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Review

Do recolonising wolves trigger non-consumptive effects in European ecosystems? A review of evidence

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Predators can affect ecosystems through non-consumptive effects (NCE) on their prey, which can lead to cascading effects on the vegetation. In mammalian communities, such cascading effects on whole ecosystems have mainly been demonstrated in protected areas, but the extent to which such effects may occur in more human-dominated landscapes remains disputable. With the recolonisation of wolves *Canis lupus* in Europe, understanding the potential for such cascading processes becomes crucial for understanding the ecological consequences of wolf recovery and making appropriate management recommendations. Here, we investigate the evidence for non-consumptive effects of wolves on their wild ungulate prey and cascading effects on the vegetation in European landscapes. We reviewed empirical studies reporting wild ungulate responses to wolves involving spatio-temporal behaviour at large and fine spatial scales, activity patterns, vigilance, grouping, physiological effects, and effects on the vegetation. We reveal that non-consumptive effects of wolves in Europe have been studied in few regions and with focus on regions with low human impact, are highly context-dependent, and might often be overruled by human-related factors. Hence, we highlight the need for a description of human influence in NCE studies. We discuss challenges in NCE research and the potential for advances in future research on NCE of wolves in a human-dominated landscape. We emphasise the need for wildlife management to restore ecosystem complexity and processes, to allow non-consumptive predator effects to occur.

Keywords: behavioural responses (to predation), human-dominated landscape, non-consumptive effects, risk effects/predation risk, trophic cascades, ungulate prey, wolf *Canis lupus*

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Introduction

Large mammalian herbivores are crucial in structuring terrestrial ecosystems (Gordon et al. 2004, Schmitz 2008). They affect vegetation structure by foraging and trampling (Kuijper et al. 2010, Hempson et al. 2015, Churski et al. 2017), by influencing nutrient cycling (Murray et al. 2013), and seed dispersal (Iravani et al. 2011, Jaroszewicz et al. 2013). In this way, herbivores can influence vegetation across multiple spatial scales, from local to landscape levels (Woodward et al. 2004, Moncrieff et al. 2016), resulting in cascading impacts on numerous species and processes (Ripple et al. 2014).

Herbivore communities themselves are influenced by bottom–up effects (e.g. food availability) and top–down effects (i.e. predation). Thus, by affecting prey communities, predators can exert indirect effects on the vegetation. Different mechanisms can induce these ecological effects of large carnivores on their prey. Historically, studies on predator–prey interactions mainly focused on consumptive effects, where predators affect population densities by killing their prey (Messier 1991, Ripple and Beschta 2012). In addition to such 'lethal' or 'consumptive' effects on the population dynamics of prey, the presence of predators can also induce antipredator responses in behaviour or physiology (Lima and Dill 1990, Boonstra et al. 1998, Creel et al. 2005). Such behavioural or physiological changes in response to predator presence are referred to as 'non-consumptive effects' (hereafter NCE).The importance of NCE of predators has often been documented in invertebrates, especially in aquatic systems, where NCE can be much stronger than consumptive effects (Preisser et al. 2005). In terrestrial vertebrate communities the interest in NCE and potential trophic cascades has increased in the past decades (Say-Sallaz et al. 2019) with the recovery of large carnivores (Chapron et al. 2014, Ripple et al. 2014).

Large carnivores have the potential to create trophic cascades (Ripple et al. 2014). However, the extent and relative contribution of NCE compared to direct lethal effects is still debated (Creel and Christianson 2008, White et al. 2008, Kauffman et al. 2010, Marshall et al. 2013, Middleton et al. 2013, Peterson et al. 2014). The main body of literature on NCE in terrestrial vertebrates originates from large protected areas (Kuijper et al. 2016). Case studies from Yellowstone National Park (USA) showed how prey species changed their behaviour when predation risk was modified by the reintroduction of wolves *Canis lupus* (Fortin et al. 2005, Creel and Christianson 2008, Kauffman et al. 2010). In response to returning predators, prey animals have been shown to change vigilance, grouping behaviour, space use, or habitat selection (Fortin et al. 2005, Winnie and Creel 2007, Thaker et al. 2011, Clinchy et al. 2013). Such changes in prey behaviour were documented to affect the ecosystem through modified feeding pressure on certain plant communities (Fortin et al. 2005) or nutrient cycling (Roux et al. 2018). Similar effects caused by the return of an apex predator have been reported in the Serengeti National Park, where the lion *Panthera leo* was reintroduced (Skinner and Hunter 1998) or in the Yosemite National Park after the recolonisation of the cougar *Puma concolor* (Ripple and Beschta 2008). However, surprisingly little is known about NCE in human-dominated landscapes, which we here define as a landscape that is substantially shaped by humans and is extensively used for a variety of human activities, including hunting, agriculture, forestry, urbanization, and industrial purposes. Compared to national parks or wilderness areas, human-dominated landscapes are characterized by the presence of human-made structures resulting in high degrees of fragmentation. In such landscapes, human impact can still vary strongly with, for example, human population density, infrastructure, habitat modifications, and the level of human disturbance (recreational activity, hunting, or forestry). In Europe (especially central Europe), the landscape is mostly human-dominated and a low-conflict coexistence between large carnivores and humans can be challenging. Cascading effects through large carnivores are often reported as important ecosystem services provided by top predators. Most NCE, however, were reported in large national parks and we need to better understand how large carnivores can affect the ecosystem in such human-dominated landscapes.

One of the most conflict-prone large carnivore species is the Eurasian wolf. The Eurasian wolf *C. l. lupus* was extirpated in the early 1900s in most European countries, but has recently recolonized large parts of its original range (Chapron et al. 2014). In many parts of Europe, wolves are returning to landscapes that are densely populated by humans and where human impact influences animal populations, behaviour, and trophic interactions (Fig. 1, Chapron et al. 2014). These landscapes present a mosaic of various types of human land use and very dense linear infrastructures. Forests, an important habitat of wolves, have been strongly modified through a substantial network of forest roads (Bojarska et al. 2021), forestry activities, or are affected by hunting practices and recreational activities.

A key question is whether, under these conditions, wolves can still create ecological impacts as documented in large national parks. Kuijper et al. (2016) reviewed how anthropogenic effects on large carnivore density or behaviour can alter their ecological function, and how human-induced changes in prey species and the landscape limit the impact of large carnivores. They concluded that the potential for density-mediated trophic cascades (mainly caused by consumptive effects) is restricted to areas where carnivores reach ecologically functional densities or where even low carnivore densities can impact prey densities, i.e. in rather unproductive areas (Kuijper et al. 2016). NCE, however, might have a higher potential for cascading through trophic levels than direct effects, since predators have been documented to affect prey behaviour even at low densities (Laundré et al. 2001). Say-Sallaz (2019) reviewed the empirical literature on NCE from large carnivore–ungulate systems worldwide and revealed a bias of studies on NCE from protected areas and with a focus on anti-predator behavioural responses. Here, we specifically focus on the NCE of wolves in Europe, including their indirect effects on the vegetation. This allows us to investigate the wolf–prey–vegetation interactions more specifically and synthesise ecosystem effects of wolves documented in Europe.

