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REVIEW

Wolves recolonize novel ecosystems leading to novel interactions

D. P. J. Kuijper[1] | T. A. Diserens[1,2] | E. Say-Sallaz[1] | K. Kasper[1] | P. A. Szafrańska[1] | M. Szewczyk[3] | K. M. Stępniak[4] | M. Churski[1]

[1]Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland

[2]Faculty of Biology, University of Warsaw, Warsaw, Poland

[3]Department of Vertebrate Ecology and Zoology, Faculty of Biology, University of Gdańsk, Gdańsk, Poland

[4]Department of Ecology, Institute of Functional Biology and Ecology, Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Warsaw, Poland

Correspondence
D. P. J. Kuijper
Email: dkuijper@ibs.bialowieza.pl

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Abstract

1. The wolf (*Canis lupus*) is arguably the most successful species at recolonizing its now human-dominated former ranges in Europe and North America. Over the centuries while the wolf was absent, humans have transformed ecosystems to a large extent. In this paper, we highlight key aspects of these human-modified ecosystems that include changes to (meso)carnivore communities, wolves themselves (genetics, behaviour), woody plant communities and the playing field for predator–prey interactions (landscape structure).
2. We argue that the recognition of the novelty of human-modified ecosystems logically leads to novel pathways of how wolves can influence ecosystem functioning. Thus far, the ecological impacts of wolves in human-dominated systems have largely been predicted based on the documented effects they have on prey species or lower trophic levels in well-preserved systems with low human impact. However, wolves in human-modified ecosystems will engage in an array of novel interactions and potential novel trophic cascades that do not occur in more natural ecosystems with lower human impact.
3. This should encourage us to re-assess the questions we ask about wolf impacts in novel systems. A promising direction for future studies is exploring what novel interactions establish and under what conditions wolves can exert their ecosystem impacts (context dependence) in the human-modified ecosystems wolves are recolonizing.
4. *Policy implications*. Understanding these novel interactions and the context dependence of ecosystem impacts could guide us to act to improve conditions to enable wolves to exert their ecosystem impacts again. These novel interactions may be the true ecological and societal value of having wolves returning to human-modified landscapes.

KEYWORDS
human-dominated landscapes, large carnivore, predator–prey interaction, trophic cascade

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1 | INTRODUCTION

In contrast to global trends (Ripple et al., 2014), the population sizes and ranges of several large carnivore species are increasing in Europe and North America (Chapron et al., 2014; Mech, 2017). This recolonization of their historical range could potentially restore their ecosystem impacts (Estes et al., 2011; Ripple et al., 2014). However, the human-dominated landscapes to which they are returning have been transformed over the decades or centuries of their absence, creating a novel playing field for predator–prey interactions (Guiden et al., 2019).

The wolf (*Canis lupus*) is arguably the most successful species at recolonizing its now human-dominated former ranges (Chapron et al., 2014; Kuijper et al., 2016). Over the centuries the wolf was absent, humans transformed European landscapes to a large extent (Fuchs et al., 2015). This has had large repercussions for the abundances, compositions and behaviour of mammal communities, including the wolf's potential prey or competitor species (for an overview see Kuijper et al., 2016). Therefore, these human-modified landscapes can be regarded as novel ecosystems (following Guiden et al., 2019), where the wolf will logically engage in potentially novel interactions and trophic cascades, as have been observed for other large carnivores (Lundgren et al., 2022).

In this paper, we highlight key aspects of these novel European ecosystems that have the potential to modify the ecological impacts of wolves. The novelty of these ecosystems is primarily driven by human-induced changes in carnivore, herbivore and (woody) plant communities, as well as changes to the physical landscape. In this paper, we argue that a new framework is required for predicting the wolf's ecological impacts in these novel, human-modified ecosystems where they are currently increasing in abundance.

