



## Europe and large carnivores: *The effect on spatial heterogeneity*



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### Abstract.

In this review we investigate the effect of large carnivores on spatial heterogeneity. As the landscape in Europe is changing, giving opportunities to restore and conserve species and ecosystems, more and more farmlands are abandoned as farmers try to find their fortune in urban areas. It is known that spatial heterogeneity is an important factor contributing to biodiversity. We looked at the effect of carnivores on spatial heterogeneity through a cascade of trophic level interactions, looking at (I) the effect of large herbivores on spatial heterogeneity, (II) the effect of large carnivores on large herbivores and finally (III) the effect of large carnivores on spatial heterogeneity. We found, by using results of various studies, that carnivores are able to regulate herbivore densities and behaviour by direct mortality and creating 'landscapes of fear'. Intermediate herbivore densities were found to have a positive effect on spatial heterogeneity as well as 'landscapes of fear', in which herbivores choose to avoid patches where they face a higher risk of predation. If herbivores exceed intermediate densities, foraging pressure will be too high, and herbivores will create a heterogeneous habitat. Additionally, herbivores of intermediate densities have a positive effect on spatial heterogeneity by the process of self-facilitation, in which they frequently forage on the same patch, creating a higher quality and quantity of the patch. There is still debate about the effectiveness of the landscape of fear theory, as found recently that hunting strategy of the predator plays a major role. More research is needed to make this topic clear.

**Keywords:** spatial heterogeneity, trophic cascade, large herbivores, large carnivores.

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### Introduction.

During the past centuries, the agricultural land use in Europe shifted from small farms with multiple crop species and animals for own use to massive commercial one-product food fabrics. This event changed the landscape and agricultural grounds dramatically (Vos and Meeke, 1999). Large herbivore and carnivore densities declined, due to the loss of their natural habitat. Additionally, large carnivores were preying on livestock and therefore intensively hunted by humans. Nowadays, Europe is changing again. More farmers are leaving the countryside trying to make fortune in the more urban areas, as agriculture isn't the money-maker anymore. Farm grounds are abandoned and neglected giving succession the chance to turn the agricultural landscape into a homogeneous climax state: forest (Vos and Meeke, 1999; IEEP final report).

These changes offer Europe new opportunities in which new ecosystems can evolve. Different species of organisms are given the chance to establish themselves again, including large herbivores and carnivores. It is important to know how these different organisms are related to each other and how population densities are regulated. The aim of this review is to determine which effects large carnivores eventually have on spatial heterogeneity. Spatial heterogeneity is a property here ascribed to a landscape. It refers to the uneven distribution of various concentrations of vegetation types within an area, creating a 'patchy' landscape. If a landscape is more heterogeneous (and thus, more patchy) it creates more different microhabitats where

different species of organisms can live (Palmer, 1994). This situation favours biodiversity, which is widely assumed as an import goal. Increasing levels of biodiversity mean more species to conserve and save from going extinct.

We are going to look at the effects of carnivores on vegetation through a cascade of trophic level interactions. Trophic cascades occur when a top trophic level predator interacts with the next lower level herbivore and this interaction in turn alters or influences vegetation (e.g. Ripple and Beschta, 2003). In this review we use results from various studies in Yellowstone National Park (USA) to address the influence of large carnivores on large herbivores. These cascades were identified as a potentially important factor affecting Yellowstone National Park's woody browse species (Laundre *et al.*, 2001). We are going to use a simplified system in which three trophic levels occur: vegetation, large herbivores and large carnivores. We address **(I)** the effects of large herbivores on spatial heterogeneity in the first place and afterwards **(II)** the effects of large carnivores on their lower level: large herbivores. Through this trophic cascade we determine eventually **(III)** the effect of large carnivores on spatial heterogeneity.

### **The effect of large herbivores on spatial heterogeneity (I)**

Spatial heterogeneity is regulated by various factors like rainfall, soil type, disturbances (e.g. herbivory and fire) and their interactions (Greig-Smith 1979, Huntley and Walker 1982, Archer 1990, Scholes and Walker 1993). We are going to have a closer look at the role of herbivores on spatial heterogeneity in grassland/woodland, as we are talking about abandoned farmlands in Europe, which mainly consist of grass and woodland and the succession phases in between.

