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Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes

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Large carnivores are frequently presented as saviours of biodiversity and ecosystem functioning through their creation of trophic cascades, an idea largely based on studies coming primarily out of relatively natural landscapes. However, in large parts of the world, particularly in Europe, large carnivores live in and are returning to strongly human-modified ecosystems. At present, we lack a coherent framework to predict the effects of large carnivores in these anthropogenic landscapes. We review how human actions influence the ecological roles of large carnivores by affecting their density or behaviour or those of mesopredators or prey species. We argue that the potential for density-mediated trophic cascades in anthropogenic landscapes is limited to unproductive areas where even low carnivore numbers may impact prey densities or to the limited parts of the landscape where carnivores are allowed to reach ecologically functional densities. The potential for behaviourally mediated trophic cascades may be larger and more widespread, because even low carnivore densities affect prey behaviour. We conclude that predator–prey interactions in anthropogenic landscapes will be highly context-dependent and human actions will often attenuate the ecological effects of large carnivores. We highlight the knowledge gaps and outline a new research avenue to study the role of carnivores in anthropogenic landscapes.

1. Introduction

The last decade has seen a strong increase in research on the ecological effects of apex predators, the results of which suggest that apex predators regulate ecosystem structure and functioning through both density-mediated and behaviourally mediated trophic cascades (figure 1) [1–3]. This research is being actively used to promote carnivore conservation and restoration efforts, including in Europe, where carnivores are rapidly recolonizing their former ranges [4]. Large carnivores are frequently presented as saviours of biodiversity and ecosystem functioning [5–7], an idea largely based on studies coming primarily out of relatively natural landscapes, especially North American national parks (figure 1). In large parts of the world, however, and in Europe in particular, large carnivores live in, or are returning to, ecosystems that are intensively modified or shaped
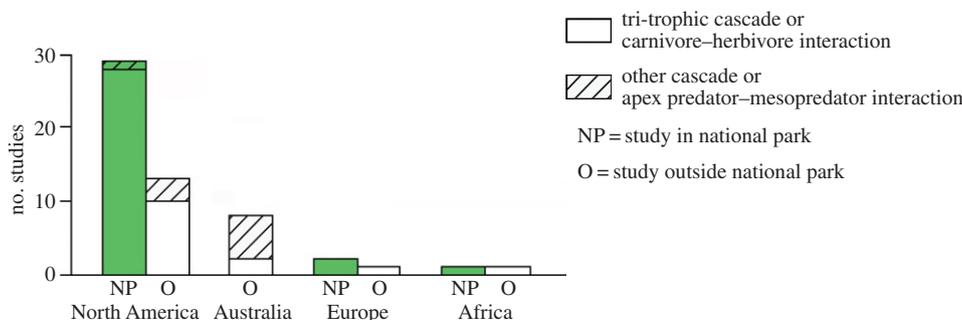
Figure 1. Evidence for large-carnivore-induced trophic cascades is biased towards a few study systems, as indicated by a search on the string 'trophic cascade' on Web of Science (4 May 2015). The search generated 1102 papers, of which 55 concerned terrestrial large carnivores (>15 kg) that either trigger trophic cascades or significantly affect the behaviour or abundance of their prey or mesopredators. (Online version in colour.)

by humans. For example, wolves (*Canis lupus*) and brown bears (*Ursus arctos*) in Sweden inhabit landscapes that are shaped through intense forestry activities and some of the highest hunting pressures on the carnivores' ungulate prey in the world. These landscapes are heavily modified by human activities, even though human population density is generally low. In Germany, wolves are returning to areas with some of the highest human population densities in the world and they inhabit landscapes with fine-scale mosaics of different types of human land use. A key question emerging from the observed recovery of large carnivores in parts of Europe and North America [3,4] is what role large carnivores play in these anthropogenic landscapes. Are they able to create trophic cascading effects as strong as those in more natural landscapes, or do various human impacts create paws without claws?

In this paper, we review how human actions may alter the ecological function of large carnivores in anthropogenic landscapes. We investigate what we know about the direct and indirect effects of humans on the number and behaviour of carnivores and their prey, as well as the food resources that both depend on. Integrating humans in a food web structure in this way is necessary if we are to better understand predator–prey interactions and their cascading effects in human-dominated landscapes [8,9]. We highlight the gaps in our knowledge and outline a new research avenue. Our approach is somewhat Europe-centric. This continent, with its large cultural, political and economical diversity, is experiencing a rapid large-scale recovery of large carnivores [4]. Europe therefore presents interesting examples of functioning of large carnivores in a variety of anthropogenic landscapes. This knowledge is relevant for other densely populated regions or areas devoid of wilderness where large carnivores coexist with humans [10].

2. Carnivores increase even in human-dominated parts of Europe

While large carnivores are still rapidly declining in most of the world [3], some species are now showing remarkable recovery across large parts of Europe [4] and North America [3]. Three large terrestrial carnivore species occur widely throughout Europe and are increasing in number: brown bear, Eurasian lynx (*Lynx lynx*) and grey wolf. In addition, the golden jackal (*Canis aureus*) is increasingly observed outside its original southeastern European range, with confirmed observations in

central and northern European countries [11]. Most European countries now have a permanent and reproducing population of at least one of these carnivore species [4]. The increases in carnivore populations coincide with strong range expansions and recolonization of former ranges largely outside protected areas. Importantly, during this process, large carnivores now enter novel landscapes that have been dramatically altered by humans during the last century or more following their extinction. Wolves have been particularly successful in settling and persisting in landscapes with relatively high human densities [4]. Numerous reproducing wolf packs have recently colonized areas near centres of human activity in countries such as Germany, France, western Poland, western Finland and south-central Sweden, with two packs now also confirmed present in Switzerland. Moreover, single wolves increasingly settle or roam in highly transformed areas in western Germany, Denmark and the Netherlands, suggesting that this expansion is continuing. These developments challenge the traditional view that human settlements and activities generally prevent the establishment of large carnivores [12,13]. In fact, public attitudes towards carnivores and the effectiveness of legal protection [4] may be stronger predictors of carnivore presence and recolonization pattern than human density and activity *per se* [14]. If current trends continue, large carnivores will become increasingly common across Europe's anthropogenic landscapes in the future. In the following section, we use a simple food web as a framework to illustrate how humans affect the ecological role of large carnivores in these anthropogenic landscapes.