Thus far, the ecological impacts of wolves in human-modified systems have largely been predicted based on the documented effects they have on prey species or lower trophic levels in well-preserved systems with low human impact (e.g., Ripple et al., 2014). However, several recent studies carried out in Europe have failed to find support, or found limited support, for these predicted changes in ungulate prey abundances (Van Beeck Calkoen et al., 2023) and behavioural responses to returning wolves (Nicholson et al., 2014; Sand et al., 2021; Van Beeck Calkoen et al., 2018) and other large carnivores (Van Beeck Calkoen et al., 2022). The impact of wolves on the behaviour of ungulates in Europe is predicted to be strongly context-dependent and can be overruled by even low levels of human impact (Kuijper et al., 2016). But does this indicate that wolves cannot re-establish the ecosystem impacts documented for more undisturbed systems, or are our predictions incorrect? Here, we argue that the recognition of the novelty of human-modified ecosystems logically leads to novel pathways of how wolves can influence ecosystem processes.

2 | WOLVES RECOLONIZING NOVEL ECOSYSTEMS

Below, we explore and describe how European ecosystems have changed across three trophic levels (i.e., predators, herbivores and plants), during the period when wolves were absent and how these changes can modify the wolf's ecological impacts (see Figures 1 and 2).

2.1 | Novel carnivore communities

The four large carnivore species occurring in Europe (brown bear *Ursus arctos*, wolf, European lynx *Lynx lynx* and wolverine *Gulo gulo*) have a discontinuous distribution with overlapping ranges in some regions, notably in Scandinavia, central Europe and the Balkans (Chapron et al., 2014). Few areas host all four species (Cretois et al., 2021) and those areas that have large carnivores do not necessarily have them at ecologically functional densities (Ordiz et al., 2013). For example, in some countries, despite legal controversies, active government-driven population control of wolf occurs, such as in Norway, Sweden and Finland (e.g., Trouwborst, Boitani, et al., 2017; Trouwborst, Fleurke, et al., 2017). Additionally, illegal killing and other human-induced mortality of wolves is widespread (Musto et al., 2021; Nowak et al., 2021).

Moreover, besides lethal control and illegal killing there is also a lot of legal recreational hunting of large carnivores in general, in northern and eastern Europe (e.g., lynx in Norway; lynx, wolf and bear in Finland and Estonia, and wolves in Latvia and Lithuania). Hence, human-caused mortality still plays a relevant role in affecting numbers of wolves and other large carnivores even in areas where they are protected (Liberg et al., 2012). Human-caused mortality affects both the abundances (density) of large carnivores and their behaviour (Ordiz et al., 2013; Oriol-Cotterill et al., 2015) and pack stability in case of social species like wolves (Cassidy et al., 2023; Wallach et al., 2009). All these factors reduce the potential for numerical and behavioural effects on prey populations and associated trophic cascades and thus downgrade their functional role (Ordiz et al., 2013; Oriol-Cotterill et al., 2015; Soulé et al., 2003). As a result, in many human-modified landscapes wolves and other large carnivores can be present without being able to perform their functional ecological role. This shows that despite recovering large carnivore populations, the functional diversity (both in numbers and in species composition) of European carnivore communities is generally impoverished.

Across the globe, regions less impacted by humans often host multi-species, large carnivore communities that are present in functional densities (Ripple et al., 2014; Say-Sallaz et al., 2019) that include species from the canid and felid families. In contrast, European systems host typically one, sometimes two and rarely three or more large carnivore species (Cretois et al., 2021). As such, these impoverished communities lack the wide array of potential intra-guild interactions that can be found in better preserved landscapes, which range from resource competition (e.g., exploitative or interference), facilitation (e.g., via carcass provisioning) and predation to behavioural suppression (Prugh & Sivy, 2020). Wolves, especially when present in the more densely human-populated regions of Europe, will in most cases occur without the modulating impacts on their ecological role that occur in areas hosting multi-species large carnivore communities (Prugh & Sivy, 2020).