Knecht (2008) investigated the role of herbivores on spatial heterogeneity. They questioned whether and through which mechanisms herbivores can induce spatial heterogeneity in savannah vegetation, which consist of grassland and shrubs. They focussed on two basic mechanisms of plant-herbivore interactions that they considered important for vegetation patterning to occur: (1) self-facilitation and (2) spatial dependency of foraging. Self-facilitation (1) is the process in which herbivores, while foraging, increase the attractiveness of a patch. This process occurs when herbivory enhances the quality or quantity of re-growth following defoliation. Quality increase has often been observed when nutrient concentration is increased in post-defoliation re-growth through the replacement of older, low-quality leaves by younger, high quality leaves (Anderson *et al.* 2007). In addition, quantity increase applies when herbivory leads to an increased amount of re-growth following defoliation (Fornara and Du Toit 2007). Spatial dependency of foraging (2) is the process in which the interaction of herbivory with the vegetation at a site is influenced by the surroundings of the site. Vegetation characteristics at larger spatial scales can, for example, influence the selection of sites to forage (Senft *et al.* 1987). Accordingly, the surrounding matrix of a site can be attractive (positive) or repellent (negative) in the herbivore's choice of a particular patch (Baraza *et al.* 2006). Additionally, Knight (2008) questioned how the role of herbivory as a determinant of spatial heterogeneity changes with variation in herbivore density and the pre-existing pattern of vegetation.

By modelling simulations they found that both self-facilitation and spatial dependency of foraging are important to induce spatial heterogeneity. This means there has to be a reason for herbivores to revisit a site and foraging at a site should relate to vegetation at larger spatial scales. They also found that herbivore densities play an important role. At low grazing pressure, the grazers create small grazed patches. At high grazing pressure (by increasing herbivore densities), the herbivores are forced to be less selective, creating larger grazed patches that ultimately leads to a homogenous, fully exploited landscape. Intermediate herbivore densities were found to increase spatial heterogeneity most. The model of Knecht (2008) also shows that the pre-existing pattern of vegetation increasingly influences vegetation patterning through herbivory when the heterogeneity of the initial landscape increases. With initially low vegetation heterogeneity, large herbivores are able to shape the vegetation, but they adhere more to the pre-existing vegetation patterns, than when the initial vegetation heterogeneity increases.

So, large herbivores can induce, at intermediate densities, spatial heterogeneity through the interactions between self-facilitation and spatial dependency of foraging, with the type of pattern being influenced by the heterogeneity of the pre-existing vegetation. Hence, the aim for landscapes to stay heterogeneous is to keep herbivore densities regulated, so that they will not exceed the intermediate range and become highly dense.

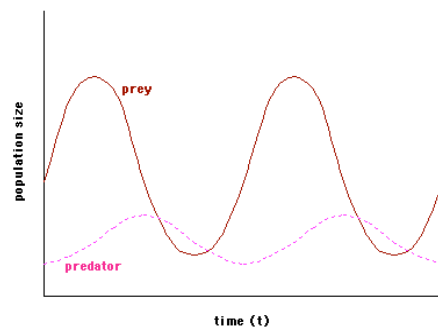
Herbivore densities are regulated through so called 'bottom-up' and 'top-down' processes. In case bottom-up processes are active, herbivore densities are regulated through limited resource availability (Coe *et al.*, 1976; East, 1984; McNaughton *et al.*, 1989; Polis, 1999). The role of bottom-up processes in herbivore dynamics is well documented in several studies in the temperate zone (e.g. Fowler 1987, Gaillard *et al.* 2000) When there are 'top-down' processes involved, herbivore densities are regulated through predation by carnivores (Estes and Duggins, 1995; Sinclair *et al.*, 2003; Owen-Smith and Mills, 2008) but in most cases in Europe, this top-down regulation has been performed by directed human hunting-activities. What if we replace the hunting by letting large carnivores take over the lead? We are now going to have a better look at the effect of large carnivores on their lower level: large herbivores.

## The effect of large carnivores on large herbivores (II)

Predators, here also known as 'large carnivores', cause the top-down regulation of large herbivores through predation, but they can also influence herbivore forage behaviour. We first go to have a look on predator-prey densities interactions. Graph 1. shows the simplest case of predator-prey relationships: The Lotka-Volterra model, which is composed of a pair of differential equations that describe predator-prey dynamics. It is characterized by oscillations in the population size of both predator and prey, with predator's oscillation peak lagging slightly behind the peak of prey's oscillation. The model makes a few assumptions:

Graph 1. Lotka - Volterra predator-prey model.

- 1) Prey population will grow exponentially when predator is absent;
- 2) Predator population will starve in absence of prey
- 3) Predators consume infinite quantities of prey
- 4) There is no environmental complexity (both populations are moving randomly through a homogenous environment).