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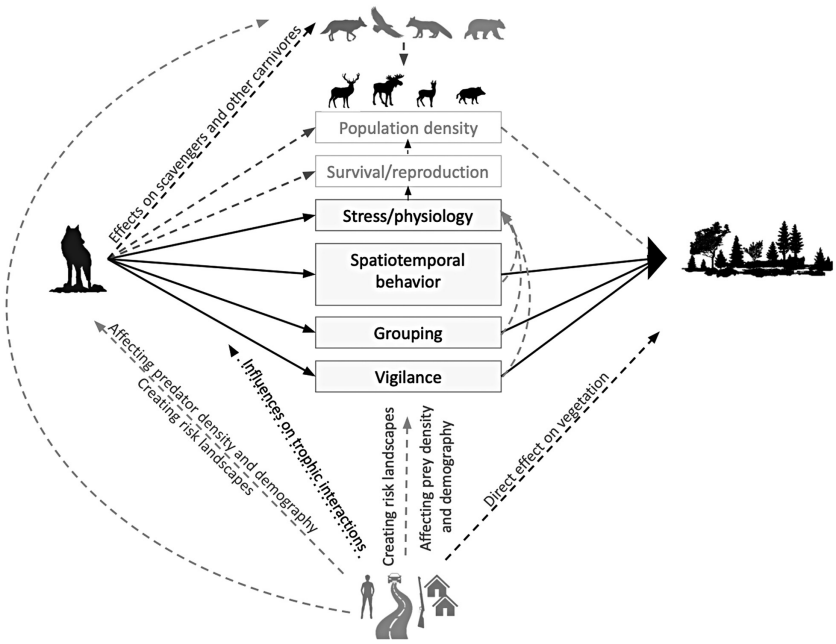


Figure 1. Simplified conceptual framework of predator effects on prey and on the vegetation. Solid lines indicate the non-consumptive effects (NCE) we considered in this study, whereas dashed lines indicate effects that were not considered in our review. Human effects on wolves or ungulate species were only considered if found as explaining variables in papers focusing on NCE of wolves on ungulate prey.

Literature search

We performed a systematic search in Web of Science that included keywords related to 'non-consumptive effects' (among others as e.g. 'risk effect*'), '*C. lupus*', 'ungulate prey', and 'Europe' (or any European country) connected with the Boolean connector AND (see Supporting information for a detailed list of searched keywords). We identified 234 studies (as of 26 September 2023). After an initial screening of title and abstracts, we selected 34 studies that were conducted at least partially in Europe and explicitly investigated NCE of wolf on large prey (> 15 kg, Ripple et al. 2014) and were published in peer reviewed journals in English. Thus, we excluded studies focusing on direct, consumptive impacts, as well as papers analysing theoretical or published data (Supporting information). To the 34 remaining studies, we added studies found in other literature databases (Google Scholar and BioOne, n = 4) and studies that were referred to in other studies (n = 3). Thus, we ended up with a total number of 41 relevant studies (Supporting information).

We classified NCE of wolves on their ungulate prey into the following categories (Table 1, Fig. 1): 1) landscape-scale spatial behaviour, 2) fine-scale spatial behaviour, 3) activity patterns, 4) vigilance behaviour, 5) grouping behaviour, 6) physiological effects, and 7) effects on the vegetation. We extracted the country where the study was performed, the prey species, and the method used to study prey behaviour. To describe the predation risk, we categorised the measure of wolf presence as follows (Moll et al. 2017 for more details): presence–absence, probabilistic occurrence, probabilistic kill occurrence, or experimental cues. We did not include direct human effects on prey species in the search terms, but assessed whether the studies on NCE included measures of anthropogenic effects (e.g. the distance to settlements, hunting, or general human activity). Given the small number of studies in each category and a diverse set of methods, a quantitative analysis was unfortunately not possible. Consequently, we summarize and discuss the findings of the studies investigating NCE of wolves in Europe qualitatively.

Where and how is our knowledge generated?

Spatial distribution and focal prey species of studies

A large number of the studies we found were performed in Białowieża Primaeval Forest in Poland (13/41, 31.7%) and Sweden (11/41, 26.8%) (Fig. 2). Thus, most of the studies were performed either in a relatively large, undisturbed system, where wolves were never completely extinct (Białowieża Primaeval Forest), or in managed forest systems with relatively low human densities (Sweden).

Since some studies looked at multiple categories of NCEs, multiple species or included different regions, we treated each investigated combination of effect, species, and region as a single observation in further analyses. If, for example, a study included data from temporal activity as well as vigilance behaviour of two different prey species, this study resulted in four observations. Thus, the 41 studies resulted in 89 observations. The most studied species was red deer *Cervus elaphus* with 23 observations in 14 studies, followed by roe deer *Capreolus capreolus* with 17 observations in 13 studies, moose *Alces alces* with 15 observations in 12 studies, and wild boar

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Table 1. Overview of non-consumptive effects in Europe for each effect category. Note that one study can have multiple observations of different categories.

Category	n	Current knowledge in Europe	Current challenges	Suggestions for future studies
2.1.1 Large-scale	15 studies 25 observations	Factors related to human activity overrule predator effects. Effects at the large spatial scale have mainly been found in national parks where human impact is reduced	Studies often focus on spatial overlap of wolves and their prey. This does not allow any conclusions about causality	Exploit the potential of telemetry data for analysing prey species behaviour. Compare prey habitat preferences between areas with and without wolves. More consideration of temporal patterns
2.1.2 Fine-scale	7 studies 14 observations	Most studies report fine-scale effects of wolves on prey (decreased visitation rate or duration). One study found no effect on visitation rate/duration, but reported increased vigilance	All studies on fine-scale responses have been performed in national parks. Human effects or context-dependence thus have not been investigated	Study human-dominated landscapes outside national parks. Camera trap studies should report visitation rates/duration and vigilance, as different strategies could be applied by prey animals
2.1.3 Temporal	6 studies 11 observations	Generally high temporal overlap between wolf and prey activity patterns (Rossa et al. 2021, Esttore et al. 2023)	Studies report temporal overlap but lack comparison with reference areas without predator presence (except Mori et al. 2020). No experimental studies	Combine studies using experimental predator cues with analyses of activity patterns. Find reference areas to study prey activity patterns when predators are absent
2.2.1 Vigilance	7 studies 9 observations	Large-scale together with small-scale risk factors can create fine-scale risk patches where vigilance is increased (and/or fine-scale spatial avoidance; section 2.1.2. above). Anthropogenic effects can overrule the effects of natural predators	Most studies have been performed in one region (Białowieża Forest) and in a protected environment (national parks)	Unveil the conditions under which NCE of wolves occur (i.e. small-scale risk factors). Different levels of human activity as well as temporal factors deserve further exploration
2.2.2 Grouping	4 studies 5 observations	Different species and sexes show different responses in grouping behaviour. Predator presence might be less important than e.g. other environmental or human-related factors	Few studies were found. Many potential alternative predictors can be responsible for effects (e.g. competition, food quality, habitat structure)	Investigate wolf effects on grouping behaviour in relation to the potential for cascading effects. Consider intraspecific differences in responses
2.3 Physiological effects	6 studies 9 observations	Wolves can affect stress levels or parasite prevalence in prey, but species differ in their responses and anthropogenic factors might be more important than wolf presence	Causality is not clear, e.g. reduced growth rates can be caused by stress but also by changes in habitat selection. Wolf presence and human presence are negatively correlated so both could be the cause of observed effects	Design experimental studies to disentangle human- and wolf-related effects
3.4 Cascading	12 studies 16 observations	Wolf presence and small-scale risk factors can result in patches with reduced browsing pressure and increased tree regeneration. These effects are most pronounced in undisturbed areas	Most research has been performed in national parks, mostly Białowieża Forest, or in Scandinavia. Hard to disentangle consumptive and non-consumptive effects	Explore interactions of wolf presence and anthropogenic factors. Evaluate the economic consequences of changes in browsing patterns. Study vegetation types other than forests. Sapling survival might be more ecologically relevant than browsing damage

Sus scrofa with 12 observations in nine studies. In Europe, the most widely distributed and most abundant prey species for wolves are red deer, roe deer, and wild boar (Okarma 1995, Zlatanova et al. 2014). Thus, most studies on NCE of wolves at the European level have been performed on the most abundant prey species, except for an overrepresentation of moose (at the European scale).