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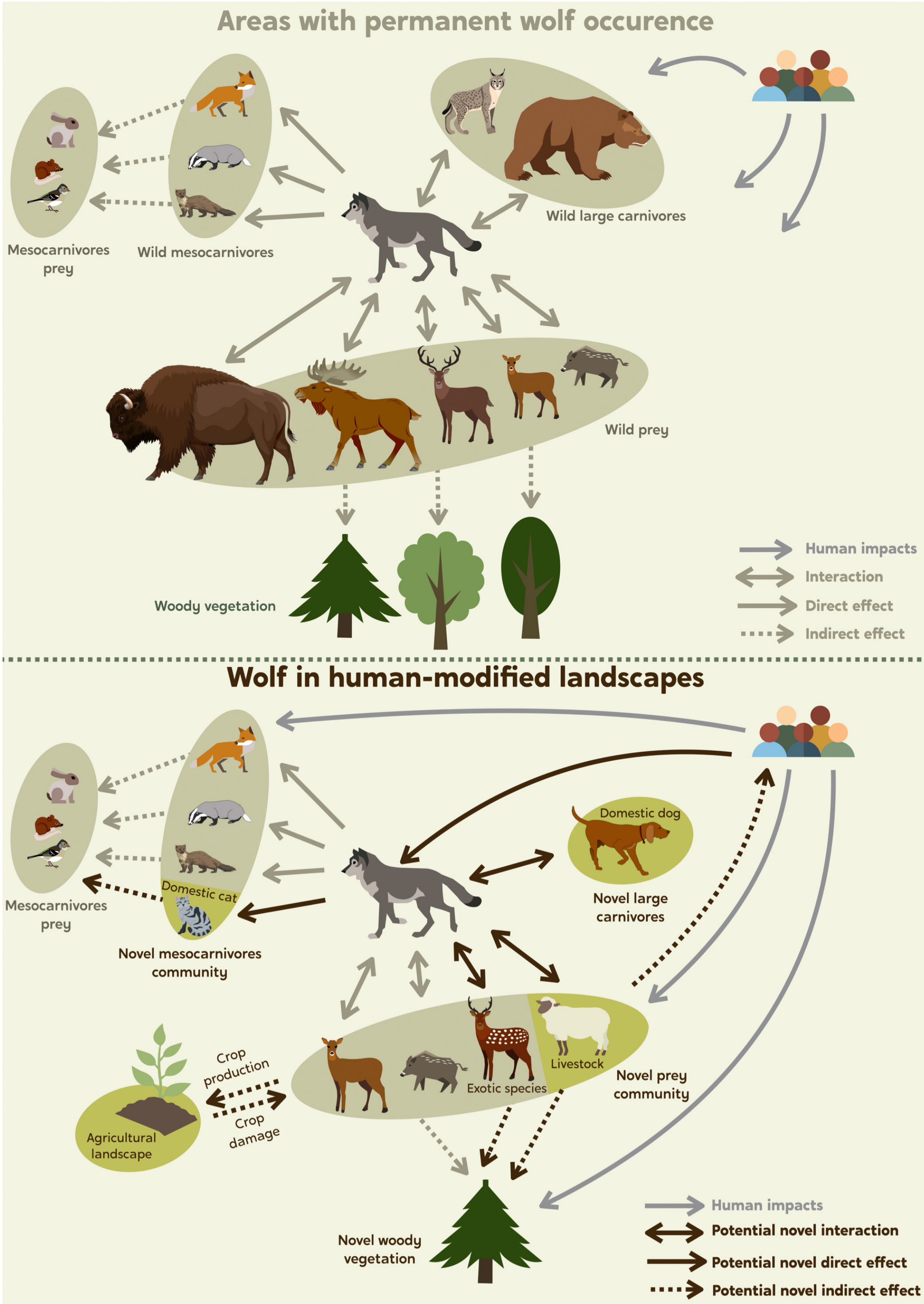

FIGURE 1 Wolves recolonize human-modified European ecosystems characterized by novel carnivore (absence of other large carnivores and modified mesocarnivore community), novel herbivore (lower diversity and potentially exotic species) and novel woody species (lower structural and species diversity) communities compared with areas with permanent wolf occurrence. Whereas the impact of man is present even in the least disturbed areas, human impacts on each trophic level are much more pronounced in novel ecosystems. Domestic animals can play a role as apex carnivores (dog) and mesocarnivores (cat), as well as providing additional prey (livestock), giving additional options for novel interactions. The interactions take place in larger and more continuous natural landscapes in areas with a permanent wolf occurrence versus in much more fragmented, agricultural landscapes in novel ecosystems. Domestic species (both animals and plants) that are integrated into ecosystems in human-modified landscapes are indicated with a green background.