This model provides a look on how predator-prey interactions are simplified related. It gives an insight in how decrease in herbivore densities influence carnivore densities (as a bottom-up process) and how an increase in carnivore densities influence herbivore densities (as a top-down process). But the highly simplified assumptions do not reflect the reality. First, predators do not consume infinite quantities of prey, as there is a trade-off between their needs to feed and the energy spend on feeding (e.g. catching a prey). Predators are satisfied at a certain point and will not spend more energy on predation. Secondly, populations are not moving randomly as the environment is often more complex as mentioned above. We found before that herbivores make decisions on forage strategies and are able to create spatial heterogeneity themselves. In the case of starvation when prey is absent; this will only happen if the predator is not able to change diet. In most cases, carnivores therefore prey on various kinds of herbivores. Table 1. shows the predator-prey relationship between a few carnivores and herbivores. As seen in this table, wolf eat a lot different kind of prey as lynx and brown bear are more focussed on few species. Herbivores mostly have to cope with more than one carnivore, except for bison, which only have to fear wolf.

	Wolf ( <i>Canis lupus</i> )	Lynx ( <i>Felis lynx</i> )	Brown bear ( <i>Ursus arctos</i> )
Bison ( <i>Bison bison</i> )	A N		
Moose ( <i>Alces alces</i> )	A N		a N
Elk ( <i>Cervus elaphus</i> )	A N	n	N
Roe deer ( <i>Capreolus capreolus</i> )	A N	A N	

**Table 1:** A = predation on adults (age > 6 months), N = predation on neonates only (age < 6 months). Capital letter indicates predation is common, a lower case letter indicates that predation has been documented, but is not a common event. (Anderson et al.)

In this part of the review we have a closer look at wolf (*Canis lupus*) predation on elk (*Cervus elaphus*), as multiple research on this predator-prey relationship has been done in Yellowstone National Park (USA) (e.g. Ripple and Beschta, 2003, 2006; Kauffman, Brodie and Jules, 2010). As Euro-American settlers colonized North America in the early 20<sup>th</sup> century, wolves were extirpated from most of their natural ranges, as one factor, allowing elk in Yellowstone to obtain high densities (Houston, 1982). Aspen and other woody species decline during that time, for instance, has spawned considerable debate (e.g. Kay, 1997; Huff and Varley, 1999) but most people recognized the role of increased elk densities as crucial. Woody plant species (like aspen, cottonwood and willow) were overexploited and not able to recover anymore from herbivory by elk (Romme *et al.*, 1995, 2005; Huff and Varley, 1999; Ripple *et al.*, 2001; Barmore, 2003). Seen as a great success, was the reintroduction of the wolf in 1995, as they were expected to restore ecosystem functions. Multiple research was done to find out if wolf presence affected elk and (indirectly) vegetation diversity by trophic cascades. These cascades were identified as a potentially important factor affecting Yellowstone's woody browse species (Laundre *et al.*, 2001). Two different predator-prey relationships have been reported (Schmitz *et al.*, 1997). The first one (and most common) is direct predation on elk by wolf, affecting prey's population size, which in turn may influence total foraging pressure on plants. The number of elk killed by wolf per unit time is a function of the time required to find an elk (search time), and the time associated with capture and feeding activities (handling time) (Messier, 1994). This means that if elk density increases, each wolf eats a decreasing proportion of elk. More wolves are in turn able to survive and reproduce, resulting in increased wolf densities that consume (all together) more elk. The foraging pressure on cottonwood and willow will decrease, giving them the chance to recover from herbivory (e.g. Ripple and Beschta, 2003 & 2006; Andersen, Linnell and Solberg, 2006). The second theory associated with trophic cascades is the, so called, 'landscape of fear' theory, whereby ungulates (like elk) alter their foraging patterns, vigilance or movements under the risk of predation (Lima and Dill, 1990; Laundre *et al.*, 2001; Hernandez and Laundre, 2005). These, although non-lethal, effects may be of bigger importance than direct mortality, assumes Schmitz *et al.* (1997). Herbivores need to balance their needs for safety and food foraging as described by the optimal foraging theory (MacArthur and Pianka, 1966; Brown *et al.*, 1999; Berger *et al.*, 2001b). When a predator sneaks upon a prey, his chance of success increases if his visibility decreases. So, herbivores grazing, for example, close to high vegetation (making predators less visible) are in more risk of predation than grazing in the open field, which makes predators more visible and noticeable at a distance, giving the prey more time to escape. Herbivores learn (in this case) to avoid, if possible, areas surrounded or close to high vegetation. This process alters the spatial dependency of foraging by herbivores. The patches close to high vegetation will have a negative attractiveness, as predation risk will be high. The foraging pressure in turn, will lower or even stop near the high vegetation, giving room for plants to recover from herbivory and seedlings to recruit. These 'spots' will ultimately create heterogeneity of the landscape, altering new microhabitats, giving biodiversity a chance to increase.

