

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

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Abstract

Predators can affect ecosystems through non-consumptive effects 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 and are highly context-dependent and might often be overruled by human-related factors. Further, 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. Further, we emphasise the need for wildlife management to restore ecosystem complexity and processes, to allow non-consumptive predator effects to occur.

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37
38 **Keywords:** wolf (*Canis lupus*), ungulate prey, non-consumptive effects, risk effects/ predation risk, human-
39 dominated landscape, trophic cascades, behavioural responses (to predation)

40

41 1. Introduction

42 Large mammalian herbivores are crucial in structuring terrestrial ecosystems (Gordon, Hester, &
43 Festa-Bianchet, 2004; Schmitz, 2008). They affect vegetation structure by foraging and trampling
44 (Kuijper *et al.*, 2010; Hempson *et al.*, 2015; Churski *et al.*, 2017), by influencing nutrient cycling
45 (Murray *et al.* 2013) and diaspore translocation (Iravani *et al.*, 2011; Jaroszewicz, Pirożnikow, &
46 Sondej, 2013). In this way, herbivores can influence vegetation across multiple spatial scales,
47 from local to landscape levels (Woodward, Lomas, & Kelly, 2004; Moncrieff, Bond, & Higgins,
48 2016), resulting in cascading impacts on numerous species and processes (Ripple *et al.*, 2014).

49
50 Herbivore communities themselves are influenced by bottom-up effects (e.g. food availability)
51 and top-down effects (i.e. predation). Thus, by affecting prey communities, predators can exert
52 indirect effects on the vegetation. Different mechanisms can induce these ecological effects of
53 large carnivores on their prey. Historically, studies on predator-prey interactions mainly focused
54 on consumptive effects, where predators affect population densities by killing their prey
55 (Messier, 1991; Ripple & Beschta, 2012). In addition to such “lethal” or “consumptive” effects on
56 the population dynamics of prey, the presence of predators can also induce antipredator
57 responses in behaviour or physiology (Lima & Dill, 1990; Boonstra *et al.*, 1998). Such behavioural
58 or physiological changes in response to predator presence are referred to as “non-consumptive
59 effects” (hereafter NCE).

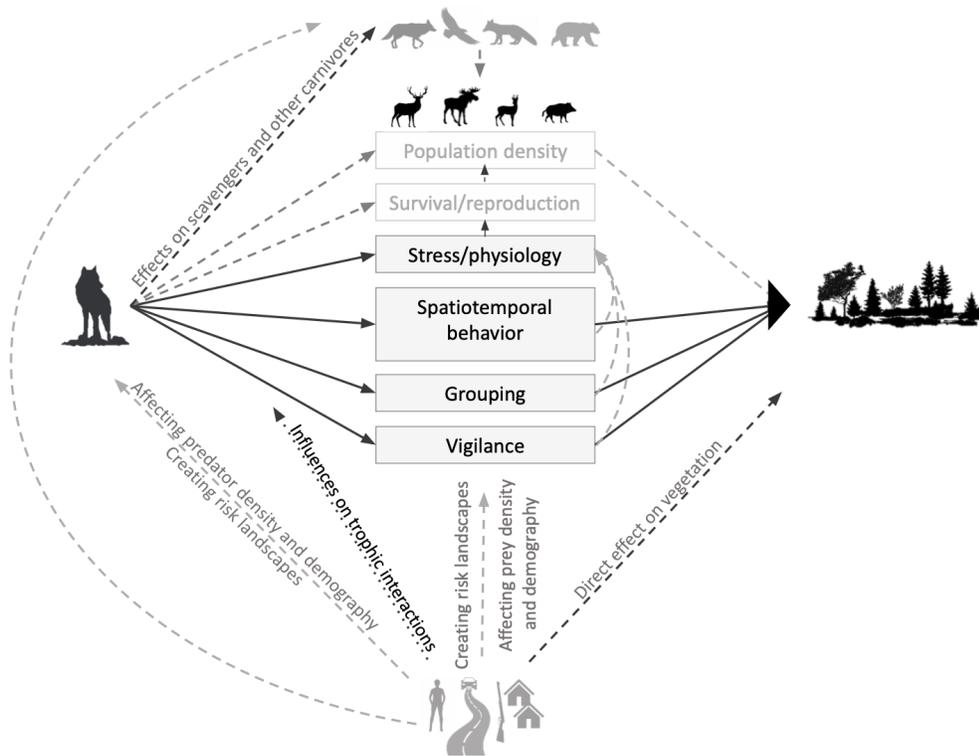
60
61 The importance of NCE of predators has often been documented in invertebrates, especially in
62 aquatic systems, where NCE can be much stronger than consumptive effects (e.g. Preisser *et al.*,

63 2005). The body of literature on predator NCE in terrestrial vertebrate communities is growing.
64 Especially with the recovery of large carnivores (Ripple *et al.*, 2014; Chapron *et al.*, 2014), the
65 interest in NCE and potential trophic cascades has increased (Say-Sallaz *et al.*, 2019). Large
66 carnivores have the potential to create trophic cascading (see Ripple *et al.*, 2014). However, the
67 extent and relative contribution of NCE compared to direct lethal effects is still debated (Creel &
68 Christianson, 2008; White *et al.*, 2008; Kauffman, Brodie, & Jules, 2010; Marshall, Hobbs, &
69 Cooper, 2013; Middleton *et al.*, 2013; Peterson *et al.*, 2014). The main body of literature on NCE
70 in terrestrial vertebrates originates from large protected areas (Kuijper *et al.*, 2016). Case studies
71 from Yellowstone National Park (USA) showed how prey species changed their behaviour when
72 predation risk was modified by the reintroduction of wolves (*Canis lupus*) (Fortin *et al.*, 2005;
73 Creel & Christianson, 2008, but see Kauffman *et al.*, 2010). In response to returning predators,
74 prey animals have been shown to change vigilance, grouping behaviour, space use or habitat
75 selection (e.g., Fortin *et al.*, 2005; Winnie & Creel, 2007; Thaker *et al.*, 2011; Clinchy, Sheriff, &
76 Zanette, 2013). Such changes in prey behaviour were documented to affect the ecosystem
77 through modified feeding pressure on certain plant communities (e.g., Fortin *et al.*, 2005) or
78 nutrient cycling (e.g., Roux, Kerley, & Cromsigt, 2018). Similar effects caused by the return of an
79 apex predator have been reported in the Serengeti National Park, where the lion (*Panthera leo*)
80 was reintroduced (Skinner & Hunter, 1998) or in the Yosemite National Park after the
81 recolonisation of the cougar (*Puma concolor*) (Ripple & Beschta, 2008). However, surprisingly
82 little is known about NCE in human-dominated landscapes, which we here define as a landscape
83 that is substantially shaped by humans and is extensively used for a variety of human activities,
84 including hunting, agriculture, forestry, urbanization and industrial purposes. Compared to
85 national parks or wilderness areas, large parts of human-dominated landscapes are not protected
86 for biodiversity conservation, and they are characterized by the presence of human-made (infra-
87)structures resulting in high degrees of fragmentation. In such landscapes, human impact can still
88 vary strongly with, for example, human population density, infrastructure, habitat modifications
89 and the level of human disturbance (recreational activity, hunting or forestry). Additionally, the
90 degree of human activities even varies strongly between national parks (van Beeck Calkoen *et al.*
91 2022).