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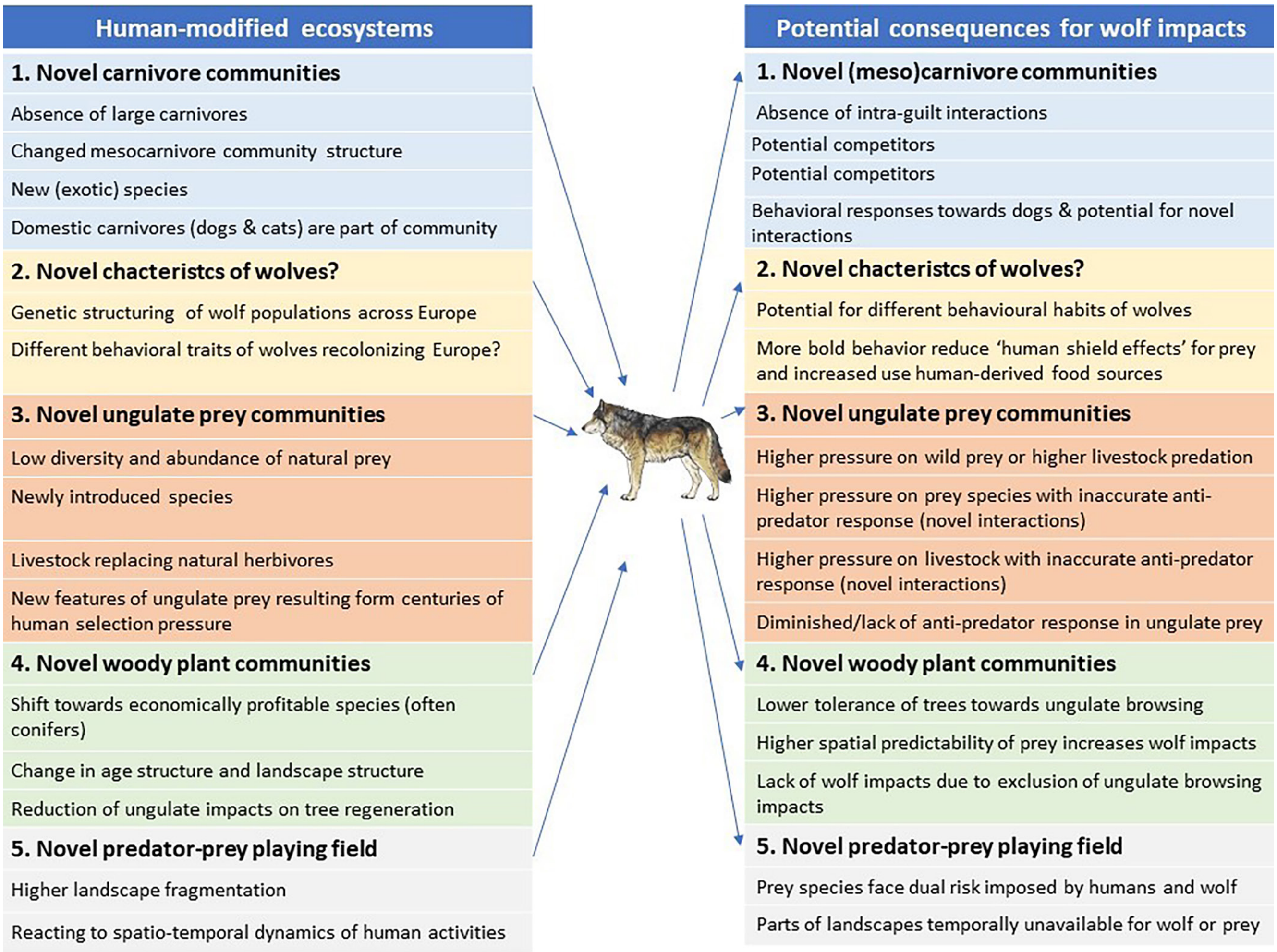

FIGURE 2 Summary of novel characteristics of ecosystems currently being recolonized by wolves. Each novel aspect has different components that either alone or in combination have the potential to modify ecosystem impacts of wolves compared with more natural systems with lower human impacts. A question mark denotes that there are indications these processes occur, but future research should confirm them.