Recently, Kauffman *et al.* (2010) examined if wolf were able to save Yellowstone's aspen. They performed a landscape-level test of a behaviourally mediated trophic cascade (BMTTC), which is a trait-mediated indirect interaction (TMII) that is strong enough to structure ecosystems (e.g. Abrams, 1984 & 1996; Werner and Peacor, 2003; Kerfoot and Sih, 1987; Beckerman *et al.* 1997). Trait-mediated interactions represent the nonlethal effects of predators. Schmitz *et al.* (2004) and Schmitz (2005) have suggested that TMII's strongly can be influenced by the hunting mode of the predator, which range from passive (sit-and-wait predators) to active predators, which chase down vulnerable individuals while coursing through groups of prey. The wolf is an example of an active predator, which is predicted to have the weakest fear-mediated effects (in contrast with passive predators, which should have the strongest indirect effects) (Schmitz 2005), as they rarely produce consistent predation risk while coursing through the landscapes. It is predicted therefore that large herbivore prey of the wolf, will not witness a 'landscape of fear' and thus will not change their foraging behaviour.

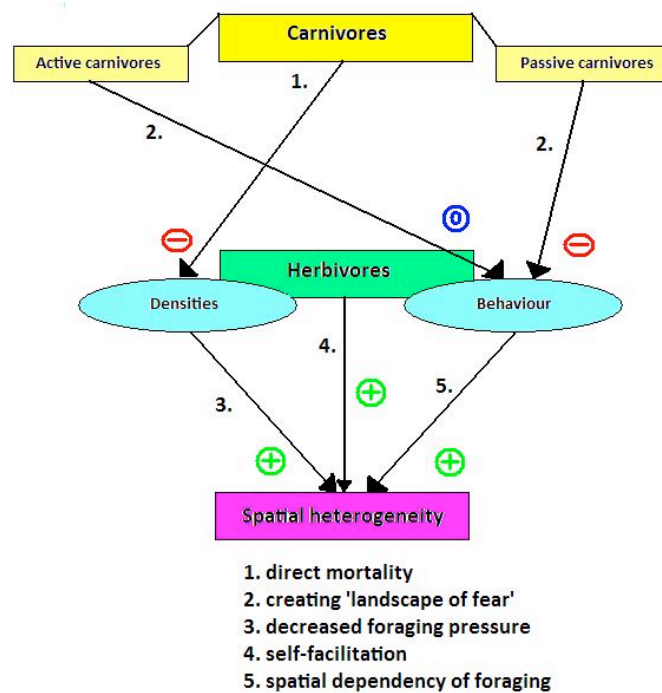
After reintroductions of the wolf in YNP in 1995, it is found though, in multiple studies, that aspen are benefiting from wolves via a BMTTC, whereby aspen are recovering in areas with a higher predation risk of wolf (e.g. Ripple *et al.*, 2001; Ripple and Beschta, 2004, 2007; Fortin *et al.*, 2005). Similar results were also found in willow recovery (Beyer *et al.*, 2007) and cottonwood

(Ripple and Beschta, 2003). These findings are contrary to the predictions that active predators produce weak or no BMTCs (Schmitz 2005). Although these findings are widely accepted and popularized, Kaufmann *et al.* (2010) claimed it was never adequately tested. They assessed whether wolves influence aspen by obtaining demographic data on aspen stands using tree rings and monitoring of browsing levels in experimental exclosures for elk arrayed across a gradient of predation risk. The research was taken over a time period of three years and they finally found that the recruitment failure of aspen was more consistent with a gradual increase of elk numbers rather than a behavioural shift (BMTC) caused by wolves. Additionally they found, in an experimental test of the BMTC hypothesis, that the impacts of elk browsing on aspen demography are not diminished in sites with a higher risk of predation by wolf.