3. Anthropogenic effects on trophic interactions

Large carnivores may influence ecosystems by directly affecting the number or behaviour of their herbivore prey, thereby influencing vegetation dynamics ('tritrophic cascades'), and/ or by affecting mesopredators and thereby their prey [3]. Such trophic cascades can be conceptualized in a simple food web diagram, including interactions between large carnivores, mesopredators, herbivores and lower trophic levels (vegetation). Humans commonly exert a direct influence on large carnivores, mesopredators or prey in anthropogenic landscapes (figure 2) by impacting their densities ('anthropogenic density-mediated effects') or their behaviour ('anthropogenic behaviourally mediated effects'). Humans may also indirectly modify the potential for trophic cascades by changing the resource landscapes or 'foodscapes' on which prey and their predators depend ('anthropogenic bottom-up effects'). This
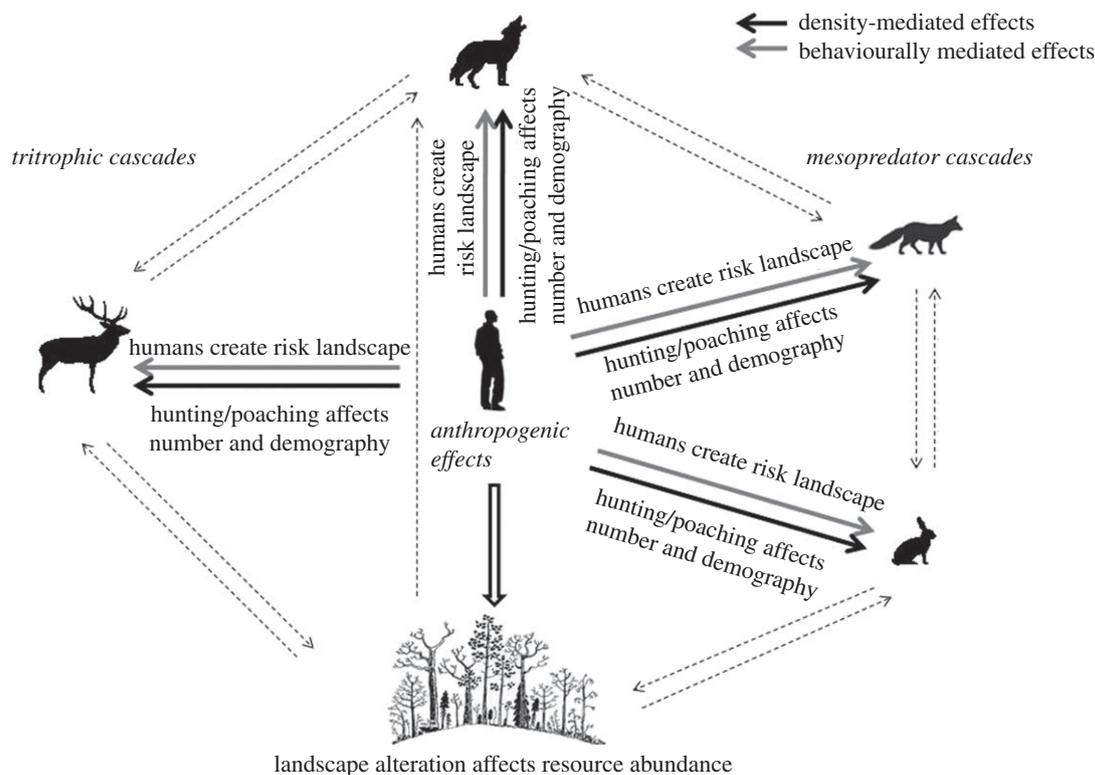
Figure 2. Apex predators can cause *tritrophic cascades* (symbolized by wolf–deer–tree) and *mesopredator cascades* (symbolized by wolf–fox–hare–tree). Bottom-up factors (upward arrows) can influence these trophic interactions in the opposite direction. Humans influence all components of this food web directly by altering animal densities or behaviour, and indirectly by influencing food resources.

framework allows us to include humans in trophic cascade theory [8,9] in a simple and informative way. In the following, we briefly review what we currently know about these anthropogenic effects.

(a) Anthropogenic top-down density-mediated effects

Despite the recovery of carnivores in Europe and parts of North America, humans clearly still have a major impact on carnivore numbers through legal hunting, poaching and traffic accidents [15]. In many anthropogenic landscapes, there is some level of legal harvest of carnivores to reduce human–carnivore conflict [16] or an increasing discussion about re-introducing such control [17]. Examples of strict carnivore control can also be found in Australia [18], where control of dingo (*Canis lupus dingo*) is particularly strict in regions with extensive sheep farming [19].

Arguably more severe than legal control, however, is the effect of poaching on population recoveries, and the genetic diversity and vital rates of small and recovering populations of large carnivores [20,21]. For example, Liberg *et al.* [20] showed that the Swedish wolf population would be four times as large without poaching. This suggests that in many human-dominated landscapes, the size of large carnivore populations is likely to be far below the potential as determined by the availability of prey [21,22]. It is questionable whether such greatly reduced carnivore populations can numerically limit or regulate prey species [16,23,24]. In social species such as wolves and dingoes, even a small reduction in the population can disrupt social stability [25,26] and reduce their functional role more sharply than would be expected based on their numbers alone [27].

The potential for numerical effects of large carnivores on prey populations is also influenced by strong numerical effects of human hunting on the same prey populations in many anthropogenic landscapes [28]. The results of this interaction between human- and carnivore-induced numerical effects are rather unclear and complex. First, hunting pressure varies widely across cultural and demographic contexts and may not always limit ungulate [29] or mesopredator populations [30], especially in more productive environments. Sometimes, hunting pressure may even increase population growth rate [31,32]. Second, the direction and magnitude of numerical effects probably differ greatly among predator–prey constellations. In Scandinavia, harvest of moose (*Alces alces*) strongly outweighs the demographic impacts of wolf and bear predation [31] (see also [33]), whereas lynx predation on roe deer (*Capreolus capreolus*) had at least as much impact as human hunting. The explanation for this difference was that lynx often prey on adult roe deer, whereas wolf and brown bear mainly prey on young moose individuals, which contribute less to future population growth. This reflects a more general difference among human hunters and various large carnivore species: the extent to which they target individuals from different sex or age classes [33,34]. Third, when large carnivores return, hunters may either reduce their harvest to limit the total mortality [35] or not change their harvest. In the latter case, the additive effect of predators and hunters may result in reduced ungulate densities [36]. Whereas the predator-induced mortality on prey might be similar in both cases, the potential for carnivores to affect ungulate abundance can be reduced or reinforced by changes in human hunting practices.

These complexities make it difficult to predict the numerical effects of recolonizing carnivores on prey densities (including mesopredators) in the presence of significant human hunting, and call for studies that compare demographic effects of large carnivores and human hunting in the same system.

