

Ignite

The paradox of searching efficiency or why are violent population cycles so uncommon in terrestrial ecosystem

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Oikos

2023: e09443

doi: [10.1111/oik.09443](https://doi.org/10.1111/oik.09443)

Subject Editor: Gregor Kalinkat

Editor-in-Chief: Pedro Peres-Neto

Accepted 10 February 2023



The searching efficiency of predators depends on the balance between the adaptations of the predator and the counter-adaptations of the prey. In this evolutionary race, the prey should normally have the upper hand, as it can perform tradeoffs between efficiency in resource use and ability to avoid predators. In terrestrial predator–herbivore systems, however, the huge difference in food quality between prey and predators seems to give predators an advantage. In productive terrestrial ecosystems, predators thus chronically overexploit herbivores, i.e. regulate them at densities far below the point of maximum sustainable yield. Assuming type II functional response, this should result in violent limit cycle dynamics. In reality, however, such cycles are only common at high latitudes, whereas the herbivory-based food webs of species-rich ecosystems at middle and low latitudes are characterized by asymptotic dynamics, where numerical changes only occur in response to external forcing. One way or another, diversity thus seems to beget stability in terrestrial grazing webs. We propose that strong, donor-controlled energy flows from the detritus web and directly from plants to predators are the key for the prevalence of asymptotic dynamics at middle and low latitudes. These flows support generalists with type III functional response and, therefore, a capacity to curb budding outbreaks at an early stage. The ongoing extinction wave could critically weaken these stabilizing interactions, which could destabilize currently stable food webs, and result in violent limit cycle dynamics in ecosystems, where the dominating species have evolved under asymptotic dynamics. This could cause secondary extinctions and inflict large economic losses.

Keywords: extinction, food webs, limit cycles, overexploitation, searching efficiency, stability

Introduction

In the evolutionary race between predators and their prey, the prey should often have the stronger hand, because they can make evolutionary and behavioral tradeoffs



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between their efficiency in resource utilization and their ability to elude predators (Oksanen 1992, Brown et al. 1999). Predators, in turn, do not usually have corresponding tradeoff options, as natural selection favors high searching efficiency regardless of the traits of the prey (Abrams 1986). Vuorinen et al. (2021) thus argued that in natural predator–prey systems, prey’s anti-predation strategies, in combination with interference between predators (Mech 1994, Cassidy et al. 2020), reduce the risk that prey would be severely overexploited, i.e. depressed below the bifurcation point, where asymptotic dynamics are replaced by violent limit cycle dynamics, accompanied by a high extinction risk (DeAngelis and Waterhouse 1987, Rosenzweig 1971, Gilpin and Rosenzweig 1972, Murdoch et al. 2003, Turchin 2003). If this applied to predator–herbivore dynamics, then increasing primary productivity would result in the replacement of vulnerable herbivores by more elusive ones and in a positive relation between the equilibrium density of herbivores and primary productivity (Oksanen 1992).

In terrestrial ecosystems, however, increasing primary productivity appears only to result in increased density of predators (Crête 1999, Ripple and Beschta 2012, Letnic and Ripple 2017). The observed pattern thus corroborates the predictions of simple, ‘laissez-faire’ food chain models (Oksanen et al. 1981, 2020), where both predator–predator interference and evolutionary responses of herbivores are ignored. The same message is carried by enclosure experiments and by data from predator-free islands (Klemola et al. 2000, Terborgh et al. 2001, 2006, Dahlgren et al. 2009, Oksanen et al. 2010): in the absence of predators, herbivore densities are often an order of magnitude higher than in their presence, implying that herbivores are chronically overexploited in many terrestrial ecosystems. A likely reason is that herbivores have a handicap that they cannot escape: their food is vastly less digestible and has much lower energy content than the food of their predators. This limits the agility of herbivores and their ability to run long distances without feeding and resting. The impacts of territoriality on predator–herbivore dynamics are, in turn, largely annulled by the high costs of territorial defense (Both and Visser 2003). This holds even for wolves that are known for their pack territoriality (McRoberts and Mech 2014).