### Conclusion/Discussion: The effect of large carnivores on spatial heterogeneity (III)

Now knowing what (I) the effect of large herbivores on spatial heterogeneity is and (II) the effect of large carnivores on large herbivores, we are able to (III) describe the trophic cascade from large carnivores to spatial heterogeneity. Graph 2. illustrates this description. Large carnivores influence spatial heterogeneity by effecting herbivore densities by (1) direct mortality. They can regulate herbivore densities so that they will not exceed intermediate densities and over exploit the vegetation (creating a homogenous habitat). Secondly, large carnivores can enhance changes in herbivore behaviour by (2) creating a 'landscape of fear'. The ability to create this landscape depends on the hunting strategy of the carnivore. Active carnivores facing weakest fear mediated effects as they rarely produce a consistent risk of predation. Passive carnivores do produce more predation risk and therefore are able to create a landscape of fear. Herbivores change their behaviour and avoid patches, which are negatively attractive (5) as they face higher risk of predation. In addition to the effect of (4) self-facilitation, spatial heterogeneity is positively stimulated. Carnivores, hence, have a major role in effecting spatial heterogeneity by effecting herbivores. Without the top-down regulation on large herbivores, densities will exceed intermediate ranges, having a negative effect on spatial heterogeneity.

Graph 2. Trophic cascade: (+) = positive effect, (-) = negative effect, (0) = no effect.



So will it be a good strategy to reduce or stop hunting and let carnivores take of the lead? We think it is, as carnivores are able to regulate herbivore densities as well. Although we did not have a closer look on maintaining densities over a longer period of time, we know large carnivores can, by looking at results of various studies (e.g. Andersen, *et al* 2006). In addition, human management will not be needed anymore, making the ecosystems fully regulated by nature (e.g. abiotic factors and different species of organisms). As wolf is enlarging his habitat recently in Europe, many countries are sceptic about his return. Some people are horrified by the idea that 'dangerous animals' are wandering around their villages, sneaking upon their kids. Frans Vera from the Dutch organisation "Staatsbosbeheer" which is responsible for overseeing Dutch nature reserves says that the chance of getting attacked by your Golden Retriever is of a higher chance than getting attacked by a wolf. People need to learn that wolves can be an addition to the ecosystems around them. In Germany for example the government started the campaign "Welcome wolves". And that is what all countries in Europe should do. Embrace the wolf!

## References.

- Abrams P. A. 1984. Foraging time optimization and interactions in food webs. *American Naturalist* 124:80-96.
- Abrams P. A. 1996. Dynamics and interactions in food webs with adaptive consumers. Pages 113-121 in G. Polis and K. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman and Hall, New York, USA.
- Adler P. B. *et al.* 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128:465-479.
- Andersen R., *et al.* 2006. The future role of large carnivores in terrestrial trophic interactions: the northern temperate view. In: *Large herbivore ecology, Ecosystem dynamics and conservation*, ed. K. Dettel, P. Duncan, R. Bergstrom & J. Pastor. Cambridge University press 2006.
- Anderson T. M. *et al.* 2007. Forage nutritive quality in the Serengeti ecosystem: the roles of fire and herbivory. *Am. Nat.* 170:343-357.
- Archer S. R. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, USA. *J. Biogeogr.* 17:111-127.
- Barmore W. J. 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park: research and synthesis 1962-1970. Yellowstone Center of Resources, Yellowstone National Park, Wyoming, USA.
- Baraza E. *et al.* 2006. Conditional outcomes in plant-herbivore interactions: neighbours matter. *Oikos* 113:148-156.
- Beckerman *et al.* 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences USA* 94: 10735-10738.
- Berger J., P. B. Stacey, L. Bellis, M. P. Johnson. 2001a. A mammalian predator/prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecol. Appl.* 11:967-980.
- Berger *et al.* 2001b. Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036-1039.
- Beyer H. L. *et al.* 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? *Ecological Applications* 17:1563-1571.
- Breitenmoser U. 1998. Large predators in the Alps: the fall and rise of man's competitors. *Biological Conservation* 83:279-289.