(b) Anthropogenic top-down behaviourally mediated effects

The potential of recolonizing large carnivores to create behaviourally mediated trophic cascades in human-dominated landscapes will be strongly modified by the effects of humans on the behaviour of large carnivores and their prey. These include indirect effects through changes in the landscape in which predator and prey interact, and direct effects on the behaviour of predator and prey.

Landscape features, particularly vegetation structure, are the main determinants of spatial patterns of predation, hunting success and the resulting predation risk [37]. Habitat openness is an important driver of perceived risk. Prey feel safer in open or closed habitats depending on the hunting strategy of their main predators (cursorial versus ambush) and their own escape tactics [38,39]. In human-dominated landscapes, habitat openness is primarily determined by activities such as agriculture, forestry and urban activities. Recently emerging studies, indeed, suggest that such human modifications to the landscape affect ungulate responses to predation risk cues (see [40,41]). For example, Sahlén et al. [41] showed that fallow deer (Dama dama) reduced their visits to plots with brown bear scent in a forest-dominated landscape, except when the habitat was opened up through human activities. We are, however, only beginning to understand how human modifications to landscapes affect predator–prey interactions.

The direct effects of human activity on the behaviour of carnivores and their prey have been subject to more studies, showing that both generally avoid human activity in space and time [42]. There is abundant evidence that several large carnivore species strongly avoid humans and change their activity and foraging patterns in areas of human activity [42–47], sometimes at fine spatio-temporal scales [48]. Because ungulates seem to be less sensitive to human activity than carnivores [42], they can reduce predation risk by increasing their use of areas of human activity, the well-known 'human shield effect' [49–51]. Does this mean that in anthropogenic landscapes large carnivores are 'downgraded to become penultimate predators' [24]? They might be so in some cases [52], but the opposite may also occur. Smith et al. [53] showed that female pumas (Puma concolor) left kills more frequently and spent less time on kills as human housing density increased. To compensate for this reduced prey consumption time, pumas in high-housing-density areas increased the number of deer they killed compared with kill rates in areas with little residential development. In this case, human-induced fear in carnivores led to stronger effects on prey populations and potentially stronger trophic cascading effects.

The picture becomes even more complex when we consider the effects of hunting by humans. Hunting strongly affects ungulate prey behaviour and spatial distribution [54–56]. When carnivores return to anthropogenic landscapes, prey will have to respond to the risk created by both carnivores and human hunters. Human hunting is often associated with different environmental factors than those associated with large carnivores [34,57]. As a result, ungulates may be squeezed between the risks imposed by apex predators and humans [57]. Thus, hunting may cancel out (at least during part of the year) the aforementioned human shield effect, although this remains to be studied. Moreover, these effects may either be further mitigated or reinforced by the human impacts on landscape features as discussed above. The full implications and impacts of the interactive effects of human hunters and large carnivores on ungulate prey behaviour in anthropogenic landscapes remain to be explored. Ungulates are likely to show the largest response to the most predictable and strongest risk, which in human-dominated landscapes would be hunting. However, hunting is typically spatially and temporally limited to fixed hunting periods and locations [54], and ungulates may learn to adjust their behaviour only during the risky times and in the risky places [58,59]. Therefore, whereas the effects of hunting on ungulate behaviour might overrule those of large carnivores during the hunting season [60], their importance is likely to decrease during the non-hunting season and in areas with less intense hunting.

A critical unresolved issue, highly relevant when considering behaviourally mediated effects in human-dominated landscapes, is the matter of prey naivety towards returning large carnivores. In most parts of Europe and North America, large carnivores have been extirpated one or more centuries ago. Several authors have suggested that prey may have lost costly antipredator behaviours towards their natural predators, after these predators were absent for centuries [40,61–63]. This is especially thought to be possible where hunting by humans presents strong, and quite different, selection pressures [64]. For example, Sand et al. [62] noted that wolves recolonizing Scandinavia had higher moose-hunting success than North American wolves and that this was associated with less effective antipredator behaviours in the Scandinavian moose. We do not know how common this form of prey naivety is. There are clear examples of prey maintaining strong antipredator responses even after a century or more of predator absence [41,65,66]. Hunting by humans probably plays a role in this variation, because hunting still largely dominates large carnivore mortality in many areas where carnivores are returning. Under these conditions, it will take a long time for antipredator behaviours to be selected for, as hunting can select against this [62]. It is interesting to note that the above-cited studies, in which prey were not naïve, either hunting did not occur [65,66] or the study was performed outside the hunting season [41].

Considering the above, an important and open question is under what conditions ungulate prey maintain or lose successful antipredator behaviours after the local extinction of their natural predators—and how quickly, if at all, they recover those behaviours when large carnivores return. Experiments in Australia suggest that some prey species remain naive 150 years after introduction of non-native predators, whereas others adapted to this new threat [67].

(c) Anthropogenic bottom-up effects via food resources

In anthropogenic landscapes, humans strongly affect food resource abundance and quality for prey, mesopredators and apex predators. In fact, during recent decades, the amount of food consciously or unconsciously provided by humans (so-called food subsidies) has increased greatly [68,69]. Humans have largely increased the productivity of systems used by ungulates through increased agricultural nitrogen subsidies and by planting nutrient-rich crops. Similarly, forestry may increase forage availability and quality by fertilization and by creating clear-cuts or other canopy gaps with a high recruitment of attractive forage species [70]. However, forestry may also lead to a reduction in forage quality and abundance by replacing high-quality deciduous species with low-quality conifers [71]. Supplementary feeding during winter is also a common practice in ungulate management across large parts of Europe

[28]. These food subsidies can weaken density-mediated effects of carnivores [72], especially when carnivore numbers are limited by factors other than food availability in human-dominated landscapes (see below). Food subsidies are considered one of the main factors behind the increasing abundance of several ungulate species in North America and Europe [28,73]. For example, it was estimated that moose density increased fivefold in response to forestry-related changes in landscape composition in boreal North America [74].