According to the predictions of Rosenzweig–MacArthur type exploitation models, high searching efficiency, leading to severe overexploitation, should result in violent limit cycle dynamics. Yet, such dynamics are only common at high latitudes. At lower latitudes, asymptotic dynamics prevail even in food webs where herbivore densities are depressed far below carrying capacity. To understand the background of the problem, let us make an excursion to the Rosenzweig–MacArthur model world. The dynamics generated by these models have been analyzed by Murdoch and Oaten 1975) and discussed in theoretical textbooks (Turchin 2003, Murdoch et al. 2003). Yet, the role of searching efficiency has obtained relatively little attention. As the same models can be used for different trophic interactions, we will use the general terms ‘exploiter’

and ‘victim’ in the next section, unless we explicitly refer to predator–herbivore interactions.

The road to overexploitation

To illustrate the analogous impacts of enrichment and increasing searching efficiency, we will assume logistic growth for the victim and type II functional response (Holling 1959) for the exploiter. Given these premises, the dynamics of victims (V) and the exploiters (E) can be described with following two differential equations:

$$\frac{dV}{dt} = rV \left(1 - \frac{V}{K} \right) - \frac{aVE}{1 + abV} \quad (1)$$

and

$$\frac{dE}{dt} = -mE + \frac{kaVE}{1 + abV} \quad (2)$$

where the state variables V and E are the densities of the victim and the exploiter, respectively, r is the victim’s intrinsic rate of population growth (for plants: intrinsic rate of biomass production), K is the victim’s carrying capacity, a is the searching efficiency of the exploiter, k is the conversion efficiency (Murdoch et al. 2003), relating the losses inflicted on victims to the energy gains of exploiters, and h is the handling time per victim. Parameter m stands for the rate of energy gain required by exploiters for zero population growth rate and for the per capita mortality rate of starving exploiters.

Setting the time derivatives equal to zero, we obtain the victim’s and exploiters zero isoclines:

$$E = -\frac{rh}{K}V^2 + \left(rh - \frac{r}{aK} \right)V + \frac{r}{a} \quad (3)$$

$$V^* = \frac{m}{a(k - mh)} \quad (4)$$

The victim isocline Eq. 3 is a downward opening parabola that meets the exploiter axis at $E = r/a$ and the victim axis at $V = K$. The exploiter isocline Eq. 4 is a vertical line. (Fig. 1).

A necessary and sufficient condition for the local stability of the exploiter–victim equilibrium (denoted by stars in Fig. 1) is that the slope of the victim isocline is negative at the equilibrium (Rosenzweig 1971, Murdoch et al. 2003, Turchin 2003). Differentiating Eq. 3 and setting the derivative equal to zero, we obtain the V -coordinate of the ‘hump’ (highest point) of the victim isocline as