Methodologies and predation risk assessment

The reviewed studies include a variety of measurements for predation risk, such as presence–absence of wolves in space (Bonnot et al. 2018, van Ginkel et al. 2019a) or time (Grignolio et al. 2019), predicted occurrence (based on habitat use, Bubnicki et al. 2019) or gradients in intensity of use by

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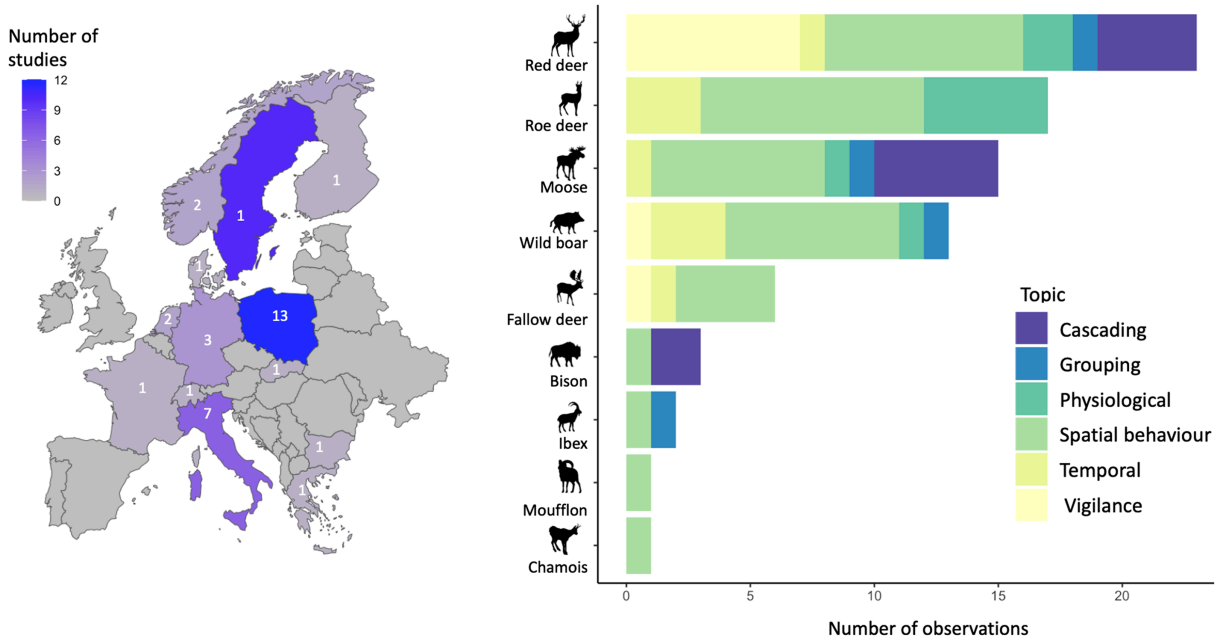


Figure 2. Number of studies on non-consumptive effects of wolves per country in Europe (left, n = 41) and number of observations (each investigated combination of effect, species and region in a study) per species and category (right, n = 89). The observations were classified according to the prey species in focus.

wolves, e.g. core areas of wolf territories versus peripheral areas (Kuijper et al. 2013). Other studies used experimental cues to simulate predation risk (Kuijper et al. 2014). Also, for prey responses, different measurements have been used. Especially for spatial behaviour, a variety of methods and different predictors have been employed, ranging from simply assessing spatial overlap of wolves and their prey based on indirect signs (Popova et al. 2018) to predicting spatial distributions based on modelled camera trap data (Bubnicki et al. 2019).

GPS information was only used in a few studies to investigate prey behaviour in response to predator presence (Eriksen et al. 2009, 2011, Nicholson et al. 2014), even though GPS tracking is probably the most common method for investigating wolf spatial behaviour. To study the fine-scale response of prey to wolf presence, camera traps and indirect signs of presence (mainly pellet counts) have been used more widely. Altogether, we document high methodological variation in the measurement of wolf predation risk as well as prey responses (Supporting information). This lack of standardisation hinders quantitative analyses and complicates drawing general conclusions from the studies (Moll et al. 2017, Prugh et al. 2019).

Assessment of human effects

Human activities might influence behaviourally mediated effects created by wolves (Kuijper et al. 2016) and, therefore, assessing the degree of human influence is important. However, studies included in this review often lack a thorough description of the type and strength of anthropogenic effects or human disturbance. Almost half of the studies (46.3%) and more than half of the observations (56.1%) were performed in protected areas where hunting, forestry, and agricultural land use were at least partially restricted. However, the degree of human activities varies strongly between national parks (van Beeck Calkoen et al. 2020). To what extent these activities are restricted is not reported in most of the studies.

Studies on habitat selection of prey species often include variables related to the intensity of human land use (e.g. forest exploitation, hunting Theuerkauf and Rouys 2008). These studies, however, mostly do not consider any interactions between anthropogenic effects and effects of wolf presence on prey behaviour. Thus, most studies do not consider whether wolf-prey interactions change in regions with high versus low human activity (Proudman et al. 2020).

Which non-consumptive effects by wolves are documented in Europe?

Spatio-temporal responses

Most studies reported only temporal or spatial results or reported them separately, which is also why we report the results in different sections, although temporal responses should not be considered isolated from spatial patterns (discussion, Kohl et al. 2018). Spatial responses to predation risk can occur at different spatial scales: at the large scale, prey might react to general presence of predators, while at a smaller scale they might avoid small-scale risk factors, such as escape impediments.

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Large-scale spatial responses

Habitat selection based on wolf habitat use / suitability

At large spatial scales (large-scale habitat use and home range selection), studies generally found that human influence, vegetation structure, and prey-related variables, such as sex and reproductive status, are more important for explaining habitat selection by large ungulates than the presence of wolves (Theuerkauf and Rouys 2008, Nicholson et al. 2014). An exception is the study of Bubnicki et al. (2019), which showed that patterns of landscape use by red deer were predominantly determined by patterns in wolf space use in the Białowieża Forest. Which environmental variables are important varies between ungulate species (Theuerkauf and Rouys 2008, Bubnicki et al. 2019). Theuerkauf and Rouys (2008) did not find evidence for a general impact of wolf presence on large-scale ungulate distribution. They concluded that anthropogenic impacts affect local intensity of use by prey stronger than predation risk by wolves. Red deer seemed to prefer areas selected by wolves. It is, however, not clear whether this is due to a lack of avoidance by prey or by the attraction of wolves to areas with high prey densities (Roder et al. 2020). In the same area, Bubnicki et al. (2019), on the other hand, found lower red deer presence and relative densities in areas with high wolf use. The intensity of wolf use did not influence relative densities of other prey species (Bubnicki et al. 2019).

In the Italian Apennines, where wild boar is the main prey of wolves, crop damage was negatively correlated with wolf habitat suitability, suggesting that wild boars avoid the most suitable wolf habitat, leading to a redistribution of crop damage in the landscape (Davoli et al. 2022).