Like their ungulate prey, large carnivores also receive increasing food subsidies from humans, including easy-to-catch prey in the form of livestock [75], human waste [68] and slaughter remains, for example from hunting activities [76]. This increased resource abundance has the potential to support larger carnivore populations than would be possible based solely on wild prey populations [69]. However, a strong response of carnivore populations to increased food availability is unlikely to occur in most anthropogenic landscapes. Human attitudes towards large carnivores are likely to set limits to carnivore population sizes below what their resources allow [16,24]. So, unless human attitudes change dramatically, food subsidies will lead to stronger increases in ungulate populations than in the populations of their carnivores in most kinds of anthropogenic landscapes. Moreover, theory suggests that carnivores should kill a smaller proportion of the prey population in systems where prey (and alternative resources) occur at high density, which means that prey may be mainly regulated by their food [77]. We predict that as a consequence of these responses, food subsidies to both carnivores and ungulate prey in anthropogenic landscapes will be likely to lead to a reduced potential for top-down density-mediated effects of carnivores on prey population size, and thus also reduced potential for trophic cascades. These effects of food subsidies may be particularly relevant for systems with low productivity, because the top-down potential of carnivores seems to be especially limited in highly productive systems [78]. However, there may be unexpected consequences from food subsidies. A recent study from Australia suggested that food subsidies by humans can alter the dietary preferences of large carnivores [79], as illustrated by the dingo's preference for small mammals in areas with food subsidies and reptiles in areas without such subsidies. The authors suggest that this may lead to unexpected ecological cascading effects, a possibility which remains largely unexplored.

4. Effects of carnivores in human-dominated landscapes: where and when?

We have discussed how humans influence large carnivores, their ungulate prey and the lower trophic levels (the resource base) in complex ways. The above-mentioned review suggests that the potential for density-mediated trophic cascades in human-dominated landscapes is rather limited for a number of reasons. First, in these landscapes, carnivore numbers are limited by other factors than prey availability alone. Their populations will thus, in many cases, not reach ecologically functional levels in terms of regulating or significantly impacting prey and mesopredator populations [16,23,24]. This potential for top-down control is further reduced because in many human-dominated landscapes, human practices increase resource abundance for the carnivore's prey. These practices include extensive nutrient subsidies in agriculture and silviculture in combination with wildlife management practices, such as supplementary

feeding. This resource abundance allows prey populations to grow even further beyond the carnivore's control [72]. Density-mediated effects in human-dominated landscapes may be limited to less productive areas, without human food subsidies, where even relatively low carnivore numbers may impact prey densities, or to the parts of the landscape where carnivores are allowed to reach meaningful densities and human interference with ungulate prey is minimal, such as large national parks or perhaps military training areas.

Following the reasoning outlined above, we suggest that the potential for behaviourally mediated trophic cascades in human-dominated landscapes may be larger and more widespread than density-mediated effects. The effects of large carnivores on prey behaviour have been noted even at relatively low densities [80], and such effects can theoretically be decoupled from predator density [1]. Fine-scale behavioural responses of ungulates to predators [41,51,81] and landscape-level responses affecting patterns of browsing [82] have been observed in landscapes with moderate human presence. In other studies at larger scales, however, changes in moose habitat selection in response to recolonizing wolves were not detected, and this was attributed to overriding effects of human hunting [63]. In addition, several studies have found that humans more strongly affect the spatial distribution of carnivores than of the ungulate prey [42,49,50]. Human presence may thus redirect predator–prey interactions to parts of the landscape that are farthest away from human activities [51,52]. In general, the predator–prey interactions in human-dominated landscapes will be highly context-dependent. Prey distribution and behaviour will depend on the combined risk landscape generated by predators and humans, which in turn depends on the predator hunting mode, prey escape tactics and the spatial configuration of the landscape. Thus, in contrast with density-mediated effects, it is currently difficult to synthesize a general conclusion about the current or future effects of predators on prey behaviour in anthropogenic landscapes.

5. A research agenda for studying predator–prey interactions in anthropogenic landscapes

The current recolonization of European and North American landscapes by several large carnivore species provides unique research opportunities to study predator–prey interactions in a variety of anthropogenic systems. These landscapes contain gradients in carnivore recolonization time and extent, human density, degree of landscape modification and productivity. This provides a unique basis for carrying out 'natural experiments' to test how and to what extent these factors affect the functional role of carnivores (figure 3). In this section, we suggest a number of avenues for research that are urgently needed to clarify the role of carnivores in anthropogenic landscapes.

(a) Interactions between wildlife management and large carnivore impact

A key question is how ungulates deal with recolonizing large carnivores in the light of intense wildlife management practices, hunting in particular. As described above, hunting strongly influences prey response and it remains unclear under what conditions and to what extent it may cancel out carnivore effects. In this situation, prey face varying
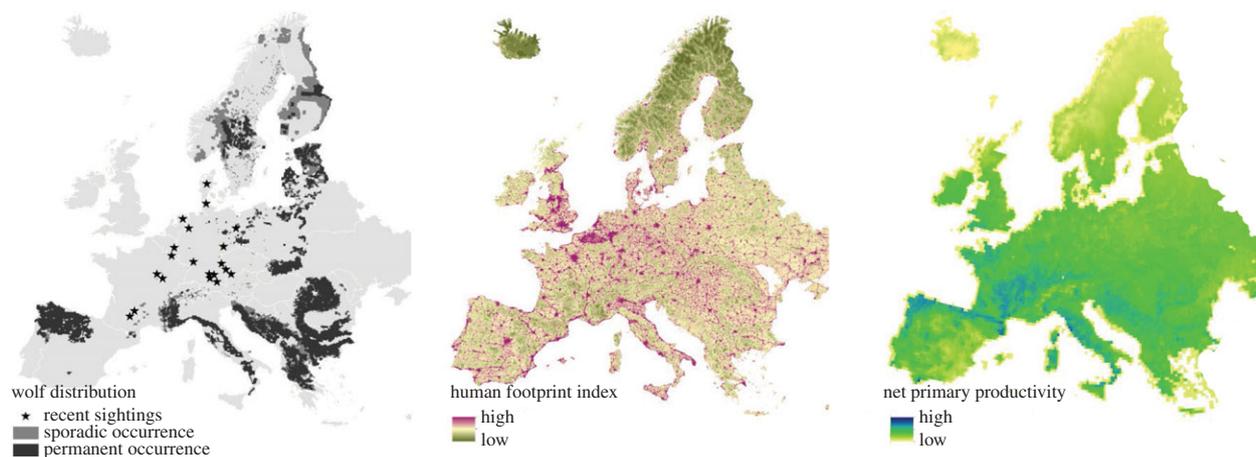
Figure 3. Large carnivores increasingly recolonize European landscapes, illustrated here for wolf based on Chapron *et al.* [4] and updated with recent confirmed sightings. Two main gradients can seriously alter carnivore impact in European landscapes: (i) anthropogenic effects as indicated by a human footprint index [83] and (ii) net primary production (NPP) [84]. The functional role of carnivores in high-human-footprint and high-NPP areas is largely unknown.

spatio-temporal patterns in the risk created by different types of predators: humans and large carnivores. How do prey species deal with a variety of landscapes of contrasting or overlapping risk in areas where both human hunters and large carnivores are present (see [57])? How do different human hunting methods interact with different carnivore types (ambush versus coursing predators)? To what extent does hunting explain variation in prey naivety to returning large carnivores? Because human hunting is generally more predictable than predation [34], would carnivore-induced risk effects be more pronounced outside the hunting season? To study these questions, one would need better and more detailed data on how human hunters, predators and their shared prey species use human-dominated landscapes, both spatially and temporally. Finally, we need to develop a better understanding of how human hunters and carnivores change their functional responses in relation to each other's presence or to human activity in general. Preliminary data suggest that both hunters [35] and carnivores [53] do respond, but the effects of these altered functional responses on more complex trophic cascades have been largely unexplored in research and wildlife management to date.