92 Europe (especially central Europe) consists largely of such human-dominated landscapes shared
93 between humans and wildlife, where human impact influences animal populations, behaviour
94 and trophic interactions. Understanding how large carnivores can affect the ecosystem in such
95 human-dominated landscapes is essential for a low-conflict coexistence of humans and large
96 carnivores.

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

106



107
108

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

113

114 A key question is whether, under such conditions, wolves can still create ecological impacts as
 115 documented in large national parks. Kuijper et al. (2016) reviewed how anthropogenic effects on
 116 large carnivore density or behaviour can alter their ecological function, and how human-induced
 117 changes in prey species and the landscape limit the impact of large carnivores. They concluded
 118 that the potential for density-mediated trophic cascades (mainly caused by consumptive effects)
 119 is restricted to areas where carnivores reach ecologically functional densities or where even low
 120 carnivore densities can impact prey densities, i.e. in rather unproductive areas (Kuijper et al.,
 121 2016). NCE, however, might have a higher potential for cascading through trophic levels than
 122 direct effects, since predators have been documented to affect prey behaviour even at low
 123 densities (Laundré, Hernández, & Altendorf, 2001). Say-Sallaz (2019) reviewed the empirical
 124 literature on NCE from large carnivore-ungulate systems worldwide and revealed a bias of studies
 125 on NCE from protected areas and with a focus on anti-predator behavioural responses. Here, we
 126 specifically focus on the NCE of wolves in Europe, including their indirect effects on the
 127 vegetation. This allows us to investigate the wolf-prey-vegetation interactions more specifically
 128 and synthesise ecosystem effects of wolves documented in Europe.

129

2. 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*”), “*Canis lupus*”, “ungulate prey” and “Europe” (or any European country) connected with the Boolean connector AND (see SI for a detailed list of searched keywords). We identified 234 studies (as of September 26th 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 (see SI for details). 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 (see Table S1).

We classified NCE of wolves on their ungulate prey into the following categories (see Table 1, Figure 1): i) landscape-scale spatial behaviour, ii) fine-scale spatial behaviour, iii) activity patterns, iv) vigilance behaviour, v) grouping behaviour, vi) physiological effects, and vii) 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 (see 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.

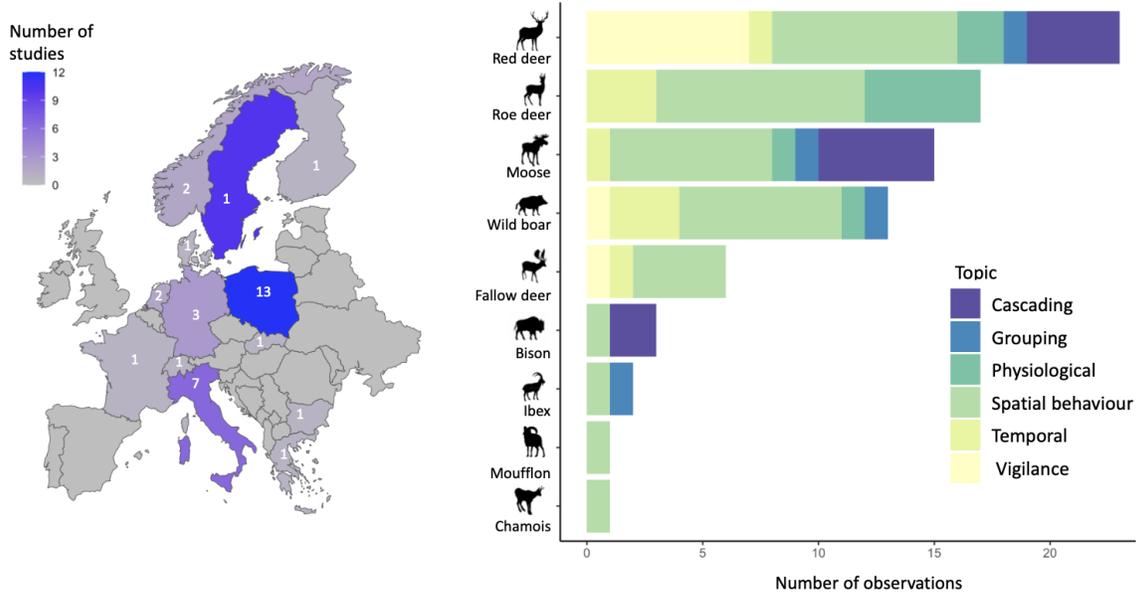
3. Where and how is our knowledge generated?