Mesocarnivore community structures have also been transformed during the decades or centuries that wolves were absent in Europe. Large carnivores can restrict mesocarnivore abundances and distributions directly by killing and indirectly by instilling fear (Ritchie & Johnson, 2009). In the absence of large carnivores, mesocarnivore populations are 'released' from this top-down control, which can lead to increases in their distributions and abundances ('the mesopredator release hypothesis'; Prugh et al., 2009; Ritchie & Johnson, 2009). Moreover, more generalist species, such as the red fox *Vulpes vulpes*, profit from human-derived food subsidies and have adapted to live in close proximity to human settlements (Contesse et al., 2004).

In addition to these changes in abundances, the species composition of mesocarnivore communities has changed since wolves were extirpated. A newcomer, the golden jackal (*Canis aureus*), is increasingly being observed outside its original southeastern European range, with confirmed sightings in western, central and northern European countries (Trouwborst et al., 2015). Coinciding with such natural species expansions, non-native (invasive) mesocarnivore species have also been introduced to the former wolf range in Europe, such as the raccoon (*Procyon lotor*, Salgado, 2018), raccoon dog (*Nyctereutes procyonoides*, Kauhala & Kowalczyk, 2011) and American mink (*Neovison vison*). Some of these new species have pronounced documented ecosystem impacts on native species, such as those of the American mink on waterbird populations (Brzeziński et al., 2020).

Domestic carnivores are omnipresent in Europe and their ecosystem impacts should also be considered when characterizing carnivore communities. Dogs are now one of the most widespread large carnivores in the world (Lescureux & Linnell, 2014) and have significant ecological impacts (Hughes & Macdonald, 2013). Besides dogs kept as pets or living in close association with humans, large numbers of free-roaming dogs occur in many regions of Europe (Spatola et al., 2023). Wolves and dogs are wild and domestic versions of the same species (*Canis lupus* and *Canius lupus familiaris*, respectively) and can potentially interact with one another in a variety of ways (Hughes & Macdonald, 2013), including hybridization (Pilot et al., 2018). Another domestic species the cat (*Felix sylvestris*) has

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also become an integral part of the carnivore community, having widely documented ecosystem impacts (Loss et al., 2022).

The return of wolves to these novel, modified (meso)carnivore communities can, on the one hand, modify the impact of wolves on mesocarnivore abundances and/or behaviour. On the other hand, novel (meso)carnivore species could suppress abundances or behaviour of prey species (Ripple et al., 2014) that form alternative food sources for wolves and act as competitors. Finally, the presence of domestic carnivores (cats, dogs) could potentially lead to novel interactions (see Figure 1).

2.2 | Novel wolves?

There are also several lines of evidence indicating that the recolonizing wolves are different from the ones that lived there before. Firstly, genetic studies show that the wolves that have been established in Central and Western Europe derive from but also genetically differ from those in areas with long-term wolf presence (Szewczyk et al., 2019, 2021). It remains to be studied if the observed spatial genetic structure is simply a consequence of stochastic demographic processes (Jarausch et al., 2021) or if it is also associated with functional adaptations. Secondly, or as a consequence of these genetic differences, recolonizing wolves likely have different behavioural traits or personalities than wolves living in less human-dominated areas (Cote et al., 2010). Despite the increasing numbers and range of wolves in more densely populated regions in Europe and despite legal protection, humans are still the main factor influencing wolf behaviour. Even in the best preserved forest in lowland Europe, Białowieża Primeval Forest, wolves avoid parts of the landscape intensively used by humans (Bubnicki et al., 2019), with the most intensively used parts of their territories typically being located far from areas of high human activity (Bubnicki et al., 2019; Jędrzejewski et al., 2001; Theuerkauf et al., 2003). Avoidance of humans, sometimes at fine spatial scales, is a pattern that occurs throughout the wolf range (Carricondo-Sanchez et al., 2020; Sazatornil et al., 2016) and likely results from human persecution over centuries that selected for shier individuals that avoid humans to survive (as has been found in deer Ciuti et al., 2012). During the recolonization of unoccupied areas, wolves select first for the most suitable habitats but with increasing wolf abundances, dispersing individuals increasingly occupy less suitable habitats with lower forest cover and a higher share of anthropogenic structures (Nowak et al., 2017). In addition to saturation of optimal habitats, we may simultaneously be experiencing a process similar to that which led to the domestication of wolves: attraction of wolves to anthropogenic food in human-dominated areas, combined with humans responding mildly to such wolves could lead to the selection of 'tamer' wolves (Newsome et al., 2017). This seems to be in accordance with wolves in Europe being increasingly seen near or in human settlements (Huber et al., 2016; Van Liere et al., 2021). Alternatively, we may be observing a consequence of the expanding wolf population in Europe, with a higher number of subadult dispersing wolves that are known to be more bold than residents (see also Cote et al., 2010), and it is these individuals that may be being observed in human-dominated landscapes. This implies that once dispersing wolves establish a pack and territory, they return to their human-shy behaviour, which has some anecdotal support (Kojola et al., 2016). Irrespective of the underlying mechanisms, individuals that established in the most human-dominated landscapes of Europe are necessarily more tolerant to the presence of humans. Whether these individuals have more bold personalities or become habituated to higher human presence (Barry et al., 2020) is a much debated but currently unanswered question.