(b) Ecosystem productivity and large carnivore impact in anthropogenic landscapes

The impact of carnivores on prey populations depends to a large extent on the productivity of the landscape, which determines the growth rates and abundance of prey populations [85]. Thus, human management regimes, and human-mediated food subsidies in particular, could be expected to interact with the impact of carnivores on prey populations [86]. The current recolonization of large carnivores in Europe occurs along large-scale gradients in productivity, human density and land-use intensity (figure 3). Demographic studies [78] on single prey species along these large-scale gradients could clarify the impact of predation relative to other factors regulating prey species abundance, as well as showing how the functional role of predators is modified under the varying levels of resource conditions. The interactive effects between human-induced productivity and 'natural' productivity deserve attention, because these may be key factors determining carnivore impact in anthropogenic landscapes.

(c) Human density and large carnivore impact

Using humans as a shield, prey species can reduce predation risk by moving closer to areas with higher human presence, and which carnivores avoid [42,49]. Humans have the potential to exclude predators (and their impact) from certain habitats or parts of the landscape [51]. However, as discussed above, predators can also profit from higher prey densities in more densely populated areas [10,87] or the predation rate might increase because of higher disturbance at kill sites [53]. The presence of humans can therefore either decrease or increase large carnivore impact on prey populations through effects on carnivore behaviour, but we currently have poor understanding of what drives the variation in these effects. Simultaneous GPS-collaring of both large carnivores and their prey species in contrasting landscapes (more natural versus highly anthropogenic) will be an important methodology to quantify carnivores' kill rates, use of prey, cause-specific prey mortality and impact on prey behaviour in these contrasting landscapes of human presence.

(d) Landscape configuration and predator – prey interactions

Another urgent question is how human modifications to the landscape shape the ecological effects of large carnivores. Human-modified landscapes across the world now contain new mixtures and mosaics of different types of land uses, including intensive and less intensively managed forestry and agriculture, networks of linear features, urban areas, less impacted natural areas and so on. Human actions can tend to make landscapes more heterogeneous or more homogeneous, depending on the location and the specific nature of the anthropogenic practices. For example, forestry practices may create more openness in previously homogeneous forests or the opposite when trees are planted in previously open habitat. These human practices reshape the risk and resource landscapes for ungulate prey. We need to learn more about how these kinds of variability and change in landscape configuration influence predator–prey interactions and the resulting trophic cascades. Detailed studies of animal movement patterns have the potential to reveal how carnivores respond to changes in the landscape and whether will they change their hunting techniques. Are prey species

better able to escape from predators or is it more difficult to escape predation because of the lack of refuge areas?

(e) Trophic cascading effects of large predators in anthropogenic landscapes

We found very few studies that investigated cascading effects of large carnivores on lower trophic levels in anthropogenic landscapes. Whereas a growing number of studies show how carnivores can affect the numbers and behaviour of herbivores and mesopredators in these landscapes, there are virtually no studies of what this means for lower trophic levels. The few studies that do exist [82,85] come from areas with relatively low human density. Future studies should address the potential for trophic cascading effects, using the recently proposed gold standard approach [88], in more intensively used anthropogenic landscapes, explicitly including humans as part of the food web and as agents altering the functional role of large carnivores. The return of large carnivores in anthropogenic landscapes may or may not mitigate human–wildlife conflict. It could, for example, reduce ungulate browsing damage or increase prey abundance by suppressing mesopredator control.

(f) Human dimensions of carnivores in anthropogenic landscapes

The suitability of landscapes for large carnivores is generally predicted based on their habitat requirements in their areas of current distribution [12,13]. However, the current recolonization by large carnivores of anthropogenic landscapes in parts of Europe indicates that carnivores may have more flexible habitat requirements than was previously thought. The future distribution and numbers of large carnivores in anthropogenic landscapes may therefore be driven more by variation in acceptance by humans [10,24] than by habitat composition and prey availability. People from urbanized areas tend to have a more positive attitude towards large carnivores [89], suggesting that these areas might provide the most suitable areas for future recolonization by carnivores; however, those positive attitudes might change dramatically when conflicts with recolonizing carnivores emerge. Indeed, anti-wolf sentiment is increasing again in some areas where wolves have recovered [89], resulting in local acceptance of poaching of carnivores across a wider sector of the population [90]. Whether or not a certain level of legal, protective hunting of large carnivores contributes to increased public acceptance of the

carnivores is also a matter of intense debate [17,21,91]. Because variation in acceptance levels may be the strongest determinant of the magnitude of carnivore effects in anthropogenic landscapes, one can hardly understate the importance of understanding its drivers.

6. Closing remarks

In general, we can make much better use of the (semi-)natural experiments that are currently arising in human-modified landscapes. As highlighted in the introduction (§1), we argue that the rapid recolonization by different large carnivore species, and strong contrasts in culture, politics, economy and anthropogenic impacts across relatively short distances, make Europe a great system to study carnivore effects in anthropogenic landscapes, as a model for human-modified landscapes elsewhere. We emphasize that both the direct and indirect predator–prey interactions, and ultimately the ecological effects of large carnivores, will undoubtedly be very different in anthropogenic when compared with more natural landscapes. Many kinds of human actions will attenuate the ecological impacts of large carnivores. It may therefore be important not to romanticize the overall ecological role of large carnivores [6,7], particularly in anthropogenic landscapes, as the scientific support for this is currently limited.

References

1. Creel S, Christianson D. 2008 Relationships between direct predation and risk effects. *Trends Ecol. Evol.* **23**, 194–201. (doi:10.1016/j.tree.2007.12.004)

2. Estes JA *et al.* 2011 Trophic downgrading of planet earth. *Science* **333**, 301–306. (doi:10.1126/science.1205106)

3. Ripple WJ *et al.* 2014 Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484. (doi:10.1126/science.1241484)

4. Chapron G *et al.* 2014 Recovery of large carnivores in Europe's modern human-dominated landscapes.

Science **346**, 1517–1519. (doi:10.1126/science.1257553)

5. Ray JC, Redford KH, Steneck RS, Berger J. 2005 *Large carnivores and the conservation of biodiversity*. Washington, DC: Island Press.