3.1 Spatial distribution and focal prey species of studies

A large amount of the studies we found were performed in Białowieża Primaeval Forest in Poland (13/41, 31.7%) and Sweden (11/41, 26.8%) (Figure 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*

168 *elaphus*) with 23 observations in 14 studies, followed by roe deer (*Capreolus capreolus*) with 17
 169 observations in 13 studies, and moose (*Alces alces*) with 15 observations in 12 studies, and wild
 170 boar (*Sus scrofa*) with 12 observations in nine studies. In Europe, the most widely distributed and
 171 most abundant prey species for wolves are red deer, roe deer and wild boar (Okarma, 1995;
 172 Zlatanova *et al.*, 2014). Thus, most studies on NCE of wolves at the European level have been
 173 performed on the most abundant prey species, except for an overrepresentation of moose (at
 174 the European scale).
 175



176 **Figure 2** Number of studies on non-consumptive effects of wolves per country in Europe (left, n=41) and number of
 177 observations (each investigated combination of effect, species and region in a study) per species and category (right,
 178 n=89). The observations were classified according to the prey species in focus.
 179
 180

181 3.2 Methodologies and predation risk assessment

182
 183 The reviewed studies include a variety of measurements for predation risk, such as presence-
 184 absence of wolves in space (e.g. (Bonnot *et al.*, 2018; van Ginkel *et al.*, 2019a) or time (e.g.
 185 (Grignolio *et al.*, 2019), predicted occurrence (based on habitat use, e.g. (Bubnicki *et al.*, 2019) or
 186 gradients in intensity of use by wolves, e.g. core areas of wolf territories vs peripheral areas (e.g.
 187 (Kuijper *et al.*, 2013). Other studies used experimental cues to simulate predation risk (e.g.
 188 (Kuijper *et al.*, 2014). Also for prey responses, different measurements have been used. Especially
 189 for spatial behaviour, a variety of methods and different predictors have been employed, ranging
 190 from simply assessing spatial overlap of wolves and their prey based on indirect signs (e.g.
 191 (Popova *et al.*, 2018) to predicting spatial distributions based on modelled camera trap data
 192 (Bubnicki *et al.*, 2019).
 193

194 Besides using different measurements to estimate wolf predation risk and prey responses,
195 different methods have been used to monitor wolf and prey distributions and behaviours (VHF
196 or GPS telemetry, camera traps, indirect signs). GPS information was only used in a few studies
197 to investigate prey behaviour in response to predator presence (Eriksen *et al.*, 2009, 2011,
198 Nicholson *et al.* 2014), even though GPS tracking is probably the most common method for
199 investigating wolf spatial behaviour. To study the fine-scale response of prey to wolf presence,
200 camera traps and indirect signs of presence (mainly pellet counts) have been used more widely.
201 Altogether, we document high methodological variation in the measurement of wolf predation
202 risk as well as prey responses (Table S1). This heterogeneity resulting in a lack of standardisation
203 impedes quantitative analyses and drawing general conclusions from the studies (see also (Moll
204 *et al.*, 2017; Prugh *et al.*, 2019).
205

206 **3.3 Assessment of human effects**

207 Anthropogenic activities might influence behaviourally mediated effects created by wolves (e.g.
208 Kuijper *et al.*, 2016). Therefore, assessing the strength of anthropogenic effects is important to
209 evaluate the potential for cascading effects of predators in the human-dominated landscape.
210 However, studies included in this review often lack a thorough description of the type and
211 strength of anthropogenic effects or human disturbance. Almost half of the studies (46.3%) and
212 more than half of the observations (56.1%) were performed in protected areas, where hunting,
213 forestry and agricultural land use were at least partially restricted. To what extent these activities
214 are restricted varies and is not reported in most of the studies.
215

216 Multiple studies in our set use the distance to human settlements as a proxy for wolf abundance
217 (e.g. (Kuijper *et al.*, 2015; Proudman *et al.*, 2020). However, less than half of the studies (42.8%)
218 mentioned human effects either on the prey/wolf habitat selection or on the interaction of
219 effects of wolf and humans on prey (e.g. (Theuerkauf & Rouys, 2008).

220 Studies on habitat selection of prey species often include variables related to the intensity of
221 human land use (e.g. forest exploitation, hunting; e.g. (Theuerkauf & Rouys, 2008). These studies,
222 however, mostly do not consider any interactions between anthropogenic effects and effects of
223 wolf presence on prey behaviour. Thus, they do not consider whether wolf-prey interactions
224 change in regions with high vs. low human activity. When measures of human activity were
225 included, by e.g. comparing the vigilance behaviour in the Białowieża National Park (Kuijper *et al.*
226 *et al.*, 2015) and in the adjacent state forest, where hunting and forestry activities occur, effects of
227 predators on prey behaviour seem to be overruled by anthropogenic effects (Proudman *et al.*,
228 2020).

229 **4. Which non-consumptive effects by wolves are** 230 **documented in Europe?**

231 **4.1 Spatio-temporal responses**

232 Spatio-temporal responses to predation risk can occur at different spatial scales: at the large
233 scale, prey might adapt their large-scale habitat use and home range selection, while at a smaller
234 scale they might avoid small-scale risk factors, such as escape impediments.
235

236 **4.1.1 Large-scale spatial responses**

237 *Habitat selection based on wolf habitat use / suitability*

238 At large spatial scales, studies generally found that human influence, vegetation structure and
239 prey-related variables, such as sex and reproductive status, are more important for explaining
240 habitat selection by large ungulates than the presence of wolves (Theuerkauf & Rouys, 2008;
241 Nicholson *et al.*, 2014). An exception is the study of Bubnicki *et al.* (2019), who showed that
242 patterns of landscape use by red deer were predominantly determined by patterns in wolf space
243 use in the Białowieża forest. Which environmental variables are important varies between
244 ungulate species (Theuerkauf & Rouys, 2008; Bubnicki *et al.*, 2019). Theuerkauf and Rouys (2008)
245 did not find evidence for a general impact of wolf presence on large-scale ungulate distribution.
246 They concluded that anthropogenic impacts affect local intensity of use by prey stronger than
247 predation risk by wolves. Red deer seemed to prefer areas selected by wolves. It is, however, not
248 clear whether this is due to a lack of avoidance by prey or by the attraction of wolves to areas
249 with high prey densities. (Roder *et al.*, 2020). In the same area, Bubnicki *et al.* (2019), on the other
250 hand, found lower red deer presence and relative densities in areas with high wolf use. The
251 intensity of wolf use did not influence relative densities of other prey species (Bubnicki *et al.*,
252 2019).