Spatial overlap

A study in the Ligurian Alps found high spatial overlap between the wolf and its main prey (roe deer and wild boar), indicating low spatial avoidance at a large landscape scale (Torretta et al. 2016). The authors document lower spatial overlap of wolves with fallow deer and chamois, which are less preyed upon by wolves, and deduce that wolves select areas of high use by their main prey. Also, no evidence for spatial avoidance of fallow deer and wolves was found in a study conducted in an Italian national park (Esattore et al. 2022). However, they found evidence for other NCE (sections below). The opposite results were found in a study conducted in a national park in southern Italy, which found low spatial overlap of wolves with their main wild prey (wild boar), which might indicate that prey avoids areas of high predation risk (Mori et al. 2020).

Popova et al. (2018) compared the selection of different habitat types between the wolf and its main prey (roe deer and wild boar). They found selection of different habitat types between wolf and roe deer and concluded that the prey avoids the predator (Popova et al. 2018). Such differences in habitat selection can, however, arise through different mechanisms including bottom-up effects, and therefore cannot be directly attributed to predation risk alone.

Habitat selection before and after wolf recolonization

Comparing habitat selection of moose before and after wolf establishment showed some effects of wolf presence: moose reduced their use of bogs after wolf recolonisation, but there was no change in the use of open or closed habitat in general (Sand et al. 2021). Thus, there are indications that the presence of wolves affects the space use of moose but, in general, studies report a lack of behavioural adjustments in response to predator presence in Scandinavia (Sand et al. 2006, Eriksen et al. 2009).

Mouflons *Ovis aries* reduced the distance to refuge areas and used patches with higher values in elevation, slope, and ruggedness since wolves recolonized the study area in the western Italian Alps (Tizzani et al. 2022). Similarly, after wolf recolonisation in Gran Paradiso National Park (Italy), male ibex started to spend less time in forage-rich, flat areas and selected more rocky slopes, which provided a refuge (Grignolio et al. 2019). However, they continued to use areas where wolves could move easily, while feeding in smaller groups. Hence, continuing to utilise higher-quality but riskier feeding sites despite the presence of predators might be compensated for by a reduction in group size (section 'Grouping behaviour').

The mixed evidence for effects of wolf presence on large-scale habitat selection by ungulates in Europe might be related to the fact that the daily home range of ungulates is much smaller than the daily home range of wolves. Thus, prey might avoid encounters with predators by high mobility within their home ranges, which might not be detected by purely spatial analyses of habitat selection. (Pusenius et al. 2020) found that moose in Finland increased their movement speed (distance between two consecutive GPS relocations/time) when predation risk was higher, but no such effect was found in moose in Scandinavia (Wikenros et al. 2016). This indicates that higher mobility may be an anti-predator mechanism not yet developed by moose in Scandinavia, where compared to Finland wolves have returned only recently (Sand et al. 2006).

Migration

We have only found one study investigating migratory behaviour of deer in the Carpathians, which showed that avoiding high winter predation risk might be a driver of downhill migration in red deer (Smolko et al. 2018). However, this study did not demonstrate behavioural shifts in direct response to predator presence by comparing areas or time periods with and without wolves.

In general, we have found inconsistent evidence for effects of wolves on large-scale habitat selection of their prey in Europe. Reported effects were mainly found in protected areas. Thus, anthropogenic factors and bottom-up effects seem to influence habitat selection of large ungulates more strongly than wolf presence.

Fine-scale responses

In cultural landscapes, the home range and habitat selection of ungulates might be constrained by human influences, and

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spatial responses to predator presence might be more evident at fine spatial scales. When predators are present, ungulates may adjust their behaviour near landscape elements that increase perceived predation risk, such as escape impediments or dense vegetation that reduces visibility (Kuijper et al. 2013 2015, van Ginkel et al. 2019a).

Observational studies of responses to fine-scale landscape structures

Kuijper et al. (2015) studied the effect of large pieces of deadwood (hereafter, tree logs) on ungulate behaviour in Białowieża Forest (Poland) and found that red deer avoided such tree logs more inside than outside of wolf core areas (Kuijper et al. 2015). This avoidance led to reduced browsing pressure around the logs and increased chances for tree recruitment (Kuijper et al. 2013, van Ginkel et al. 2019a, Section 'Cascading effects on vegetation').

Responses to experimental cues

van Beek Calkoen et al. (2021) showed that at sites with predator cues (scat and urine), visitation duration (but not visitation rate) by red deer was reduced. This again indicates that deer might increase mobility to avoid predation risk (van Beeck Calkoen et al. 2021). Another study on free-ranging deer in Białowieża, however, found no evidence for decreased visitation rate or duration on sites with wolf scent (scat) but only observed higher vigilance (Kuijper et al. 2014). Accordingly, van Ginkel et al. (2019a) found no effect of the presence of wolf urine on the visitation rate/duration of red deer, both in areas with and without resident wolves (van Ginkel et al. 2019a). These studies, however, also studied other responses than visitation rate/duration, such as vigilance behaviour. Given that there are multiple strategies to avoid predation risk, the responses should not be analysed independently, as –depending on the context – different strategies might be applied (Kuijper et al. 2014).

Strong context-dependence became also evident in a study on prey responses to wolf sound playbacks. While cervids did not lower visitation rates, wild boar showed lower visitation rates with wolf sounds than with sheep sounds, but only in broadleaved forest and over a short time period (Weterings et al. 2022). Also, in Sweden the trapping rate of ungulates (roe deer and fallow deer) and the damage to crops was lower when playback sounds of dogs, wolves, and humans were played (Widén et al. 2022). However, there was no comparison with a control sound.

Temporal avoidance

We found eight studies considering temporal avoidance. In the Pollino National Park in southern Italy, the activity overlap of ungulates and wolves was generally high and, for the main prey, the wild boar, even higher in areas of high wolf occurrence (Mori et al. 2020). In the Maremma National Park in central Italy, however, fallow deer (the main prey of wolves in the region) had lower temporal overlap with wolves at sites where wolf activity was high (Rossa et al. 2021). This effect was, however, only visible in winter and not in summer (Rossa et al. 2021). Both studies were performed in protected areas but showed opposite results for different prey species. Mori et al. (2020) explain their results with wolves trying to maximise activity overlap with their prey, whereas Rossa et al. (2021) argued that fallow deer avoided time periods of high wolf activity. A factor that might affect different temporal overlap could be the different recolonisation history of wolves in both Italian national parks. While wolves have never been extinct in the Pollino National Park, the Maremma National Park was recently recolonised by wolves (Ferretti et al. 2019), which could present another factor affecting the potential for NCE.

In a study in the Italian western Alps, seasonal differences in temporal overlap between wolves and their main prey (roe deer and wild boar) were documented. The activity overlap increased during the non-denning season of wolves compared to the denning season. This increase was significant for roe deer, indicating that roe deer changed their activity patterns to avoid wolves during the wolf denning season (Torretta et al. 2016). However, shifts in the wolves' space use or other factors could have influenced this effect.

In Moldavia and Greece high temporal overlap of wolves and roe deer was found; however, roe deer activity peaked when wolf activity decreased (Popova et al. 2018, Petridou et al. 2023). In a study looking at activity synchronisation between wolves and moose in Norway, moose activity peaked at dusk, whereas the wolves' activity peaked at dawn (Eriksen et al. 2011). Also a study on fallow deer in an Italian national park found different activity patterns of wolves and fallow deer, with fallow deer being mainly active during daylight, whereas wolves were mainly nocturnal (Esattore et al. 2023). However, simply looking at activity overlap cannot inform about the underlying mechanisms and cannot be solely used to conclude about temporal avoidance or to assess the NCE of wolves on their prey.