6. Mech LD. 2012 Is science in danger of sanctifying the wolf? *Biol. Conserv.* **150**, 143–149. (doi:10.1016/j.biocon.2012.03.003)

7. Allen BL, Fleming PJS, Allen LR, Engeman RM, Ballard G, Leung LK-P. 2013 As clear as mud: a critical review of evidence for the ecological roles of Australian dingoes. *Biol.*

Conserv. **159**, 158–174. (doi:10.1016/j.biocon.2012.12.004)

8. Dorresteijn I, Schultner J, Nimmo DG, Fischer J, Hanspach J, Kuemmerle T, Kehoe L, Ritchie EG. 2015 Incorporating anthropogenic effects into trophic ecology: predator–prey interactions in a human-dominated landscape. *Proc. R. Soc. B* **282**, 20151602. (doi:10.1098/rspb.2015.1602)

9. Haswell PM, Kusak J, Hayward M. In press. Large carnivore impacts are context-dependent. *Foodwebs*. (doi:10.1016/j.fooweb.2016.02.005)

8

rspb.royalsocietypublishing.org Proc. R. Soc. B 283: 20161625

10. Carter NH, Linnell JDC. 2016 Co-adaptation is key to coexisting with large carnivores. *Trends Ecol. Evol.* **31**, 575–578. (doi:10.1016/j.tree.2016.05.006)

11. Trouwborst A, Krofel M, Linnell JDC. 2015 Legal implications of range expansions in a terrestrial carnivore: the case of the golden jackal (*Canis aureus*) in Europe. *Biodivers. Conserv.* **24**, 2593–2610. (doi:10.1007/s10531-015-0948-y)

12. Niedziałkowska M, Jędrzejewska W, Mysłajek RW, Nowak S, Jędrzejewska B, Schmidt K. 2006 Environmental correlates of Eurasian lynx occurrence in Poland: large scale census and GIS mapping. *Biol. Conserv.* **133**, 63–69. (doi:10.1016/j.biocon.2006.05.022)

13. Huck M, Jędrzejewski W, Borowik T, Miłosz-Cielma M, Schmidt K, Jędrzejewska B, Nowak S, Mysłajek RW. 2010 Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. *Acta Theriol.* **55**, 177–192. (doi:10.4098/j.at.0001-7051.114.2009)

14. Linnell JDC, Swenson JE, Andersen R. 2001 Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Anim. Conserv.* **4**, 345–349. (doi:10.1017/S1367943001001408)

15. Nowak S, Mysłajek RW. 2016 Wolf recovery and population dynamics in Western Poland, 2001–2012. *Mammal Res.* **61**, 83–98. (doi:10.1007/s13364-016-0263-3)

16. Ordiz A, Bischof R, Swenson JE. 2013 Saving large carnivores, but losing the apex predator? *Biol. Conserv.* **168**, 128–133. (doi:10.1016/j.biocon.2013.09.024)

17. Treves A. 2009 Hunting for large carnivore conservation. *J. Appl. Ecol.* **46**, 1350–1356. (doi:10.1111/j.1365-2664.2009.01729.x)

18. Ritchie EG, Elmhagen B, Glen AS, Letnic M, Ludwig G, McDonald RA. 2012 Ecosystem restoration with teeth: what role for predators? *Trends Ecol. Evol.* **27**, 265–271. (doi:10.1016/j.tree.2012.01.001)

19. Johnson CN, Isaac JL, Fisher DO. 2007 Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proc. R. Soc. B* **274**, 341–346. (doi:10.1098/rspb.2006.3711)

20. Liberg O, Chapron G, Wabakken P, Pedersen HC, Hobbs NT, Sand H. 2012 Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proc. R. Soc. B* **279**, 910–915. (doi:10.1098/rspb.2011.1275)

21. Kaltenborn BP, Brainerd SM. 2016 Can poaching inadvertently contribute to increased public acceptance of wolves in Scandinavia? *Eur. J. Wildl. Res.* **62**, 179–188. (doi:10.1007/s10344-016-0991-3)

22. Fuller TK. 1989 Population dynamics of wolves in north-central Minnesota. *Wildl. Monogr.* **105**, 3–41.

23. Soulé ME, Estes JA, Berger J, Del Rio CM. 2003 Ecological effectiveness: conservation goals for interactive species. *Conserv. Biol.* **17**, 1238–1250. (doi:10.1046/j.1523-1739.2003.01599.x)

24. Oriol-Cotterill A, Valeix M, Frank LG, Riginos C, Macdonald DW. 2015 Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* **124**, 1263–1273. (doi:10.1111/oik.02224)

25. Fryxell JM, Mosser A, Sinclair ARE, Packer C. 2007 Group formation stabilizes predator–prey dynamics. *Nature* **449**, 1041–1043. (doi:10.1038/nature06177)

26. Wallach AD, Johnson CNJ, Ritchie EG, O'Neill AJ. 2010 Predator control promotes invasive dominated ecological states. *Ecol. Lett.* **13**, 1008–1018. (doi:10.1111/j.1461-0248.2010.01492.x)

27. Wallach AD, Ritchie EG, Read J, O'Neill AJ. 2009 More than mere numbers: the impact of lethal control on the social stability of a top-order predator. *PLoS ONE* **4**, e6861. (doi:10.1371/journal.pone.0006861)

28. Apollonio M, Andersen R, Putman R. 2010 *European ungulates and their management in the 21st century*. Cambridge, UK: Cambridge University Press.