253
254 In the Italian Apennines, where wild boar is the main prey of wolves, crop damages were
255 negatively correlated with wolf habitat suitability, suggesting wild boars to avoid the most
256 suitable wolf habitat, leading to a redistribution of crop damage in the landscape (Davoli *et al.*
257 2022).

258 259 *Spatial overlap*

260 A study in the Ligurian Alps found high spatial overlap between the wolf and its main prey (roe
261 deer and wild boar), indicating low spatial avoidance at a large landscape scale (Torretta *et al.*,
262 2017). The authors document lower spatial overlap of wolves with fallow deer and chamois,
263 which are less preyed upon by wolves, and deduce that wolves select areas of high use by their
264 main prey. No evidence for spatial avoidance of fallow deer and wolves was found in a study
265 conducted in an Italian National Park (Esattore *et al.* 2022). However, they documented other
266 NCE (see sections below). Opposite results were found in a study conducted in a National Park in

267 southern Italy, which found low spatial overlap of wolves with their main wild prey (wild boar),
268 which might indicate that prey avoids areas of high predation risk (Mori *et al.*, 2020).

269
270 Popova *et al.* (2018) compared the selection of different habitat types between wolf and its main
271 prey (roe deer and wild boar). They found selection of different habitat types between wolf and
272 roe deer and concluded that the prey avoids the predator (Popova *et al.*, 2018). Such differences
273 in habitat selection can, however, arise through different mechanisms including bottom up
274 effects and therefore we think that it can not directly be attributed to predation risk.

275
276 *Habitat selection before and after wolf recolonization*

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

283
284 Mouflons (*Ovis aries*) reduced the distance to refuge areas and used patches with higher values
285 in elevation, slope and ruggedness since wolves recolonized the study area in the Western Italian
286 Alps (Tizzani *et al.* 2022). Similarly, after wolf recolonisation in Gran Paradiso National Park (Italy),
287 male ibex started to spend less time in forage-rich, flat areas and selected more rocky slopes,
288 which provided a refuge (Grignolio *et al.*, 2019). However, they continued to use areas where
289 wolves could move easily, while feeding in smaller groups. Hence, continuing to utilise higher
290 quality but riskier feeding sites despite the presence of predators might be compensated by a
291 reduction in group size (see section *group size* below) to reduce predator encounters.

292
293 The mixed evidence for effects of wolf presence on large-scale habitat selection by ungulates in
294 Europe might be related to the fact that the daily home range of ungulates is much smaller than
295 the daily home range of wolves. Thus, prey might avoid encounters with predators by high
296 mobility within their home ranges, which might not be detected by purely spatial analyses of
297 habitat selection. (Pusenius *et al.*, 2020) found that moose in Finland increased their movement
298 speed (distance between two consecutive GPS relocations/time) when predation risk was higher,
299 but no such effect was found in moose in Scandinavia (Wikenros *et al.*, 2016). This indicates that
300 higher mobility may be an anti-predator mechanism not yet developed by moose in Scandinavia,
301 where compared to Finland wolves have returned only recently (see also (Sand *et al.*, 2006).

302
303 *Migration*

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

309

310 In general, we have found inconsistent evidence for effects of wolves on large-scale habitat
311 selection of their prey in Europe. Reported effects were mainly found in protected areas. Thus,
312 anthropogenic factors and bottom-up effects seem to influence habitat selection of large
313 ungulates more strongly than wolf presence. The general rarity of evidence for large-scale
314 behavioural responses of prey does not preclude that more fine-scale behavioural responses to
315 wolf presence occur (see below).
316

317 **4.1.2 Fine-scale responses**

318 In cultural landscapes, the home range and habitat selection of ungulates might be constrained
319 by human influences, and behavioural responses to predator presence might be more evident at
320 fine spatial scales. When predators are present, ungulates may adjust their behaviour near
321 landscape elements that increase perceived predation risk, such as escape impediments or dense
322 vegetation that reduces visibility (Kuijper *et al.*, 2013, 2015; van Ginkel *et al.*, 2019a).
323

324 *Observational studies of responses to fine-scale landscape structures*

325 Kuijper *et al.* (2015) studied the effect of tree logs on ungulate behaviour in Białowieża forest
326 (Poland) and found that red deer avoided such tree logs more inside than outside of wolf core
327 areas (Kuijper *et al.*, 2015). This avoidance led to reduced browsing pressure around the logs and
328 increased chances for tree recruitment (Kuijper *et al.*, 2013; van Ginkel *et al.*, 2019a), which we
329 discuss in detail in the section *Cascading effects*.
330

331 *Experimental cues*

332 Van Beek Calkoen *et al.* (2021) showed that at sites with predator cues (scat and urine), visitation
333 duration (but not visitation rate) by red deer was reduced. This again indicates that deer might
334 increase mobility to avoid predation risk (van Beeck Calkoen *et al.*, 2021). Another study on free-
335 ranging deer in Białowieża, however, found no evidence for decreased visitation rate or duration
336 on sites with wolf scent (scat) but only observed higher vigilance (Kuijper *et al.*, 2014).
337 Accordingly, van Ginkel *et al.* (2019a) found no effect of the presence of wolf urine on the
338 visitation rate/duration of red deer, both in areas with and without resident wolves (van Ginkel
339 *et al.*, 2019a). These studies, however, also studied other responses than visitation rate/duration,
340 such as e.g. vigilance behaviour. Given that there are multiple strategies to avoid predation risk,
341 the responses should not be analysed independently, as depending on the context, different
342 strategies might be applied (e.g. (Kuijper *et al.*, 2014).
343

344 Strong context-dependence became also evident in a study on prey responses to wolf sound
345 playbacks. While cervids did not lower visitation rates in response to wolf sounds compared to
346 sheep sounds, wild boar showed lower visitation rates with wolf sounds than with sheep sounds,
347 but only in broadleaved forest and for a few days (Weterings *et al.*, 2022). Also, in Sweden the
348 trapping rate of ungulates (roe deer and fallow deer) and the damage on crops was lower when
349 playback sounds of dogs, wolves and humans were played (Widén *et al.* 2022). However, there
350 was no comparison with a control sound.
351

352

353 **4.1.3 Temporal avoidance**

354 Most studies investigated either temporal or spatial avoidance. Thus, we report those effects in
355 separate sections.