$$V_{hump} = \frac{K}{2} - \frac{1}{2ah} \quad (5)$$

The equilibrium is thus locally stable if

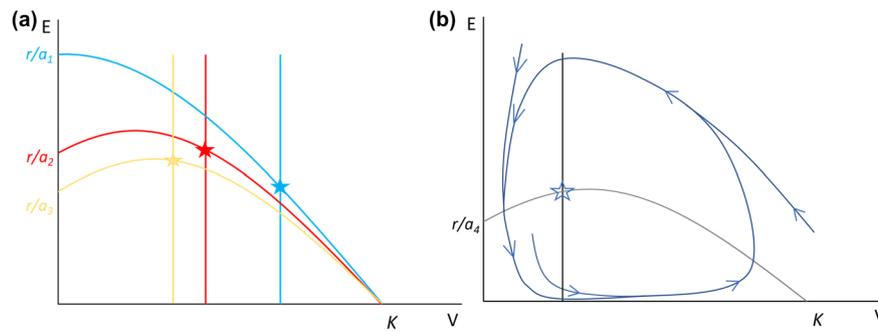


Figure 1. Exploiter (E) and victim (V) isoclines after successive increases in exploiters' searching efficiency. Exploiter isoclines are vertical lines, perpendicular to the victim axis. Victim isoclines are pieces of a parabola. Different colors are used for each isocline pair. The equilibrium points, i.e. the intersection between exploiter and victim isoclines, are denoted by stars. (a) Systems with a locally stable equilibrium. Blue isoclines represent the initial situation, where searching efficiency (a_1) is low. Red isoclines represent the situation after a 30% increase in searching efficiency from a_1 to a_2 , resulting in an increase of exploiter's equilibrium density. Yellow isoclines represent the situation after an additional, small increase in searching efficiency from a_2 to a_3 , now resulting in a reduction of exploiter's equilibrium density. (b) The situation after a further, small increase in searching efficiency from a_3 to a_4 . The equilibrium is now destabilized, and the system starts to display limit cycle dynamics. The limit cycle is mathematically stable, i.e. the system tends to return to this oscillation path if removed from it. In each cycle, however, the exploiter faces a long period of high mortality due to starvation, resulting in very low minima. With the slightest amount of stochasticity or with any Allee-effect, these minima could amount to extinction.

$$\frac{K}{2} - \frac{1}{2ab} < \frac{m}{a(k-mb)} \quad (6)$$

i.e. if

$$aK < \frac{2m}{k-mb} + \frac{1}{h} \quad (7)$$

The stability of the equilibrium point depends on the magnitude of the product aK relative to parameters m and h . While high searching efficiency is good for an individual exploiter, it threatens the stability of the system just as enrichment does. Another parameter with a strong impact on stability is handling time (parameter h). If the value of this parameter were close to zero, the value of the right-hand side of inequality Eq. 7 would be high enough to ensure the stability of the equilibrium point for almost any values of a and K . However, terrestrial predators have usually long handling times, as they spend much time in pursuing detected prey, often in vain, and rest after a successful capture. The value of the term $1/2ab$ in inequality Eq. 6 is therefore small in terrestrial food webs, i.e. the equilibrium is likely to be destabilized if searching efficiency is high enough to pass the equilibrium victim density substantially below $K/2$ (the point of maximal sustainable yield, Sutherland 2001).

To illustrate the consequences of increasing searching efficiency, let us successively increase the value of parameter a , starting with a low value (Fig. 1a, the blue isocline pair). This decreases the equilibrium density of victims but, as long as victims' equilibrium density exceeds $K/2$, the productivity of the victim stock increases, and so does the equilibrium density of exploiters (the red isocline pair). So far, the increase in searching efficiency has been good for the individual exploiter and for the exploiter population. When the value of

parameter a is high enough to depress the equilibrium victim density below $K/2$, the equilibrium density of exploiters starts to decrease (the yellow isocline pair). The victims start now to be overexploited.

When the equilibrium density of victims decreases below $K/2 - 1/2ab$, the system has passed the bifurcation point at which equilibrium is destabilized (Fig. 1b), and asymptotic dynamics are replaced by a limit cycle. The amplitude of the cycle increases rapidly with further increases in parameters a or K (Morozov et al. 2020), especially for the exploiter as it faces periods of heavy mortality due to starvation when victim densities are at their lowest. As the lows of the exploiter deepen, it will face an imminent risk of extinction (Gilpin and Rosenzweig 1972, DeAngelis and Waterhouse 1987, Murdoch et al. 2003, Turchin 2003).

The enigma of stability

In concordance with the implications of the model, the boreal zone is characterized by high amplitude predator–herbivore and parasitoid–folivore cycles (Hanski et al. 1991, 2001, Krebs et al. 1995, Korpimäki and Norrdahl 1998, Boulanger and Arseneault 2004, Jepsen et al. 2008, Klemola et al. 2010, Myers and Cory 2013). In some less productive arctic-alpine ecosystems, corresponding cycles are driven by herbivore–plant interactions (Batzli et al. 1980, Turchin et al. 2000, Olofsson et al. 2012, 2014, Ruffino et al. 2016, but see Fauteux et al. 2016). To survive the low phases, exploiters driving boreal and arctic population cycles have evolved a strong tendency to disperse during population peaks (Oksanen et al. 1992, Henttonen and Kaikusalo 1993). This also reduces the amplitude of the cycle and enhances the chances of the species to persist as a metapopulation (Huffaker 1958, Holyoak and Lawler 1996, Gurney et al. 1998, Klepac et al. 2007).