Living in close proximity to humans or avoiding them at finer spatio-temporal scales can modify the ecosystem impacts of wolves in human-dominated landscapes compared with more natural areas (Figures 1 and 2), for example, by increasing hybridization or sharing of parasites with domestic or feral dogs (Hughes & Macdonald, 2013), or by changing the playing field for predator–prey interactions (see Section 5).

2.3 | Novel ungulate prey communities

European ungulate population sizes are generally increasing and ungulate communities are becoming more diverse (Apollonio et al., 2010; Linnell et al., 2020), leading to not only increased ungulate-human conflicts (Carpio et al., 2021) but also opportunities (Linnell et al., 2020). Nevertheless, we argue that from an ecological perspective many regions of Europe still have greatly impoverished ungulate communities, both with respect to their abundances and diversities.

The more productive regions of Europe are characterized by the highest human footprint indexes (Kuijper et al., 2016), due to, among other factors, agriculture. To prevent crop damage in these regions, ungulate population densities are generally controlled via hunting. Without hunting, these productive parts of Europe would host the highest abundances and diversities of ungulates. While roe deer and wild boar are common in these agricultural landscapes, larger species like the red deer is less common and European bison, and moose are generally absent (Bluhm et al., 2023; Linnell et al., 2020). The largest ungulates in particular, such as the European bison, went extinct in these open landscapes and are now restricted to forests (Kerley et al., 2012). Additionally, across Europe there is a widespread policy of preventing conflict-prone ungulate species from recolonizing so-called 'zero-policy areas'. This mainly concerns the red deer (the main prey species across a large part of the wolf range, Jędrzejewski et al., 2012) and wild boar (the main prey species especially in the Mediterranean region, Meriggi & Lovari, 1996) in Germany, Netherlands and France. But ungulate densities even in the more natural or forested regions of Europe are well below the potential densities set by the environment as hunting limits their numbers (see Van Beeck Calkoen et al., 2023). Notably, even in areas with the highest protection status (i.e., national parks) ungulate numbers are usually controlled as part of conservation management. In 68% of national parks across Europe, ungulates are regulated by

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culling (40%) or hunting (11%) or both (17%). Only 29% of the national parks contain no hunting zones covering at least 75% of the area (van Beeck Calkoen et al., 2020). Ungulate management policies not only affect the spatial patterns or densities and diversities of ungulate prey species, but likewise can modify the seasonal availability of ungulate prey for wolves. In some mountainous regions of central Europe (e.g., Germany, Austria and Czechia), the traditional system of red deer management involves keeping the majority of animals in enclosures in winter, where they are supplementarily fed, to prevent browsing damage in forests (Rivrud et al., 2016). This creates artificial fluctuations in ungulate prey availability, generating very low prey abundances in winter that contrast with the natural fluctuations, which normally entail the highest deer densities being present at the beginning of winter. Moreover, this restricts prey availability during the season when food requirements for wolves are highest due to larger pack sizes with subadults that need to be fed.