356

357 *Activity overlap*

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

371

372 In a study in the Italian Western Alps, seasonal differences in temporal overlap between wolves
373 and their main prey (roe deer and wild boar) were documented. The activity overlap increased
374 during the non-denning season of wolves compared to the denning season. This increase was
375 significant for roe deer, indicating that roe deer changed their activity patterns to avoid wolves
376 during the wolf denning season (Torretta *et al.*, 2017). However, shifts in the wolves' space use
377 or other factors could have influenced this effect.

378

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

388

389

390 **4.2 Other behavioural adaptations**

391 **4.2.1 Vigilance**

392 Vigilance behaviour presents a potential trade-off between foraging and risk avoidance.
393 Especially when animals stop foraging to engage in vigilance (Blanchard & Fritz, 2007), they spend
394 less time foraging. This might affect individual survival and population dynamics, but also reduce
395 biomass removal and thus affect vegetation growth.

396
397 Fallow deer in an Italian national park showed more often and longer vigilance behaviour at sites
398 with higher wolf activity (Esattore *et al.* 2023). Red deer in the Polish Białowieża Forest increased
399 their vigilance close to tree logs representing small-scale escape impediments. However, this
400 effect was only visible in core areas of wolf territories (Kuijper *et al.*, 2015). Predator cues, such
401 as the presence of wolf scats, also led to increased vigilance levels in red deer but not in wild boar
402 (Kuijper *et al.*, 2014). These results indicate that in areas where wolves are frequently present,
403 cues of their presence together with the habitat structure can create risky patches and thus alter
404 the vigilance behaviour and spatial avoidance of prey at a fine spatial scale. In contrast to these
405 results, a study testing the vigilance behaviour in response to wolf urine in wolf-free areas in
406 National Park Veluwezoom in the Netherlands and in areas with wolf presence in the Białowieża
407 National Park did not find any effect of wolf urine on the vigilance behaviour of red deer (van
408 Ginkel, Smit, & Kuijper, 2019b). The authors argue that the lack of response might be a result of
409 the quality of wolf urine. Also in other experimental studies, wolf scent had no effect on vigilance
410 behaviour (van Beeck Calkoen *et al.*, 2021; van Ginkel *et al.*, 2021). However, the visitation
411 duration and browsing intensity in plots with wolf scent was reduced, indicating that deer might
412 increase mobility to avoid predation risk (see section on spatiotemporal responses above).

413
414 The above-mentioned studies documenting effects of wolf presence on deer vigilance were all
415 performed in national parks or enclosures. In a recent study, however, Proudman *et al.* (2020)
416 investigated vigilance behaviour of red deer in response to humans and wolves on a large scale
417 in the commercially used parts of Białowieża forest adjacent to the national park. In the non-
418 protected areas, i.e. hunting reserves, deer showed higher levels of vigilance during the hunting
419 season and at diurnal hours. In contrast, in protected areas, red deer were more vigilant at night,
420 possibly related to higher wolf activity in areas where human disturbances are strongly restricted.
421 These results indicate that wolves' impacts on red deer vigilance behaviour seem to be
422 superimposed by anthropogenic effects in areas with high human disturbance and hunting.

423 **4.2.2 Grouping behaviour**

424 We found four studies investigating grouping behaviour of ungulates in response to wolf
425 predation risk. Red deer and male moose tended to form larger groups in the presence of wolves
426 (Jędrzejewski *et al.*, 1992; Månsson *et al.*, 2017), while group size of male ibex decreased
427 (Grignolio *et al.*, 2019). Moose grouping behaviour generally seemed to be little affected by
428 predator presence, which aligns with results from other studies (Nicholson *et al.*, 2014; Wikenros
429 *et al.*, 2016). Male ibex changed their behaviour in response to wolf recolonisation within a
430 relatively short period of time. However, female ibex and moose with calves did not change their

431 grouping behaviour in response to predation risk (Månsson *et al.*, 2017; Grignolio *et al.*, 2019).
432 This leads to the assumption that their behaviour is either determined by other factors, such as
433 forage quality, or - in case of moose - that they have lost their antipredator behaviour in the
434 absence of predators. Also an experimental study in the Netherlands, where prey was naïve to
435 wolves, found no effect of wolf acoustic playbacks on group sizes of wild boar or cervid species
436 (Weterings *et al.*, 2022).

437
438 Other factors such as population density, snow depth and hunting were important predictors of
439 grouping behaviour (Dzięciołowski, 1979; Månsson *et al.*, 2017; Grignolio *et al.*, 2019), indicating
440 that grouping in wild ungulates is influenced by a complex set of factors (Creel, Schuette, &
441 Christianson, 2014).

442 **4.3 Physiological effects and parasite prevalence**

443 In the French Alps, roe deer fawn body mass was consistently lower in wolf core areas compared
444 to peripheral areas (Randon *et al.*, 2020). The mechanisms of such a difference in body mass in
445 response to wolf presence are unclear. They could be related to increased stress, but also to
446 changes in habitat selection or higher vigilance levels. However, the effect size was relatively
447 small (~1 kg) compared to effects of, e.g. population density (>3 kg, (Douhard *et al.*, 2013)), and
448 the variation was correlated with variation in roe deer abundance in both areas. Thus, this effect
449 had likely been caused by an unmeasured factor (Randon *et al.*, 2020).

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

464
465 Predator presence might also influence parasite prevalence in ungulates. They can lead to
466 healthier ungulate populations as reduced population size might hinder parasite spread, and
467 infected and old individuals might be removed from the population (Packer *et al.*, 2003). In
468 contrast, the life cycle of some parasites depends on two specific hosts, with ungulates as the
469 intermediate host (e.g. *Sarcocystis* sp.). Infected ungulates might become more vulnerable prey
470 for carnivores, which then serve as the definitive host. Thus, the presence of wolves might be
471 linked to parasite infections in ungulates as they add to the guild of definite hosts.