Other behavioural adaptations

Vigilance

Vigilance behaviour presents a potential trade-off between foraging and risk avoidance. Especially when animals stop foraging to engage in vigilance (Blanchard and Fritz 2007), they spend less time with energy intake. This might affect individual survival and thus population dynamics, but also reduce biomass removal by herbivores and thus affect vegetation growth. Thus, increased vigilance of prey has the potential to induce trophic cascades.

We found seven studies investigating vigilance behaviour in response to wolf cues. Fallow deer in an Italian national park showed more often and longer vigilance behaviour at sites with higher wolf activity (Esattore et al. 2023). Also, red deer in the Polish Białowieża Forest increased their vigilance close to risky places (i.e. tree logs representing small-scale escape impediments). However, this effect was only visible in core areas of wolf territories (Kuijper et al. 2015).

Predator cues, such as the presence of wolf scats, also led to increased vigilance levels in red deer but not in wild boar in Białowieża (Kuijper et al. 2014). In contrast to these results, a study testing the vigilance behaviour in response to

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wolf urine in wolf-free areas in National Park Veluwezoom in the Netherlands, and in areas with wolf presence in the Białowieża National Park, did not find any effect of wolf urine on the vigilance behaviour of red deer (van Ginkel et al. 2019b). The authors argue that the lack of response might be a result of the quality of wolf urine. Also in other experimental studies, wolf scent had no effect on vigilance behaviour (van Beeck Calkoen et al. 2021, van Ginkel et al. 2021). However, the visitation duration and browsing intensity in plots with wolf scent was reduced, indicating that deer might increase mobility to avoid predation risk (section 'Spatiotemporal responses').

The above-mentioned studies documenting effects of wolf presence on deer vigilance were all performed in national parks or enclosures. When comparing protected and non-protected areas in Białowieża, deer showed higher levels of vigilance during the hunting season and at diurnal hours in non-protected areas (Proudman et al. 2020). In contrast, in protected areas, red deer were more vigilant at night, possibly related to higher wolf activity in areas where human disturbances are strongly restricted. These results indicate that wolves' impacts on red deer vigilance behaviour seem to be superimposed by anthropogenic effects in areas with high human disturbance and hunting.

Grouping behaviour

We found four studies investigating grouping behaviour of ungulates in response to wolf predation risk. Red deer and male moose tended to form larger groups in the presence of wolves (Jędrzejewski et al. 1992, Månsson et al. 2017), while group size of male ibex decreased (Grignolio et al. 2019). Moose grouping behaviour generally seemed to be little affected by predator presence, which aligns with results from other studies (Nicholson et al. 2014, Wikenros et al. 2016). Male ibex changed their behaviour in response to wolf recolonisation within a relatively short period of time. However, female ibex and moose with calves did not change their grouping behaviour in response to predation risk (Månsson et al. 2017, Grignolio et al. 2019). This leads to the assumption that their behaviour is either determined by other factors, such as forage quality, or – in the case of moose – that they have lost their antipredator behaviour in the absence of predators. Also, an experimental study in the Netherlands, where prey was naïve to wolves, found no effect of wolf acoustic playbacks on group sizes of wild boar or cervid species (Weterings et al. 2022).

Other factors such as population density, snow depth, and hunting were important predictors of grouping behaviour (Dzięciołowski 1979, Månsson et al. 2017, Grignolio et al. 2019), indicating that grouping in wild ungulates is influenced by a complex set of factors (Creel et al. 2014).

Physiological effects and parasite prevalence

We found six studies related to physiological effects and one study related to parasite prevalence in response to wolf presence. In the French Alps, roe deer fawn body mass was consistently lower in wolf core areas compared to peripheral areas (Randon et al. 2020). The mechanisms of such a difference in body mass in response to wolf presence are unclear. They could be related to increased stress, but also to changes in habitat selection or higher vigilance levels. However, the effect size was relatively small (~ 1 kg) compared to effects of, for example, population density (> 3 kg, Douhard et al. 2013), and the variation was correlated with variation in roe deer abundance in both areas. Thus, this effect had likely been caused by an unmeasured factor (Randon et al. 2020).

In roe deer populations in Poland, Zbyryt et al. (2017) found lower and less variable faecal glucocorticoid metabolite (FGM) concentration in areas with high predator presence (wolf and Eurasian lynx *Lynx lynx*) compared to areas with low predator presence. However, human-related factors had more substantial effects on the stress level of ungulates than effects of predators (Zbyryt et al. 2017). In eastern Poland, roe deer expressed elevated stress levels in areas with wolves present, but the effect of wind farms on stress levels seemed to be more important than the effect of predators (Klich et al. 2020). In contrast, moose in Sweden reacted more strongly to predator presence than to human-related factors: hair cortisol levels decreased with the distance to wolf territories, whereas anthropogenic effects did not affect hair cortisol levels (Spong et al. 2020). In contrast, the blood cortisol level of roe deer captured in wooden box traps was 30% higher in areas with wolves and lynx present compared to a predator-free and human-dominated landscape (Bonnot et al. 2018). These findings are based on blood cortisol, which reflects how roe deer reacted to acute stressors, indicating that differences are rather due to handling than to a general stress level.

Parasite prevalence

Predator presence might also influence parasite prevalence in ungulates. They can lead to healthier ungulate populations, as reduced population size might hinder parasite spread, and infected and old individuals might be removed from the population (Packer et al. 2003). In contrast, the life cycle of some parasites depends on two specific hosts, with ungulates as the intermediate host (e.g. *Sarcocystis* sp.). Infected ungulates might become more vulnerable prey for carnivores, which then serve as the definitive host. Thus, the presence of wolves might be linked to parasite infections in ungulates as they add to the guild of definite hosts. Higher probabilities of *Sarcocystis* sp. infection were found for red deer in areas with wolves present, but not for roe deer or wild boar (Lesniak et al. 2018). For other diseases, however, predation can reduce the prevalence of infection without leading to a reduction in prey population density, because disease-induced mortality can compensate for predation mortality (Tanner et al. 2019).

Cascading effects on vegetation

In central Europe, cascading effects of wolves on lower trophic levels have only been studied extensively in the Polish Białowieża Forest. Studies measuring indirect effects of

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wolves on the vegetation found that, inside wolf core areas, browsing intensity was reduced near structures that might impede escape or hinder visibility (i.e. coarse woody debris or fallen tree logs (Kuijper et al. 2013, van Ginkel et al. 2019a), resulting in a higher percentage of trees growing out of reach of browsing ungulates. The effect of fine-scale habitat structures was much more robust in high-risk areas for prey inside of wolf territories than in low-risk areas outside of wolf core areas (Kuijper et al. 2013, van Ginkel et al. 2019a). These studies were performed in the most undisturbed parts of the Białowieża Forest, i.e. in the national park that excludes hunting and forestry activities. A recent experimental study outside the Białowieża National Park, in an adjacent area where hunting and forestry occur, illustrated that visual obstructions (similar to tree logs) strongly reduced deer browsing pressure and led to increased tree growth (van Ginkel et al. 2021), indicating that similar risk effects can also occur in a more human-disturbed environment.

Also at the landscape scale, changes in patterns of space use by red deer caused by wolf presence led to a measurable reduction of browsing intensity and changes in the relative recruitment of different tree species inside and outside the Białowieża National Park (Bubnicki et al. 2019). Consequently, tree species that were most vulnerable to deer browsing had a higher chance of recruitment in places with frequent wolf presence (Bubnicki et al. 2019) or, at a smaller scale, in places hindering deer browsing due to (visual) impediments (van Ginkel et al. 2021).

