody plant growth at a forest–moorland transition. – *Ecol. Appl.* 2020: e02119.
- Walker, D. A. et al. 2005. The circumpolar arctic vegetation map. – *J. Veg. Sci.* 16: 267–282
- Walsh, J. R. et al. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. – *Proc. Natl Acad. Sci. USA* 113: 4081–4085.
- Walter, H. 1964. Die Vegetation der Erde in öko-physiologischer Sicht: I Die tropischen und subtropischen Zonen. – Gustav Fischer Verlag.
- Walter, H. 1968. Die Vegetation der Erde in öko-physiologischer Sicht: II Die arktischen und gemäßigten Zonen. – Gustav Fischer Verlag.
- Walter, H. et al. 1967. Klimadiagramm Weltatlas. – Fischer.
- Watson, A. 1983. Eighteenth century deer numbers and pine regeneration near Braemar, Scotland. – *Biol. Conserv.* 25: 289–305.
- Werth, E. 1928. Überblick über die Vegetationsgliederung von Kerguelen sowie von Possession-Eiland (Crozet-Gruppe) und Heard-Eiland. – In: von Drygalski, E. (ed.), Deutsche Südpolar-Expedition 1901–1903. Teil 8. de Gruyter, pp. 300–326.
- White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. – *Oecologia* 3: 71–86.
- White, T. C. R. 2013. Experimental and observational evidence reveals that predators in natural environments do not regulate their prey: they are passengers, not drivers. – *Acta Oecol.* 53: 73–87.
- Wielgolaski, F. E. 1975. Primary productivity of alpine meadow communities. – In: Wielgolaski, F. E. (ed.), Fennoscandian tundra ecosystems. Part 1. Plants and microorganisms. Ecological studies 16. Springer, pp. 121–128.
- Yalden, D. 1999. The history of British mammals. – Poyser.
- Zeder, M. A. and Hesse, B. 2000. The initial domestication of goats (*Capra hircus*) in the Zagros Mountains 10 000 years ago. – *Science* 287: 2254–2257.
- Zimov, N. S. et al. 2009. Carbon storage in permafrost and soils of the mammoth tundra-steppe biome: role in the global carbon budget. – *Geophys. Res. Lett.* 36: L02502.

Supplementary material (available online as Appendix ecog-05076 at <[www.ecography.org/appendix/ecog-05076](http://www.ecography.org/appendix/ecog-05076)>). Appendices 1–7.