472 (Lesniak *et al.*, 2018) analysed tissue samples of wolves, red deer, roe deer and wild boar in
473 Germany and found higher probabilities of *Sarcocystis* sp. infection for red deer in areas with
474 wolves present (but not for roe deer or wild boar). For other diseases, however, predation can
475 reduce the prevalence of infection without leading to a reduction in prey population density
476 because disease-induced mortality can compensate for predation mortality (Tanner *et al.*, 2019).
477

478 **4.4 Cascading effects on vegetation**

479 In Central Europe, cascading effects of wolves on lower trophic levels have only been studied
480 extensively in the Polish Białowieża forest. Studies measuring indirect effects of wolves on the
481 vegetation found that inside wolf core areas, browsing intensity was reduced near structures that
482 might impede escape or hinder visibility (i.e. coarse woody debris or fallen tree logs (Kuijper *et*
483 *al.*, 2013; van Ginkel *et al.*, 2019a), resulting in a higher percentage of trees growing out of reach
484 of browsing ungulates. The effect of fine-scale habitat structures was much more robust in high-
485 risk areas for prey inside of wolf territories than in low-risk areas outside of wolf core areas
486 (Kuijper *et al.*, 2013; van Ginkel *et al.*, 2019a). These studies were performed in the most
487 undisturbed parts of the Białowieża forest, i.e. in the national park that excludes hunting and
488 forestry activities. A recent experimental study outside the Białowieża National Park, in an
489 adjacent area where hunting and forestry occur, illustrated that visual obstructions (mimicking
490 the tree log effect) strongly reduced deer browsing pressure and led to increased tree growth
491 (van Ginkel *et al.*, 2021), indicating that similar risk effects can also occur in a more human-
492 disturbed environment.

493 Also at the landscape scale, changes in patterns of space use by red deer caused by wolf presence
494 led to a measurable reduction of browsing intensity and changes in the relative recruitment of
495 different tree species inside and outside the Białowieża National Park (Bubnicki *et al.*, 2019).
496 Consequently, tree species that were most vulnerable to deer browsing had a higher chance of
497 recruitment in places with frequent wolf presence (Bubnicki *et al.*, 2019) or, at a smaller scale, in
498 places hindering deer browsing due to (visual) impediments (van Ginkel *et al.*, 2021).
499

500 Wolf presence can also affect forage selection, potentially leading to shifts in the plant
501 community. Red deer foraged more on broadleaved tree species and less on forbes in high-risk
502 than in low-risk areas (Churski *et al.*, 2021). This effect, however, was only present in the national
503 park and not in the managed forest.
504

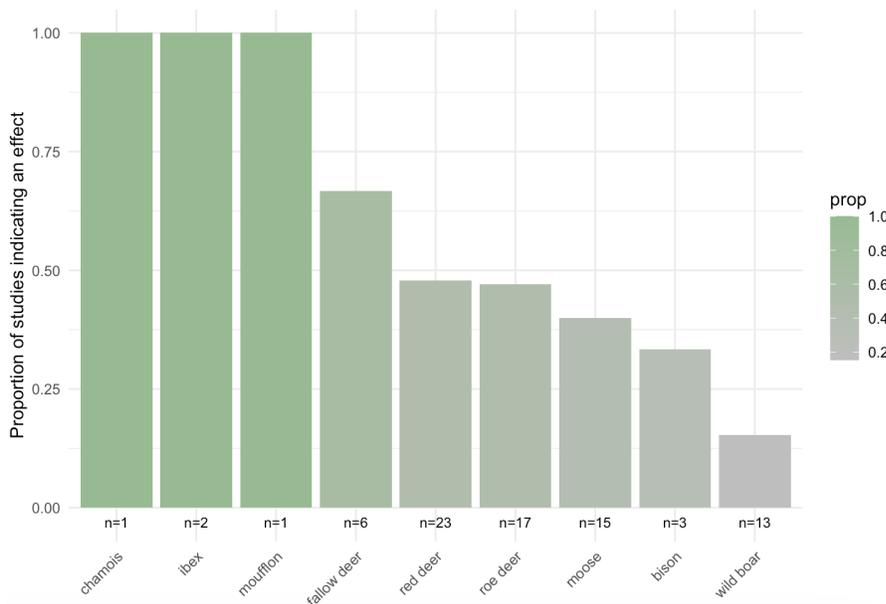
505 In an area more recently recolonized by wolves in Switzerland, a pilot study on the local tree
506 regeneration showed that ungulate densities, as indicated by local hunting bags, and the
507 percentage of saplings with browsed leader shoot decreased in the wolves' summer core zone
508 (Kupferschmid, 2017). Due to the pilot character of the study, data were lacking to evaluate if
509 this might have been related to indirect effects of wolf presence, i.e. shifts in ungulates' spatio-
510 temporal, social or foraging behaviour, or potential other factors, such as changes in hunting
511 effort. An experimental study on captive red deer in the Bavarian Forest, Germany, did not
512 document a shift in selectivity for certain tree species in proximity to simulated wolf cues.
513 However, visitation duration and browsing intensity decreased in the presence of wolf scent,

514 which might impact woody plant communities and affect forest ecosystems in the long term (van
515 Beeck Calkoen *et al.*, 2021).

516
517 Interestingly, results from moose, the main prey of wolves in Sweden, show a different pattern
518 than observed in red deer in other parts of Europe: The probability of moose browsing was higher
519 inside wolf territories compared to outside of wolf territories (Gicquel *et al.*, 2020; Ausilio *et al.*,
520 2021), which seems related to higher moose abundance inside wolf territories (Ausilio *et al.*,
521 2021). Also, van Beeck Calkoen *et al.* (2018) found higher browsing damage in high-
522 wolf-utilisation areas. The authors related their findings to a confounding effect, as these areas
523 were characterised by lower productivity (because of higher elevation) that led to reduced tree
524 density and height, which are associated with an increase in moose browsing intensity (van Beeck
525 Calkoen *et al.*, 2018). They also related their finding to anthropogenic effects as high-
526 wolf-utilisation areas are characterised by a lower human influence index and situated at higher
527 altitudes than low-wolf-utilisation areas. From this, the authors deduced that human activities
528 could push wolves into less productive parts of the landscape with lower overall tree densities,
529 resulting in higher moose browsing levels. These findings illustrate that comparing areas with and
530 without wolves might lead to erroneous conclusions when no other (human-related)
531 confounding factors are considered.

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

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Figure 3 Proportion of observations indicating NCE and number of observations per prey species.