Wolf presence can also affect forage selection, potentially leading to shifts in the plant community. Red deer foraged more on broadleaved tree species and less on forbs in high-risk than in low-risk areas (Churski et al. 2021). This effect, however, was only present in the national park and not in the managed forest.

In an area more recently recolonized by wolves in Switzerland, a pilot study on the local tree regeneration showed that ungulate densities, as indicated by local ungulate harvest, and the percentage of saplings with browsed leader shoot, decreased in the wolves' summer core zone (Kupferschmid 2017). Due to the pilot character of the study, data were lacking to evaluate if this might have been related to indirect effects of wolf presence, i.e. shifts in ungulates' spatio-temporal, social, or foraging behaviour, or other potential factors such as changes in hunting effort. An experimental study on captive red deer in the Bavarian Forest, Germany, did not document a shift in selectivity for certain tree species in proximity to simulated wolf cues. However, visitation duration and browsing intensity decreased in the presence of wolf scent, which might impact plant growth rates and thus affect forest ecosystems in the long term (van Beeck Calkoen et al. 2021).

Results from moose, the main prey of wolves in Sweden, show a different pattern than observed in red deer in other parts of Europe. The probability of moose browsing was higher inside wolf territories compared to outside of wolf territories (Gicquel et al. 2020, Ausilio et al. 2021), which seems related to higher moose abundance inside wolf territories (Ausilio et al. 2021). Also, van Beeck Calkoen et al. (2018) found higher browsing damage in high-wolf–utilisation areas. The authors related their findings to a confounding effect, as these areas were characterised by lower productivity (because of higher elevation) that led to reduced tree density and height, which are associated with an increase in moose browsing intensity (van Beeck Calkoen et al. 2018). They also related their finding to anthropogenic effects, as high-wolf–utilisation areas are characterised by a lower human influence index and situated at higher elevations than low-wolf–utilisation areas. Thus, human activities could push wolves into less productive parts of the landscape with lower overall tree densities and higher moose browsing levels (caused by bottom–up processes). These findings illustrate that simply comparing areas with and without wolves might lead to erroneous conclusions when no other (human-related) confounding factors are considered.

Not only human settlements, but also roads present key features of anthropogenic impacts. Inside wolf territories, however, browsing of rowan *Sorbus aucuparia*, the tree species most preferred by moose, decreased close to secondary roads, while increasing close to secondary roads outside wolf territories (Loosen et al. 2021). The roadsides thus appear to be perceived as riskier by moose in the presence of predators.

Discussion

Complexity and context-dependence of non-consumptive effects

We found inconsistent evidence for NCE of wolves on their large ungulate prey in Europe, highlighting the context-dependence of NCE. There is evidence that, under certain conditions, wolves can affect patterns of space use and behaviour of their prey, which in turn can affect the vegetation (Kuijper et al. 2013, 2015, Bubnicki et al. 2019, van Ginkel et al. 2019a). Less intense use of risky feeding areas has the potential to create a fine-scale mosaic of patches with lower grazing/browsing pressure and thus promote a more heterogeneous landscape (sections 'Fine-scale responses' and 'cascading effects'). These effects have been found mainly at a small spatial scale (landscape-scale patterns in Bubnicki et al. 2019) and in relatively undisturbed systems (i.e. no hunting/forestry), suggesting that NCE are easily overruled by human-related factors. Thus, humans can influence and alter predator–prey relationships, limiting the potential ecological role of predators (Ciucci et al. 2020). Most evidence for NCE in Europe comes from the Białowieża Forest, and there are indications that NCE can lead to measurable cascading effects. However, outside of non-disturbed areas, anthropogenic effects might quickly overrule these effects of natural predators.

In addition to anthropogenic impacts, further factors lead to context-dependence of NCE. Species – or even sexes, age classes, or individuals in different states – might vary in their sensitivity to risk effects from either human or non-human predators. While red deer, roe deer, and fallow deer showed changes in their behaviour in response to predator presence under certain conditions, other species such as wild boar or

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moose seemed less sensitive to predator presence (Fig. 3). Moose and wild boar might have higher changes of surviving an encounter with wolves, so there might be less selective pressure to avoid such encounters. For smaller prey, mortality after an encounter might be much higher and, thus, they might have been selected to have increased avoidance behaviour. Different species (or even individuals) might adopt different strategies, and some might specialise in avoidance of risky places while others specialise in early detection (e.g. through vigilance or grouping) or other defence mechanisms (Makin et al. 2017, Gaynor et al. 2019).

Quantifying the risk landscape and human influences

To document effects of predation risk on prey behaviour, we need to quantify the risk landscape. The presented studies used different methods to measure predation risk by wolves, but it is questionable if these measures are equivalent to the landscape of fear perceived by the prey (Moll et al. 2017, Prugh et al. 2019). For example, habitat suitability of predators is often used to predict predation risk, but might not be a good predictor for the landscape of fear. Thus, there might be a mismatch between what we measure and what is perceived by prey.

Not only quantifying the risk landscape, but also quantifying human impact is challenging. Human impact can vary with, for example, human density, infrastructure, the level of hunting, forestry, and recreational activity and each of those variants of human impact might affect wildlife differently. Many studies included here did not estimate human impact in the study region, thus making comparing different studies considerably challenging.

The majority of European studies investigating wolves' effects on herbivore behaviour were conducted in national parks, where human impact is assumed to be weaker than in non-protected areas. However, European national parks are subject to relatively high human impact (especially compared to the large national parks in North America), and truly undisturbed areas are rare (van Beeck Calkoen et al. 2020). In human-dominated landscapes, the effects of humans on wildlife behaviour can exceed those of natural predators (Theuerkauf and Rouys 2008, Ciuti et al. 2012) and human risk factors can interact with predator-induced risk factors (Proffitt et al. 2009, Rogala et al. 2011, Kuijper et al. 2015). Human activities can directly affect the behaviour and spatial distribution of ungulates (Benhaiem et al. 2008, Rogala et al. 2011) or indirectly by affecting predator distribution (Theuerkauf et al. 2003, Theuerkauf and Rouys 2008, Rogala et al. 2011). Thus, we must be very careful when interpreting study results on NCE of wolves in the presence of anthropogenic effects without the recognition of potential indirect effects of human–carnivore–prey interactions. It is challenging to interpret the effects of predators isolated from anthropogenic effects, since they generally coexist in Europe. Thus, there is a need for studies in more human-dominated landscapes, which allow us to study the interacting effects of humans and natural predators.

Additionally, the correlation of human activity with wolf presence makes it very difficult to disentangle wolf-induced effects and human-induced effects, emphasizing the need to consider indirect effects of humans on carnivore behaviour. While the presence of wolves may not have a significant impact on forest vegetation in human-dominated areas, it can have effects in undisturbed forest systems.