- Brown *et al.* 1999. The ecology of fear: optimal foraging, game theory and trophic interactions. *J. Mammal.* 80:385-399.
- Coe M. J. *et al.* 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22:341-354.
- Estes, J. A. and D. O. Duggins. 1995. Sea Otters and kelp forests in Alaska - Generality and variation in a community ecological paradigm. *Ecol. Monogr.* 65:75- 100.
- Fornara D. A. And J. T. Du Toit. 2007. Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology* 88:200-209.
- Fowler C. W. 1987. A review of density dependence in populations of large mammals. *Current Mammalogy*, Vol. I, ed. H. H. Genoways. New York, USA. Plenum:401-441.
- Fortin D. *et al.* 2005. Wolves influence elk movements: behavior shapes and trophic cascade in Yellowstone National Park. *Ecology* 86:285-298.
- Gailard J. M. *et al.* 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual review of Ecology and Systematics* 31:367-393.
- Greig-Smith P. 1979. Pattern in vegetation. *J. Ecol.* 67:775-779.
- Huff D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. *Ecological Applications* 9:17-29.
- Hernandez L., J. W. Laundre. 2005. Foraging in the landscape of fear and its implications for habitat use and diet quality of elk (*Cervus elaphus*) and bison (*Bison bison*). *Wildl. Ecol.* 11:215-220.
- Huntley B. J. and B. H. Walker. 1982. *Ecology of tropical savannas*. Springer.
- Institute for European Environmental Policy. Final report IEEP, ENV. B.1 / ETU / 2008 / 0030
- Kauffman M. J., J. F. Brodie and E.S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviourally mediated trophic cascade. *Ecology*, 91(9):2742-2755.
- Kay C. E. 1997. Viewpoint: ungulate herbivory, willows, and political ecology in Yellowstone. *Journal of Range Management* 50:139-145.
- Kerfoot W. C., A. Sih. 1987. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Larsen E. J., W. J. Ripple. 2003. Aspen age structure in the northern Yellowstone ecosystem, USA. *Forest Ecol. Manage.* 179:469-482.
- Laundre *et al.* 2001. Wolves, elk and bison: re-establishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79:1401-1409.
- Lima S. L., L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619-640.
- MacArthur R. H., E. R. Pianka. 1966. On optimal use of a patchy environment. *Am. Nat.* 100:603-609.
- McLaren B. E., R. O. Peterson. 1994. Wolves, moose and tree rings on Isle Royale. *Science* 266:1555-1558.
- McNaughton S. J. 1984. Grazing lawns: animals in herds, plant form and coevolution. *Am. Nat.* 124:863-886.
- McNaughton S. J. *et al.* 1989. Ecosystem-level patterns of primary productivity and herbivory in

- terrestrial habitats. *Nature* 341:142-144.
- Messier F. 1994. Ungulate population models with predation: a case study with the American
- Owen-Smith N. and M. G. L. Mills. 2008. Predator-prey size relationships in an African large-mammal food web. *J. Anim. Eco.* 77:173-183.
- Polis G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86:3-15.
- Ripple *et al.* 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological conservation* 102:227-234.
- Ripple W. J., R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184:299-313.
- Ripple W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* 54:755-766.
- Ripple W. J., R. L. Beschta. 2005b. Linking wolves and plants: Aldo Leopold on trophic cascades. *Bioscience* 55:613-621.
- Ripple W. J., R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* 230:96-106.
- Ripple W. J., and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138:514-519.
- Romme *et al.* 1995. Aspen, elk and fire on the northern range of Yellowstone National Park. *Ecology* 76:2097-2106.
- Senft R. L. *et al.* 1987. Large herbivore foraging and ecological hierarchies: landscape ecology can enhance traditional foraging theory. *BioScience* 37:789-799.
- Scholes R. J. and S. R. Walker. 1993. *An African savanna: synthesis of the Nylsvely study.* Cambridge Univ. Press.
- Schmitz *et al.* 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388-1399.
- Schmitz *et al.* 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* 7:153-163.
- Schmitz O. J. 2005. Behavior of predators and prey and links with population level processes. Pages 256-278 in P. Barbosa and I. Castellanos, editors. *Ecology of predator-prey interactions.* Oxford University Press, Oxford UK.
- Sinclair A. R. E. *et al.* 2003. Patterns of predation in a diverse predator-prey system. *Nature* 425:288-290.
- Trouwborst A. and C. J. Bastmeijer. 2010. Lynxen en wolven; Het natuurbeschermingsrecht en de terugkeer van grote roofdieren naar Nederland. *Milieu & Recht*, 37(5):272-283.
- Vos W., H. Meekes. 1999. Trends in European cultural landscape development: perspectives for a sustainable future. *Landscape and Urban Planning* 46:3-14.
- Werner E. E., S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083-1100



Woodroffe R. 2000. Predators and people: using human densities to interpret decline of large carnivores. *Animal Conservation* 3:165-173.

(Photo wolf: google search: wolf trophic cascade, no author found).