<i>Category</i>	<i>n</i>	<i>Current knowledge in Europe</i>	<i>Current challenges</i>	<i>Suggestions for future studies</i>
2.1.1 <i>Large-scale</i>	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 <i>Fine-scale</i>	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 <i>Temporal</i>	6 studies 11 observations	Generally high temporal overlap between wolf and prey activity patterns (but see 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 <i>Vigilance</i>	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; see 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 <i>Grouping</i>	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 <i>Physiological effects</i>	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 <i>Cascading</i>	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.

541 Table 1: Overview of non-consumptive effects in Europe for each effect category, note that one study can have multiple observations of different categories

542

5. Discussion

543

544 **Complexity and Context-Dependence of Non-Consumptive Effects (NCE)**

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

559

560 In addition to anthropogenic impacts, further factors lead to context-dependence of NCE. Species
561 - or even sexes, age classes, or individuals in different states - might vary in their sensitivity to
562 risk effects from either human or non-human predators. While red deer, roe deer and fallow deer
563 showed changes in their behaviour in response to predator presence under certain conditions,
564 other species, such as wild boar or moose, seemed less sensitive to predator presence. Different
565 species or even individuals might also adopt different strategies, and some might specialise in
566 avoidance of risky places while others specialise in early detection (e.g. through vigilance or
567 grouping) or other defence mechanisms (e.g. (Makin, Chamaillé-Jammes, & Shrader, 2017;
568 Gaynor *et al.*, 2019).

569

570

571 **Quantifying the Risk Landscape and Human Influences**

572

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

579

580 Not only quantifying the risk landscape, but also quantifying human impact is challenging.
581 Human impact can vary with, for example, human density, infrastructure, the level of hunting,
582 forestry and recreational activity and each of those variants of human impact might affect wildlife

583 differently. Many studies included here did not estimate human impact in the study region, thus
584 making comparing different studies considerably challenging.

585 The majority of European studies investigating wolves' effects on herbivore behaviour were
586 conducted in national parks, where human impact is assumed to be weaker than in non-
587 protected areas. However, European national parks are subject to relatively high human impact
588 (especially compared to the large national parks in North America) and truly undisturbed areas
589 are rare (van Beeck Calkoen *et al.*, 2020). In human-dominated landscapes, the effects of humans
590 on wildlife behaviour can exceed those of natural predators (Theuerkauf & Rouys, 2008; Ciuti *et*
591 *al.*, 2012) and human risk factors can interact with predator-induced risk factors (Proffitt *et al.*,
592 2009; Rogala *et al.*, 2011; Kuijper *et al.*, 2015). Human activities can directly affect the behaviour
593 and spatial distribution of ungulates (e.g., (Benhaiem *et al.*, 2008; Rogala *et al.*, 2011) or indirectly
594 by affecting predator distribution (Theuerkauf *et al.*, 2003; Theuerkauf & Rouys, 2008; Rogala *et*
595 *al.*, 2011). Thus, we must be very careful when interpreting study results on NCE of wolves in the
596 presence of anthropogenic effects without the recognition of potential indirect effects of human-
597 carnivore-prey interactions. It is challenging to interpret the effects of predators isolated from
598 anthropogenic effects since they generally coexist in Europe. Thus, there is a need for studies in
599 more human-dominated landscapes, which allow for studying the interacting effects of humans
600 and natural predators.

601
602 Additionally, the correlation of human activity with wolf presence makes it very difficult to
603 disentangle wolf-induced effects and human-induced effects, emphasizing the need to consider
604 indirect effects of humans on carnivore behaviour. While the presence of wolves may not have a
605 significant impact on forest vegetation in human-dominated areas, it can have effects in
606 undisturbed forest systems.

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611 **Spatial scales and constraints**

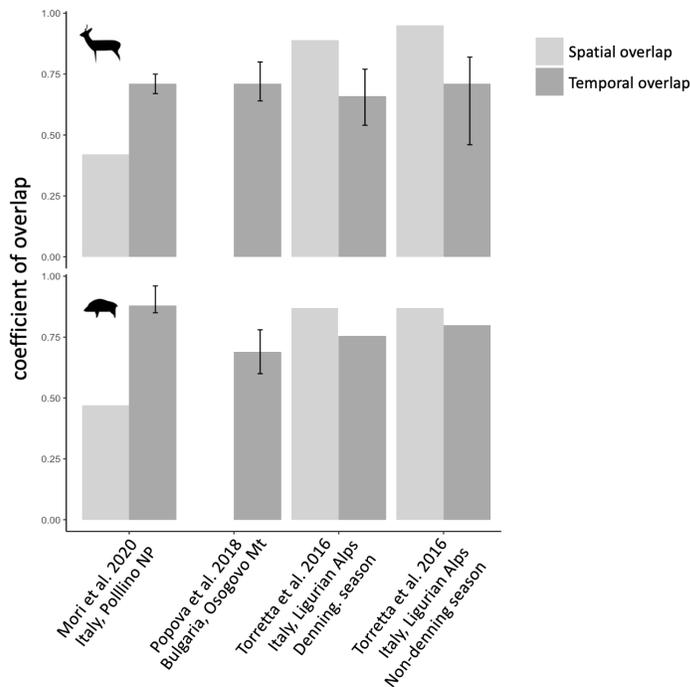
612
613 Most studies we found here indicate that risk factors for ungulate prey act at different spatial
614 scales—impediments acting as a risk factor at a fine scale and carnivore distribution shaping the
615 perceived risk at the landscape scale. Most importantly, these factors interact and shape the
616 functional role of large carnivores in ecosystem processes. We thus would expect NCE to mainly
617 appear in response to small-scale risk factors when combined with the presence of wolves at
618 larger scales. In many cases, large-scale habitat selection of ungulates seems to be strongly
619 affected by anthropogenic factors, such as hunting or forest exploitation, whereas predation risk
620 by wolves seems to have relatively minor effects. To understand how large carnivores indirectly
621 affect the vegetation in ecosystems, it is crucial to consider interactive effects between fine- and
622 landscape-scale risk factors, as we might see effects only under certain conditions (Wirsing *et al.*,
623 2021).