Spatial scales and constraints

Most studies we found here indicate that risk factors for ungulate prey act at different spatial scales – impediments acting as a risk factor at a fine scale and carnivore distribution

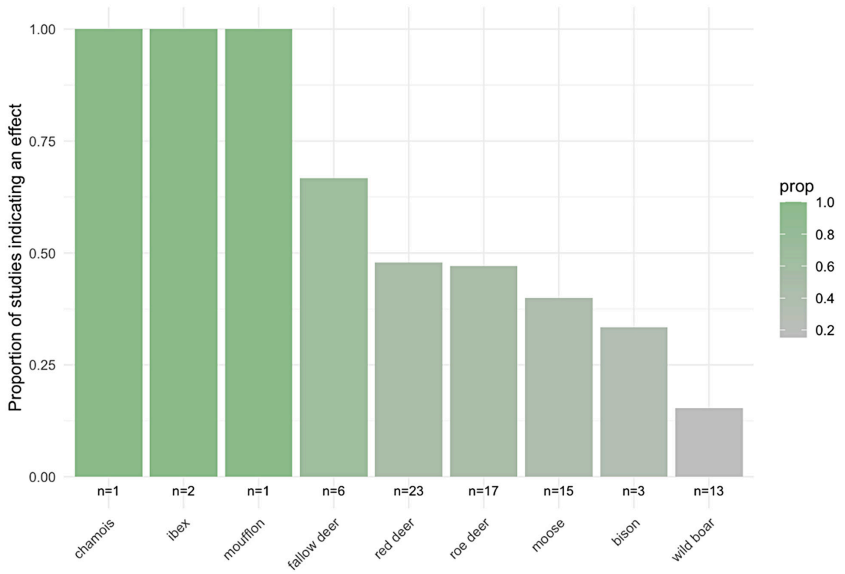


Figure 3. Proportion of observations indicating non-consumptive effects (NCE) and number of observations per prey species.

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shaping the perceived risk at the landscape scale. Most importantly, these factors interact and shape the functional role of large carnivores in ecosystem processes. We thus would expect NCE to mainly appear in response to small-scale risk factors when combined with the presence of wolves at larger scales. In many cases, large-scale habitat selection of ungulates seems to be strongly affected by anthropogenic factors, such as hunting or forest exploitation, whereas predation risk by wolves seems to have relatively minor effects. To understand how large carnivores indirectly affect the vegetation in ecosystems, it is crucial to consider interactive effects between fine- and landscape-scale risk factors, as we might see effects only under certain conditions (Wirsing et al. 2021).

In addition, spatial constraints (e.g. through anthropogenic structures) might prevent the occurrence of large-scale changes, so that even though prey might perceive predation risk from returning predators, it may not be able to react to it (Gaynor et al. 2019). Prey species in the human-dominated landscape of Europe live in a complex environment with multiple (human and non-human) predators and competitors, and further anthropogenic stressors (Lone et al. 2014). Thus, an important question is how much potential the prey has left to adapt their habitat selection to a new risk factor such as the wolf. In Europe, for example, suitable wildlife habitat areas are often small and homogenised due to intense forestry. Large herbivores are mainly present in forest-dominated landscapes, while most of the open landscape is used for agricultural production. Anthropogenic factors thus limit the potential for large-scale behavioural changes, as a heterogeneous landscape of fear (i.e. including low-risk regions) is crucial for NCE to be detectable (Cromsigt et al. 2013). Within the constraints on large-scale space use, prey might avoid predation by high mobility or a more heterogeneous habitat use. Such subtle changes can be hard to detect with the methods used in most studies. But also increased mobility or more heterogeneous habitat use could have consequences for browsing and grazing pressure, seed dispersal, nutrient fluxes, and transmission of parasites or diseases (Winnie et al. 2006), and lead to cascading effects at the larger scale. This has, however, not been directly demonstrated in Europe yet, although there are hints towards higher prey mobility (Pusenius et al. 2020, van Beeck Calkoen et al. 2021) and large-scale effects on browsing patterns in the presence of wolves (Bubnicki et al. 2019). Generally, in human-dominated landscapes, prey species might prioritise adaptation to the risk landscape imposed by humans, which could weaken responses to other risk landscapes (e.g. from large carnivores).

Studies investigating temporal and spatial overlap generally found mixed results (Fig. 4, Popova et al. 2018, Mori et al. 2020; except for Esattore et al. 2023). In general, we need to be careful with the interpretation of causal relationships of spatial and temporal overlap, especially if there are no data from reference areas/time periods. Additionally, activity patterns of herbivores are already strongly adapted to the presence of humans, and there might be few opportunities left for avoiding the activity periods of carnivores. How complex and dynamic NCE can turn out to be is illustrated by the fact that herbivores might even increase their space use close to human settlements to reduce wolf predation risk (Kuijper et al. 2015, Proudman et al. 2020), while temporarily avoiding humans during the day.

Limitations and methodological challenges

Unfortunately, we were not able to quantitatively analyse factors leading to the documentation of NCE. We only found a limited number of studies per section/species. Even more challenging was that different studies within a section applied different methods, complicating a quantitative analysis. Ideally, we would have been able to test indications of human disturbance on the documentation of NCE. This was, however, not possible, as for most of the studies we were not able to extract information on human activities. Even a comparison of studies within national parks with studies outside of national parks is debatable, as human disturbance has multiple dimensions (hunting, forestry, recreational activities), which can strongly vary in national parks (van Beeck Calkoen et al. 2020).

Another factor hampering quantitative analysis is the multidimensionality of prey response. Prey can use different strategies for dealing with increased predation risk. In this review, we presented the results on different NCE in separate sections (similar to most of the papers reported). However, NCE in one section cannot be separated from effects in another section. For example, spatial and temporal avoidance cannot be isolated from each other or other behavioural adaptations (i.e. grouping or vigilance). All these effects can interact, and one mechanism can compensate for another (Torretta et al. 2016, Grignolio et al. 2019). For example, risky places can be used at safe times, indicating that the landscape of fear is dynamic over time (Kohl et al. 2018). Additionally, NCE might be dependent on the season. For example, in winter, prey might have to accept higher predation risk as they cannot afford to trade lower predation risk with lower energy intake. Furthermore, there are multiple strategies to solve the same dilemma. Some individuals/populations/species might apply alternative strategies and, while some prey might increase their vigilance while using risky places, others might rather avoid such places while keeping their vigilance behaviour constant. Given that there might be individual variation in these strategies, effects can stay undetected depending on the scale we are looking at.

Studies investigating temporal avoidance mostly measured temporal overlap. Even though there are indications for temporal avoidance of wolves by prey, it is challenging to show causal relationships from activity overlap data, and we advocate interpreting these results carefully when no reference area is available or when no comparative data exist from times when wolves were not present in the study area. Furthermore, it needs to be clarified whether prey are adapting their activity patterns to avoid predation, or wolves are adapting their activity to increase hunting success, or both. Additionally, the potential for adaptations in activity patterns might be overruled by human influence, which is known to

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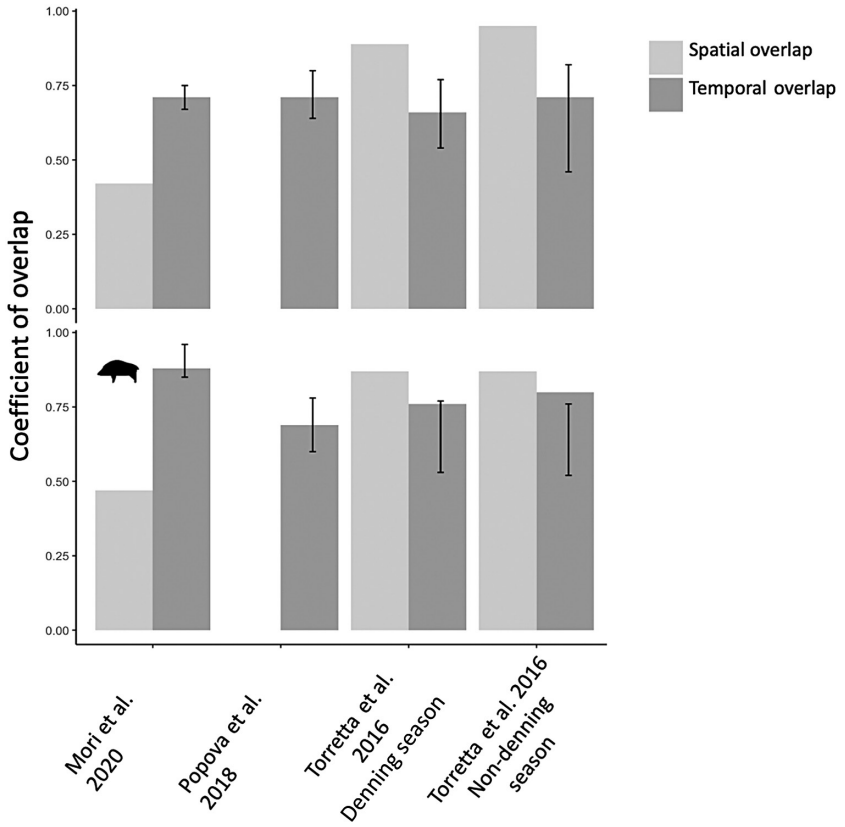


