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Review and synthesis

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

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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 artic–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 Satgé 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 λ_1 and λ_2 are positive constants; λ_1 reflects the fraction of energy channeled into digestible tissues and λ_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:

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

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

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

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 μ. 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 μ 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 μ 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 λ_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 λ_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
λ_1 = the fraction of primary production channeled to perennial, protoplasm-rich aboveground plant biomass.
λ_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.
β = 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.
α = the searching efficiency of predators.
κ = predators' constant of proportionality, relating their energy gains to losses inflicted on herbivores.
η = the average per prey handling time of predators.
μ = 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, β, 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, β, as $\beta = a_1 h/(a_1 + a_2)$, 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 β 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 μ. 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 μ. 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:

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

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

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 ↓
K ↓
a ↑
β ↓
k ↓
m ↑
α ↓
κ =
η =
μ ↑↑

↓ negative
= no obvious impact
↑ positive
↑↑ strongly positive

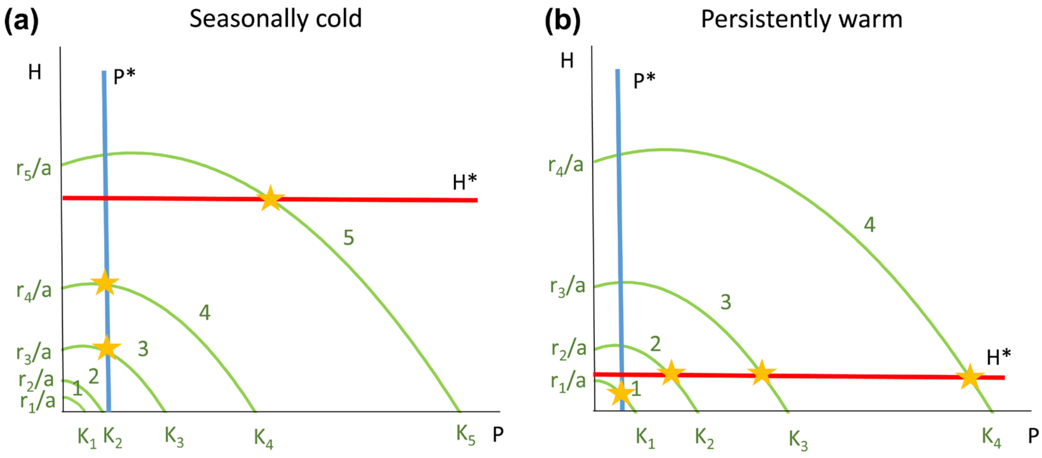

Figure 1. Plant isoclines (green curved lines) for five ecosystems differing in primary productivity, and their shared herbivore ($P = P^*$) and predator ($H = H^*$) isoclines in the $C = 0$ phase plane. Non-trivial equilibrium points with $H > 0$ are denoted by a yellow star. For three trophic level 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).

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

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 μ, 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

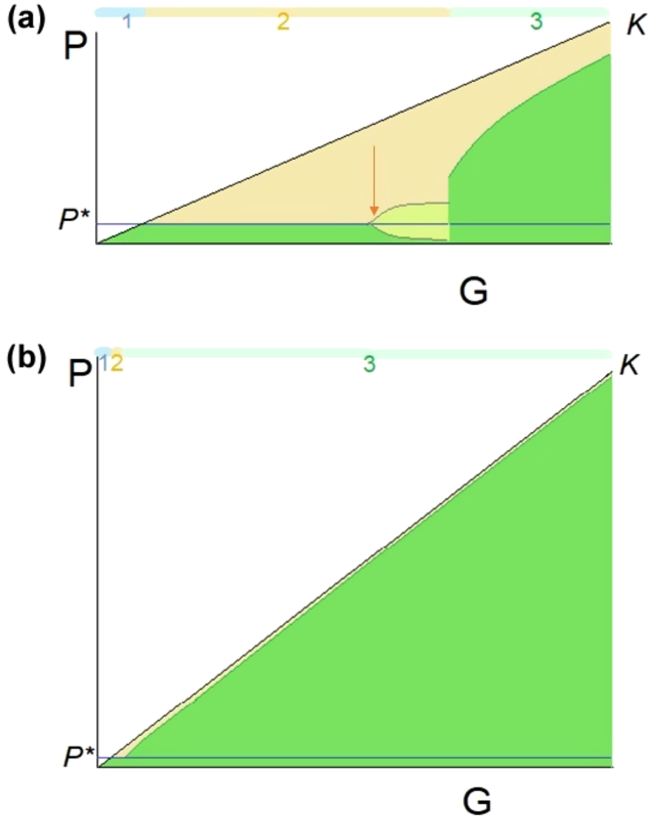

Figure 2. Predicted relation of plant carrying capacity (*K*, black oblique line), above ground plant biomass at the herbivore isocline (P^*, horizontal blue line), equilibrium above ground plant biomass (the width of the green field) and the predicted impact of natural herbivory on above ground plant 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 $\mathrm{g\,m^{-2}\,yr^{-1}}$, (Miller et al. 1980), whereas NASA's dataset yielded 102 $\mathrm{g\,m^{-2}\,yr^{-1}}$. 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 $g m^{-2} yr^{-1}$, to 20 and 400 $g m^{-2} yr^{-1}$.