29. Milner JM, Bonenfant C, Mysterud A, Gaillard J-M, Csányi S, Stenseth NC. 2006 Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J. Appl. Ecol.* **43**, 721–734. (doi:10.1111/j.1365-2664.2006.01183.x)

30. Baker PJ, Harris S. 2006 Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? *Eur. J. Wild. Res.* **52**, 99–108. (doi:10.1007/s10344-005-0018-y)

31. Gervasi V *et al.* 2012 Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore–ungulate systems in Scandinavia. *J. Anim. Ecol.* **81**, 443–454. (doi:10.1111/j.1365-2656.2011.01928.x)

32. Sand H, Vucetich JA, Zimmermann B, Wabakken P, Wikenros C, Pedersen HC, Peterson RO, Liberg O. 2012 Assessing the influence of prey–predator ratio, prey age structure and packs size on wolf kill rates. *Oikos* **121**, 1454–1463. (doi:10.1111/j.1600-0706.2012.20082.x)

33. Wright GJ, Peterson RO, Smith DW, Lemke TO. 2006 Selection of northern Yellowstone elk by gray wolves and hunters. *J. Wildl. Manage.* **70**, 1070–1078. (doi:10.2193/0022-541X(2006)70[1070:SONYEB]2.0.CO;2)

34. Cromsigt JPGM *et al.* 2013 Hunting for fear: innovating management of human–wildlife conflicts. *J. Appl. Ecol.* **50**, 544–549. (doi:10.1111/1365-2664.12076)

35. Wikenros C, Sand H, Bergström R, Liberg O, Chapron G. 2015 Response of moose hunters to predation following wolf return in Sweden. *PLoS ONE* **10**, e0119957. (doi:10.1371/journal.pone.0119957)

36. Jędrzejewski W, Jędrzejewska B, Okarma H, Schmidt K, Zub K, Musiani M. 2000 Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. *J. Mammal.* **81**, 197–212. (doi:10.1644/1545-1542(2000)081<0197:PSAPBW>2.0.CO;2)

37. Kauffman MJ, Varley N, Smith DW, Stahler DR, MacNulty DR, Boyce MS. 2007 Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecol. Lett.* **10**, 690–700. (doi:10.1111/j.1461-0248.2007.01059.x)

38. Moreno S, Delibes M, Villafuerte R. 1996 Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. *Can. J. Zool.* **74**, 1656–1660. (doi:10.1139/z96-183)

39. Creel S, Winnie J, Maxwell B, Hamlin K, Creel M. 2005 Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**, 3387–3397. (doi:10.1890/05-0032)

40. Gervasi V, Sand H, Zimmermann B, Mattisson J, Wabakken P, Linnell JDC. 2013 Decomposing risk: Landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecol. Appl.* **23**, 1722–1734. (doi:10.1890/12-1615.1)

41. Sahlén E, Noell S, DePerno CS, Kindberg J, Spong G, Cromsigt JPGM. 2016 Phantoms of the forest: legacy risk effects of a regionally extinct large carnivore. *Ecol. Evol.* **6**, 791–799. (doi:10.1002/ece3.1866)

42. Rogala JK, Hebblewhite M, Whittington J, White CA, Coleshill J, Musiani M. 2011 Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. *Ecol. Soc.* **16**, 16. (doi:10.5751/ES-04251-160316)

43. Theuerkauf J, Jędrzejewski W, Schmidt K, Gula R. 2003 Spatiotemporal segregation of wolves from humans in the Białowieża Forest (Poland). *J. Wildl. Manage.* **67**, 706–716. (doi:10.2307/3802677)

44. Wam HK, Eldegard K, Hjeljord O. 2012 From overlooking to concealed: predator avoidance in an apex carnivore. *Eur. J. Wildl. Res.* **58**, 1001–1003. (doi:10.1007/s10344-012-0670-y)

45. Ordiz A, Støen O-G, Delibes M, Swenson JE. 2011 Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* **166**, 59–67. (doi:10.1007/s00442-011-1920-5)

46. Sunde P, Stener SØ, Kvam T. 1998 Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. *Wildl. Biol.* **4**, 177–183.

47. Brook LA, Johnson CN, Ritchie EG. 2012 Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *J. Appl. Ecol.* **49**, 1278–1286. (doi:10.1111/j.1365-2664.2012.02207.x)

48. Carter NH, Shrestha BK, Karki JB, Pradhan NMB, Liu J. 2012 Coexistence between wildlife and humans at fine spatial scales. *Proc. Natl Acad. Sci. USA* **109**, 15 360–15 365. (doi:10.1073/pnas.1210490109)

49. Berger J. 2007 Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.* **3**, 620–623. (doi:10.1098/rsbl.2007.0415)

50. Muhly TB, Semeniuk C, Massolo A, Hickman L, Musiani M. 2011 Human activity helps prey win the predator–prey space race. *PLoS ONE* **6**, e17050. (doi:10.1371/journal.pone.0017050)

51. Kuijper DPJ, Bubnicki JW, Churski M, Mols B, van Hooft P. 2015 Context-dependence of risk effects: wolves and tree logs create patches of fear in an old-growth forest. *Behav. Ecol.* **26**, 1558–1568. (doi:10.1093/beheco/arv107)

52. Hebblewhite M, White CA, Nietvelt CG, McKenzie JA, Hurd TE, Fryxell JM, Bayley SE, Paquet PC. 2005 Human activity mediates a trophic cascade caused by wolves. *Ecology* **86**, 2135–2144. (doi:10.1890/04-1269)

53. Smith JA, Wang Y, Wilmers CC. 2015 Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proc. R. Soc. B* **282**, 20142711. (doi:10.1098/rspb.2014.2711).

54. Proffitt KM, Grigg JL, Hamlin KL, Garrott RA. 2009 Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *J. Wildl. Manage.* **73**, 345–356. (doi:10.2193/2008-210)

55. Tolon V, Dray S, Loison A, Zeileis A, Fischer C, Baubet E. 2009 Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. *Can. J. Zool.* **87**, 1129–1137. (doi:10.1139/Z09-101)

56. Padié S, Morellet N, Hewison AJM, Martin J-L, Bonnot N, Cargnelutti B, Chamaillé-Jammes S. 2015 Roe deer at risk: teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. *Oikos* **124**, 1536–1546. (doi:10.1111/oik.02115)

57. Lone K, Loe LE, Gobakken T, Linnell JDC, Odden J, Remmen J, Mysterud A. 2014 Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos* **123**, 641–651. (doi:10.1111/j.1600-0706.2013.00938.x)

58. Sönnichsen L, Bokje M, Marchal J, Hofer H, Jędrzejewska B, Kramer-Schadt S, Ortmann S. 2013 Behavioural responses of European roe deer to temporal variation in predation risk. *Ethology* **119**, 233–243. (doi:10.1111/eth.12057)

59. Lone K, Loe LE, Meisingset EL, Stamnes I, Mysterud A. 2015 An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Anim. Behav.* **102**, 127–138. (doi:10.1016/j.anbehav.2015.01.012)

60. Ciuti S, Northrup JM, Muhly TB, Simi S, Musiani M, Pitt JA, Boyce MS. 2012 Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE* **7**, e50611. (doi:10.1371/journal.pone.0050611)

61. Berger J, Swenson JE, Persson IL. 2001 Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science* **291**, 1036–1039. (doi:10.1126/science.1056466)

62. Sand H, Wikenros C, Wabakken P, Liberg O. 2006 Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proc. R. Soc. B* **273**, 1421–1427. (doi:10.1098/rspb.2005.3447)