624
625

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

648
649 Studies investigating temporal and spatial overlap generally found mixed results (Figure 4,
650 Popova *et al.*, 2018; Mori *et al.*, 2020, except for Esattore *et al.* 2023). In general, we need to be
651 careful with the interpretation of causal relationships of spatial and temporal overlap, especially
652 if there is no data from reference areas/ time periods. Additionally, activity patterns of herbivores
653 are already strongly adapted to the presence of humans, and there might be little opportunities
654 left for avoiding the activity periods of carnivores. How complex and dynamic NCE can turn out
655 is illustrated by the fact that herbivores might even increase their space use close to human
656 settlements to reduce wolf predation risk (see e.g. Kuijper *et al.*, 2015; Proudman *et al.*, 2020),
657 while temporarily avoiding humans during the day.

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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. 2017; 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.

666

667 Limitations and Methodological Challenges

668

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

678

679 Another factor hampering quantitative analysis is the multidimensionality of prey response. Prey
680 can use different strategies for dealing with increased predation risk. In this review, we presented
681 the results on different NCE in separate sections (similarly to most of the papers reported).
682 However, NCE in one section cannot be separated from effects in another section. For example,
683 spatial and temporal avoidance cannot be isolated from each other or other behavioural
684 adaptations (i.e. grouping or vigilance). All these effects can interact, and one mechanism can
685 compensate for another (see e.g. Torretta *et al.*, 2017; Grignolio *et al.*, 2019). For example, risky
686 places can be used at safe times, indicating that the landscape of fear is dynamic over time (Kohl

687 *et al.*, 2018). Additionally, NCE might be dependent on the season. For example, in winter, prey
688 might have to accept higher predation risk as they cannot afford to trade lower predation risk
689 with lower energy intake. Furthermore, there are multiple strategies to solve the same dilemma.
690 Some individuals/populations/species might apply alternative strategies and while some prey
691 might increase their vigilance while using risky places, others might rather avoid such places while
692 keeping their vigilance behaviour constant. Given that there might be even individual variation
693 in these strategies, effects can stay undetected depending on the scale we are looking at.

694
695 Studies investigating temporal avoidance mostly measured temporal overlap. Even though there
696 are indications for temporal avoidance of wolves by prey, it is challenging to show causal
697 relationships from activity overlap data, and we advocate interpreting these results carefully
698 when no reference area is available or when no comparative data exist from times when wolves
699 were not present in the study area. Furthermore, it needs to be clarified whether prey are
700 adapting their activity patterns to avoid predation, or wolves are adapting their activity to
701 increase hunting success, or both. Additionally, the potential for adaptations in activity patterns
702 might be overruled by human influence, which is known to be an important driver of temporal
703 activity patterns in ungulates and carnivores (Stankowich, 2008; van Doormaal *et al.*, 2015).
704 Moreover, temporal avoidance might reduce spatial effects, as prey might use risky places at safe
705 times (Kohl *et al.*, 2018). Thus, temporal responses should not be considered isolated from spatial
706 patterns.

707
708 Effects of predators on the vegetation have so far only been studied in forest systems (except for
709 (Davoli *et al.* 2022)) and the extent of cascading effects in vegetation types other than forests,
710 such as shrub or open grassland, remains unclear. Such open areas in Europe are typically
711 occupied by humans and low-disturbance open areas are much rarer than undisturbed forested
712 areas, so that the potential for observing cascading effects of wolves in vegetation types other
713 than forest seems limited.

714
715 We are aware that there might be a publication bias and that more results that find NCE might
716 be published compared to studies that found no effect. Further, we have missed grey literature
717 and literature that was not published in English. We found some reports investigating NCE in
718 Germany and Switzerland (Gärtner & Noack, 2009; Nitze, 2012; Kupferschmid, Beeli, &
719 Thormann, 2018a, 2018b), but excluded them from the systematic review as they were not
720 published in English, and we are not able to include grey literature in other languages.

721
722

723 **Future Research and Methodological Advancements**

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

731
732 Not only large herbivores, but also other trophic levels such as scavengers can be affected by
733 apex predators through competition (Wikenros *et al.*, 2010, 2017; Krofel *et al.*, 2017), facilitation
734 (Selva & Fortuna, 2007; van Dijk *et al.*, 2008; Wikenros *et al.*, 2013; Focardi *et al.*, 2017; Rossa *et*
735 *al.*, 2021, 2021)) or hybridisation (Moura *et al.*, 2014). Such effects in turn can have indirect
736 effects on the herbivore community. In this review, however, we have not considered effects of
737 wolves on scavengers, mesopredator or other apex predators, or potential combined effects of
738 several apex predators in more complex food webs, because the majority of studies only
739 considered one predator species. In future studies, however, we need to account for multiple
740 predators when investigating ungulate responses to predation risk (Moll *et al.*, 2017). Moreover,
741 we have not taken into account the complexity of the prey guild, which might influence the
742 potential for behaviourally mediated effects, since in ecosystems with high complexity,
743 redundancy effects might mask trophic cascades through compensation by other species
744 (Fahimipour, Anderson, & Williams, 2017).

745
746
747 Advances in technology will allow for higher-resolution data collection. We have documented
748 very few studies using GPS telemetry for the assessment of space use of wolves and their prey.
749 This technology can provide essential insights by providing data for the whole home range of the
750 collared individuals, but is limited to the collared individuals. Thus, combining multiple
751 approaches, e.g. GPS-telemetry and camera traps, can be very powerful. However, with new
752 possibilities for data collection and the combination of multiple approaches, it will become more
753 and more essential to have common standards that allow for comparing different studies and
754 synthesising the knowledge generated in different regions and under different environmental
755 conditions (Moll *et al.*, 2017; Prugh *et al.*, 2019).

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758 **Conclusions and Implications**

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

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772 If we aim to restore the complexity of ecosystems and ecosystem processes, we should think
773 about creating more landscapes with a lower human impact and therefore a higher potential for
774 these carnivore-induced impacts to occur. In the humans-dominated landscape of Europe, this is

775 however currently not the most realistic scenario. Regarding a land-sharing view, we need more
776 knowledge on effects of carnivores on the ecosystem with focusing on the influence of human
777 activities on predator-prey relationships and resulting cascading effects.

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7. References

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