Predictions to be tested

1) For all ecosystems with primary productivity > 400 $g m^{-2} yr^{-1}$ and, in persistently warm environments, for all ecosystems with primary production > 20 $g m^{-2} yr^{-1}$, 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 $g m^{-2} yr^{-1}$, 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 $g m^{-2} yr^{-1}$. In persistently warm environments, felids are present everywhere, except for extreme deserts, with primary production < 20 $g m^{-2} yr^{-1}$.

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

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 exclosure 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 NPP < 400 $g m^{-2} yr^{-1}$, predicted to have two trophic level dynamics, and 2) studies from persistently warm environments with NPP > 20 $g m^{-2} yr^{-1}$ and from seasonally cold ones with NPP > 400 $g m^{-2} yr^{-1}$, 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>). 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°N or 45°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,

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

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 ≥ 45° or not. The estimates for the four parameters $\beta_0, \ldots, \beta_3$ are shown in the rows of Table 2. The model was fit to a total of 12 642 observations (8171 with latitude < 45° and 4471 with absolute latitude ≥ 45°). Moreover, we tested whether the regression differs between high (≥ 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 NPP < $400\,\mathrm{g\,m^2\,yr^{-1}}$ (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, $p = 4.006\ 10^{-8}$).

According to the IUCN distribution maps, felids are present in most ecosystems with primary productivity exceeding $400\,\mathrm{g\,m^2\,yr^{-1}}$ (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°) and a 250.7% (218.3%, 287.5%) increase at high latitudes (absolute latitude ≥ 45°) (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 Jungrun 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	Morrissette-Boileau et al. 2018
Riviere George	SLB	144	Seasonal	2	4	Manseau et al. 1996, Crête and Doucet 1998, Campeau et al. 2019
Zackenberg	SLB	19	Seasonal	2	5	Mosbacher et al. 2019
Brøggerhalvøya	SLB	32	Seasonal	2	4	Hansen et al. 2007
Čoalbma-Likčajávri	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
Lássijunjávri (Joatka Lowland)	SLB	162	Seasonal	2	1	Olofsson et al. 2004b, 2009, Kaarlejärvi et al. 2015
Skirvinjárga (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
Ieávri*	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,

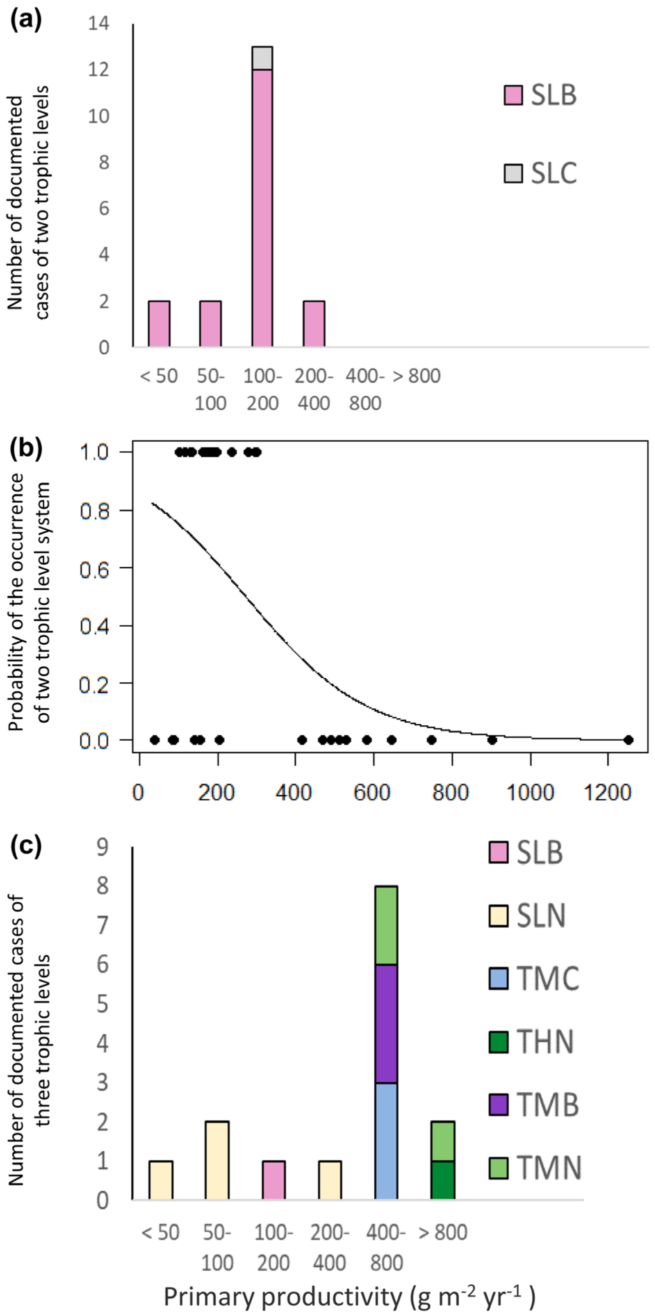

Figure 3. Numbers of documented cases of two (a) and three (c) trophic level trophic dynamics along terrestrial primary productivity gradients. The (b)-panel shows the locations of the site on the primary productivity axis and also displays the cumulative probability of two trophic level dynamics in 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 g m^{-2} 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