63. Nicholson KL, Milleret C, Månsson J, Sand H. 2014 Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. *Oecologia* **176**, 69–80. (doi:10.1007/s00442-014-3004-9)

64. Ciuti S, Muhly TB, Paton DG, McDevitt AD, Musiani M, Boyce MS. 2012 Human selection of elk behavioural traits in a landscape of fear. *Proc. R. Soc. B* **279**, 4407–4416. (doi:10.1098/rspb.2012.1483)

65. Li C, Yang X, Ding Y, Zhang L, Fang H, Tang S, Jiang Z. 2011 Do Père David's deer lose memories of their ancestral predators? *PLoS ONE* **6**, e23623. (doi:10.1371/journal.pone.0023623)

66. Chamaillé-Jammes S, Malcuit H, Le Saout S, Martin J-L. 2014 Innate threat-sensitive foraging: black-tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100 years of wolf absence. *Oecologia* **174**, 1151–1158. (doi:10.1007/s00442-013-2843-0)

67. Carthey AJR, Banks PB. 2016 Naiveté is not forever: responses of a vulnerable native rodent to its long term alien predators. *Oikos* **125**, 918–926. (doi:10.1111/oik.02723)

68. Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013 Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* **16**, 1501–1514. (doi:10.1111/ele.12187)

69. Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR. 2015 The ecological effects of providing resource subsidies to predators. *Glob. Ecol. Biogeogr.* **24**, 1–11. (doi:10.1111/geb.12236)

70. Kuijper DPJ, Cromsigt JPGM, Churski M, Adam B, Jędrzejewska B, Jędrzejewski W. 2009 Do ungulates preferentially feed in forest gaps in European temperate forest? *For. Ecol. Manage.* **258**, 1528–1535. (doi:10.1016/j.foreco.2009.07.010)

71. Jędrzejewska B, Okarma H, Jędrzejewski W, Miłkowski L. 1994 Effects of exploitation and protection on forest structure, ungulate density and wolf predation in Białowieża Primeval Forest, Poland. *J. Appl. Eol.* **31**, 664–676. (doi:10.2307/2404157)

72. Muhly TB, Hebblewhite M, Paton D, Pitt JA, Boyce MS, Musiani M. 2013 Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. *PLoS ONE* **8**, e64311. (doi:10.1371/journal.pone.0064311)

73. Coté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM. 2004 Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* **35**, 113–147. (doi:10.1146/annurev.ecolsys.35.021103.105725)

74. Serrouya R, McLellan BN, Boutin S, Seip DR, Scott EN. 2011 Developing a population target for an overabundant ungulate for ecosystem restoration. *J. Appl. Ecol.* **48**, 935–942. (doi:10.1111/j.1365-2664.2011.01998.x)

75. Torres RT, Silva N, Brotas G, Fonseca C. 2015 To eat or not to eat? The diet of the endangered Iberian wolf (*Canis lupus signatus*) in a human-dominated landscape in Central Portugal. *PLoS ONE* **10**, e0129379. (doi:10.1371/journal.pone.0129379)

76. Mateo-Tomas P, Olea PP, Moleon M, Vicente J, Botella F, Selva N, Viñuela J, Sánchez-Zapata JA. 2015 From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Divers. Distrib.* **21**, 913–924. (doi:10.1111/ddi.12330)

77. Messier F. 1994 Ungulate population models with predation: a case study with the north American moose. *Ecology* **75**, 478–488. (doi:10.2307/1939551)

78. Melis C *et al.* 2009 Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Glob. Ecol. Biogeogr.* **18**, 724–734. (doi:10.1111/j.1466-8238.2009.00480.x)

79. Newsome TM, Ballard G-A, Fleming PJS, van de Ven R, Story GL, Dickman CR. 2014 Human-resource subsidies alter the dietary preferences of a mammalian top predator. *Oecologia* **175**, 139–150. (doi:10.1007/s00442-014-2889-7)

80. Laundré JW, Hernández L, Altendorf KB. 2001 Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Can. J. Zool.* **79**, 1401–1409. (doi:10.1139/z01-094)

81. Kuijper DPJ, Verwijmeren M, Churski M, Zbyryt A, Schmidt K, Jędrzejewska B, Smit C. 2014 What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE* **9**, e84607. (doi:10.1371/journal.pone.0084607)

82. Kuijper DPJ, de Kleine C, Churski M, van Hooft P, Bubnicki J, Jędrzejewska B. 2013 Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* **36**, 1263–1275. (doi:10.1111/j.1600-0587.2013.00266.x)

83. Wildlife Conservation Society and Center for International Earth Science Information Network. 2005 Last of the Wild project: Global Human Footprint dataset. See http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic. (doi:10.7927/H4M61H5F)

84. Imhoff ML, Bounoua L, Ricketts T, Loucks C, Harriss R, Lawrence WT. 2004 *HANPP collection: global patterns in net primary productivity*. Palisades, NY: NASA Socioeconomic Data and Applications Center.

85. Elmhagen B, Ludwig G, Rushton SP, Helle P, Lindén H. 2010 Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *J. Anim. Ecol.* **79**, 785–794. (doi:10.1111/j.1365-2656.2010.01678.x)

86. Gagné C, Mainguy J, Fortin D. 2016 The impact of forest harvesting on caribou–moose–wolf interactions decreases along a latitudinal gradient. *Biol. Conserv.* **197**, 215–222. (doi:10.1016/j.biocon.2016.03.015)

87. Basille M, Herfindal I, Santin-Janin H, Linnell JDC, Odden J, Andersen R, Arild Høgda K, Gaillard J-M. 2009 What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography* **32**, 683–691. (doi:10.1111/j.1600-0587.2009.05712.x)

88. Ford AT, Goheen JR. 2015 Trophic cascades by large carnivores: a case for strong inference and mechanism. *Trends Ecol. Evol.* **30**, 725–735. (doi:10.1016/j.tree.2015.09.012)

89. Williams CK, Ericsson G, Heberlein TA. 2002 A quantitative summary of attitudes toward wolves and their reintroduction. *Wildl. Soc. Bull.* **30**, 575–584.

90. Gangaas KE, Kaltenborn BP, Andreassen HP. 2013 Geo-spatial aspects of acceptance of illegal hunting of large carnivores in Scandinavia. *PLoS ONE* **8**, e68849. (doi:10.1371/journal.pone.0068849)

91. Chapron G, Treves A. 2016 Blood does not buy goodwill: allowing culling increases poaching of a large carnivore. *Proc. R. Soc. B* **283**, 20152939. (doi:10.1098/rspb.2015.2939)