At the transition from the boreal to the temperate zone, the diversity of the predator community increases, so does the connectivity of the food web, and limit cycles are replaced by asymptotic dynamics. There seems to be a causal connection between the change in food web structure and in dynamics: the generalists of the temperate zone have broad diets and can therefore have a stabilizing type III functional response (Erlinge et al. 1983, Erlinge 1987, Hanski 1987, Hanski et al. 1991, 2001, Tanhuanpää et al. 1999, Klemola et al. 2002, Dwyer et al. 2004, Bjørnstad et al. 2010, Kollberg et al. 2014). The exceptions that confirm the rule are species-poor, heavily human impacted ecosystems, where limit cycle dynamics are common in the temperate zone, too (Turchin et al. 1991, Turchin 2003, Lambin et al. 2006).

A weakness of the Erlinge–Hanski hypothesis is that it does not explain the nature of the alternative resources supporting these generalists. Increasing diversity and food web connectivity per se does not promote stability (Pimm 1979, Thébaud and Fontaine 2010). Switching between different prey species that are vulnerable to predation can only synchronize community level dynamics. To promote stability, increasing connectivity must thus be accompanied by qualitative changes in food web interactions (Neutel et al. 2002, Abrams 2004, Williams and Martinez 2004, Rall et al. 2008, Neutel and Thorne 2014, Kadoya et al. 2018). In order to obtain stabilizing, type III functional responses via switching, the generalists must have alternative resources that are constantly available and cannot be collapsed (Oksanen et al. 2001). In other words, the Erlinge–Hanski hypothesis requires that the generalists of the temperate zone are supported by stabilizing, donor-controlled energy flows (DeAngelis 1975, Barabás et al. 2017, Polis and Strong 1996, Oksanen et al. 2020).

In concordance with the above reasoning, donor-controlled energy flows seem to play a major role in the stabilization of herbivory-based food webs at the transition from the boreal to the temperate zone, where generalists supported by the detritus-based food web and by high quality plant organs curb budding outbreaks by switching to potential outbreak species at the right time. Badgers switch to field voles at their peak reproductive season (Erlinge 1987). Wood mice and shrews start to exploit the pupae of autumnal moth that has massive outbreaks at high latitudes (Tenow 1972), when the density of the pupae exceeds a critical level (Tanhuanpää et al. 1999). In both cases, the interactions appear weak if averaged over time but can rapidly grow stronger when the density of the herbivore increases.

Conclusions

Due to the high searching efficiency of terrestrial predators, terrestrial herbivores are often overexploited i.e. regulated at densities far below the point of maximum sustainable yield, contrary to the arguments of Vuorinen et al. (2021). Assuming type II functional response, this ought to result in violent limit cycle dynamics, as is the case in high latitude ecosystems. Conversely, species-rich temperate zone ecosystems are

characterized by asymptotic dynamics. Empirical evidence indicates that the ultimate causes for the replacement of limit cycles by asymptotic dynamics are donor-controlled energy flows. In the temperate zone, these flows support numerous generalists with type III functional response. A subset of these generalists constitute keystone modules (Kadoya et al. 2018). In these modules, the predator interacts, at average, only weakly with potential outbreak species but switches to them when their density increases, thus curbing budding outbreaks. The ongoing extinction wave (Pimm et al. 2014, Díaz et al. 2019) could destroy these modules, destabilizing previously stable food webs, where predominating species are not adapted to limit cycle dynamics. This could trigger secondary extinctions and inflict economic damages (Hansson 1985, Boulanger and Arseneault 2004).

Acknowledgements – We are grateful for the Subject Editor G. Kalinkat for constructive comments.

Author contributions

Lauri Oksanen: Conceptualization (equal); ; Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); ; Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (lead). **Tarja Oksanen:** Conceptualization (equal); Formal analysis-Supporting, ; Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing-Supporting. **Katariina E. M. Vuorinen:** Conceptualization (equal); ; Formal analysis-Supporting, Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization(lead); Writing – original draft (equal); Writing – review and editing supporting.

Data availability statement

There are no additional data for this paper.

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