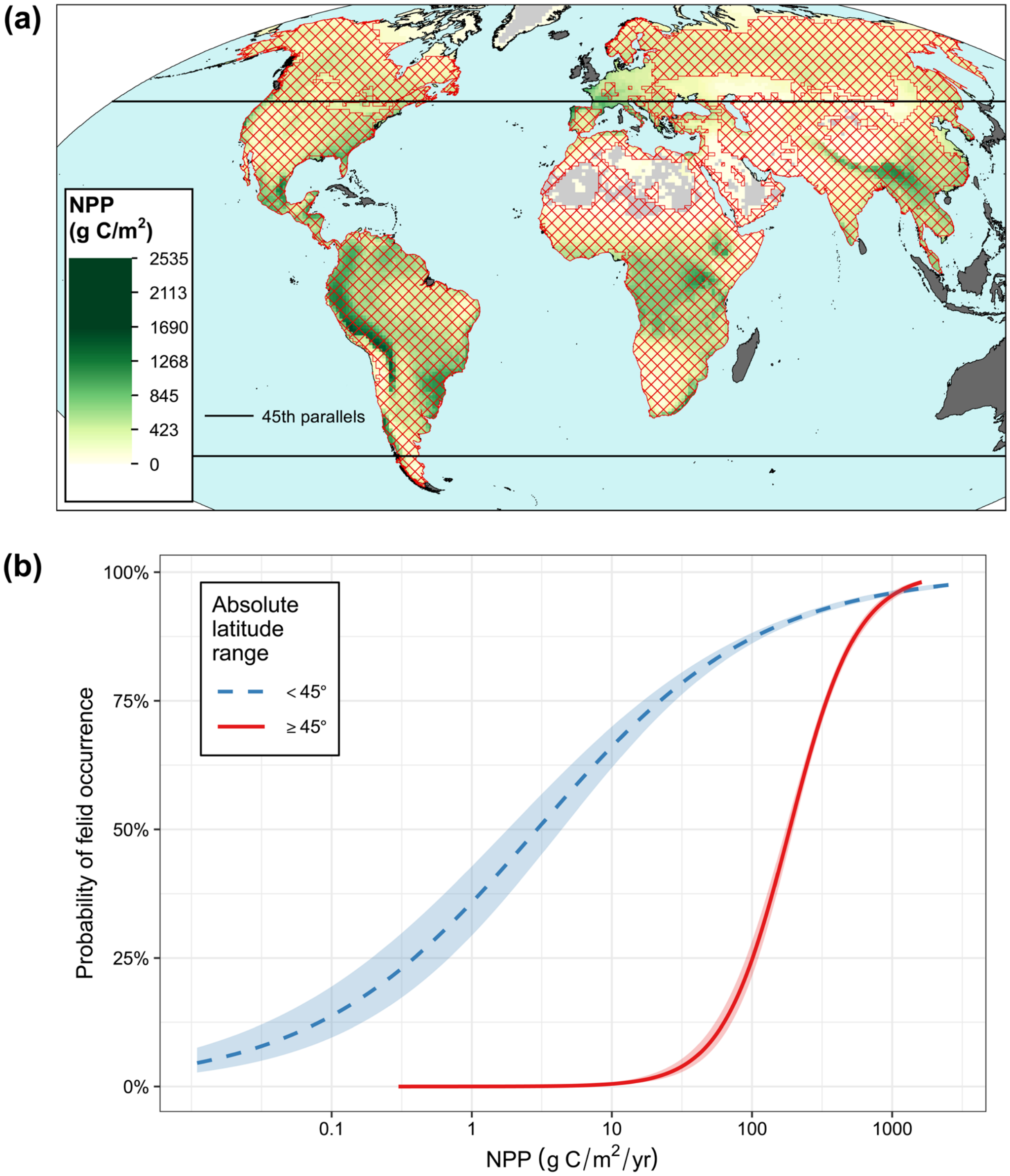

Figure 4. (a) Areas within the collective distribution of felids (cross raster), superimposed on a global primary productivity map. Islands not reachable by ice bridge (shown in dark gray) have been excluded from the analysis. (b) Logistic regression with 95% confidence intervals describing the relationship 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 ocurrence as a function of NPP and whether or not absolute latitude is ≥ 45° (abs. lat. ≥ 45°). 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. ≥ 45°	−0.118	−0.341	0.107	0.114	−1.034	0.301
log NPP:abs. lat. ≥ 45°	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 (10^6 km^2)	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 μ). The need to avoid herders reduced searching efficiency (parameter α). 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 ecosystems 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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Supplementary material (available online as Appendix ecog-05076 at <www.ecography.org/appendix/ecog-05076>). Appendices 1–7.

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