Figure 4. Spatial and temporal overlap coefficients with wolves provided by the respective studies for roe deer (upper panel) and wild boar (lower panel). Error bars show standard errors for temporal overlap (as reported in the studies), but no measure of uncertainty is provided for spatial overlap; in Torretta et al. 2016 the uncertainty measures were not clearly reported and are thus not provided here. The studies provided two different estimates for spatial overlap (UDOI in Torretta et al. 2016, Pika index in Mori et al. 2020), but both are bound between 0 and 1, with 1 indicating high overlap and 0 low spatial overlap. Popova et al. (2018) did not provide an estimate of spatial overlap.

be an important driver of temporal activity patterns in ungulates and carnivores (Stankowich 2008, van Doormaal et al. 2015). Moreover, temporal avoidance might reduce spatial effects, as prey might use risky places at safe times (Kohl et al. 2018). Thus, temporal responses should not be considered isolated from spatial patterns.

Effects of predators on the vegetation have so far only been studied in forest systems (except for Davoli et al. 2022) and the extent of cascading effects in vegetation types other than forests, such as shrub or open grassland, remains unclear. Such open areas in Europe are typically occupied by humans, and low-disturbance open areas are much rarer than undisturbed forested areas, so that the potential for observing cascading effects of wolves in vegetation types other than forest seems limited.

We are aware that there might be a publication bias and that more results that find NCE might be published compared to studies that found no effect. Further, we have missed grey literature and literature that was not published in English. We found some reports investigating NCE in Germany and Switzerland (Gärtner and Noack 2009, Nitze 2012, Kupferschmid et al. 2018a, b), but excluded them from the systematic review as they were not published in English, and we are not able to include grey literature in other languages.

Future research and methodological advancements

Future research on NCE in Europe should try to quantify human impact in the studies to allow for a synthesis from multiple regions with varying predator presence as well as varying human impact on different levels (tourism, forestry, hunting). Further, different strategies to lower predation risk should be considered in the same study, and factors should not be looked at in isolation. Considering vigilance and grouping behaviour, as well as spatial and temporal dynamics, together and not separately in future studies would allow a more integrated understanding of wolf NCE, in line with the landscape of fear as a dynamic concept (Palmer et al. 2022).

Not only large herbivores, but also other trophic levels such as scavengers, can be affected by apex predators through competition (Wikenros et al. 2010, 2017, Krofel et al. 2017), facilitation (Selva and Fortuna 2007, van Dijk et al. 2008, Wikenros et al. 2013, Focardi et al. 2017, Rossa et al. 2021), or hybridisation (Moura et al. 2014). Such effects in turn can have indirect effects on the herbivore community. In this review, however, we have not considered effects of wolves on scavengers, mesopredator, or other apex predators, or potential combined effects of several apex predators in more complex food webs, because the majority of studies only

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considered one predator species. In future studies, however, we need to account for multiple predators when investigating ungulate responses to predation risk (Moll et al. 2017). Moreover, we have not taken into account the complexity of the prey guild, which might influence the potential for behaviourally mediated effects since, in ecosystems with high complexity, redundancy effects might mask trophic cascades through compensation by other species (Fahimipour et al. 2017). In addition, cascading effects through non-ungulate prey should be explored. In particular, beavers are commonly preyed upon by wolves where the species overlap and can have strong effects on the ecosystem (Gable et al. 2018).

Advances in technology will allow for higher-resolution data collection. We have documented very few studies using GPS telemetry for the assessment of space use of wolves and their prey. This technology can provide essential insights by providing data for the whole home range of the collared individuals, but is limited to the collared individuals. Thus, combining multiple approaches, e.g. GPS-telemetry and camera traps, can be very powerful. However, with new possibilities for data collection and the combination of multiple approaches, it will become increasingly essential to have common standards that allow for comparing different studies and synthesising the knowledge generated in different regions and under different environmental conditions (Moll et al. 2017, Prugh et al. 2019).

Conclusions and implications

Our review shows that wolves recolonizing Europe rarely led to critical changes in the ecosystems (Table 1), so that exaggerating or romanticising their role in ecosystem functioning does not seem appropriate (Mech 2012). However, in addition to changing the population dynamics and/or the behaviour of prey, wolves might have other effects on the ecosystem, such as controlling the spread of infectious diseases in prey populations (Packer et al. 2003) or providing carcasses for the scavenger community (Wikenros et al. 2013). Here we documented a strong context-dependence of NCE on prey behaviour and stronger effects in areas with relatively low human impact. In Europe, such areas are extremely rare as, in more than two thirds of the national parks, wildlife is regulated and less than 30% of the national parks have a non-intervention zone of at least 75% of the area (van Beeck Calkoen et al. 2020).

If we aim to restore the complexity of ecosystems and ecosystem processes, we should think about creating more landscapes with a lower human impact and therefore a higher potential for these carnivore-induced impacts to occur. In the human-dominated landscape of Europe, this is, however, currently not the most realistic scenario. Regarding a land-sharing view, we need more knowledge on the effects of carnivores on the ecosystem with a focus on the influence of human activities on predator–prey relationships and resulting cascading effects.

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Nina Gerber: Conceptualization (lead); Writing – original draft (lead); Data collection (equal); Writing – review sections (lead); Writing – general sections (lead); Interpretation and structural editing (equal). **Friederike Riesch**: Conceptualization (equal); Writing – original draft (lead); Data collection (equal); Writing – review sections (lead); Writing – general sections (equal); Interpretation and structural editing (lead). **Katarzyna Bojarska**: Interpretation and structural editing (lead). **Maria Zetsche**: Conceptualization (supporting); Writing – original draft (supporting); Data collection (equal); Writing – review sections (equal). **Nina-K. Rohwer**: Writing – original draft (supporting); Data collection (equal); Writing – review sections (supporting). **Johannes Signer**: Conceptualization (supporting); Interpretation and structural editing (equal). **Johannes Isselstein**: Conceptualization (supporting); Interpretation and structural editing (equal). **Sven Herzog**: Conceptualization (supporting); Interpretation and structural editing (equal). **Henryk Okarma**: Conceptualization (supporting); Interpretation and structural editing (equal). **Dries P. J. Kuijper**: Conceptualization (supporting); Interpretation and structural editing (equal). **Niko Balkenhol**: Conceptualization (lead); Writing – original draft (supporting); Writing – general sections (supporting); Interpretation and structural editing (lead).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

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