While several native ungulates have disappeared from many European landscapes, new species have often been introduced in their place (Linnell et al., 2020). The mouflon (*Ovis orientalis*) has been introduced to several areas (e.g., in the Netherlands, Belgium, Germany and Poland) as a game species and to maintain open, grazed landscapes. This species originating from rocky, Mediterranean landscapes now occurs in a variety of large carnivore-free, lowland areas. Humans have also introduced fallow (*Dama dama*) and Sika deer (*Cervus nippon*) to several European countries (including Estonia, Latvia, Lithuania, Austria, Belgium, Denmark, France, Germany, Ireland, the Netherlands, Poland, Norway, Switzerland and Romania) as game species. Sporadically, other exotic ungulates occur, such as Reeves's muntjac (*Muntiacus reevesi*, in the UK and the Netherlands) and the Chinese water deer (*Hydropotes inermis*, in the UK and France). Contributing to the changes in ungulate community compositions, climate change is also expanding the ranges of native ungulate species, especially in the northern and mountainous regions of Europe (Herfindal et al., 2019).

Moreover, in regions of Europe where large carnivores do not occur or have not occurred until recently, livestock is kept in meadows with low fences (not wolf-proof) without shepherds or guard dogs making them vulnerable to predation (Linnell & Cretois, 2018). This includes regions with high livestock densities, such parts of Belgium, the Netherlands, Germany, France, Italy and Denmark. This also applies to areas with free-ranging livestock, such as cows and sheep on alpine meadows without shepherds, or semi-wild reindeer in Scandinavia. Such unprotected livestock creates easily accessible prey that in some regions comprises an important food source for wolves (Lagos & Bárcena, 2018; Vos, 2000). The availability of wild relative to domestic prey is an important factor determining the proportion of livestock in the wolf diet (Imbert et al., 2016; Meriggi & Lovari, 1996). Moreover, there is a growing interest in rewilding projects in Europe aiming to restore trophic interactions (Bakker & Svenning, 2018). As large wild ungulates are absent in many regions, wildlife managers often use cattle, sheep and horses as substitute species to restore or maintain half-open, grazed landscapes characterized by high biodiversity. With the ongoing recolonization of large carnivores across Europe, there is a growing interest in using more primitive livestock breeds in rewilding projects that are better at protecting themselves against large carnivore attacks.

For many ungulate species (including important prey species for wolves: red deer, roe deer and wild boar), hunting by humans has been and is an important or main mortality factor affecting their densities across Europe (Keuling et al., 2013; Melis et al., 2009; Van Beeck Calkoen et al., 2023). The centuries of ungulate management in human-dominated landscapes (van Beeck Calkoen et al., 2020), which followed millennia of their harvesting for food, have selectively shaped ungulate morphology (Crosmary et al., 2013) and behaviour (Ciuti et al., 2012; Sand et al., 2006). During the decades or centuries of absence of large carnivores in large parts of Europe, humans were the sole predator imposing a selective pressure. Next to changes in morphology and behaviour, this selective pressure in the absence of wolves may have reduced the natural anti-predator responses of some ungulate species (Sand et al., 2006).

2.4 | Novel woody plant communities

The presence of wolves can indirectly affect woody plant communities by modifying ungulate prey density or behaviour (Ripple et al., 2014). These trophic cascading impacts have been observed in well-preserved systems with low human impact (Bubnicki et al., 2019; Ripple et al., 2014). Therefore, in this section we focus on changes only in the woody plant communities in human-modified systems as they could modify these trophic cascading impacts of wolves.

This does not exclude that also in other parts of the landscape trophic cascading impacts could potentially occur, for example, via affecting crop damage in agricultural landscapes (see Figure 1). Moreover, how changes in other plant communities, including those in agricultural landscapes, can modify wolf's ecosystem impacts we discussed under ‘Novel playing field for predator–prey interactions’.

Despite the growing interest in nature-based silviculture, most (central) European forests are managed to maximize timber production according to strict forestry management practices that largely exclude natural processes (Kenderes et al., 2008). The cutting of canopy trees is often followed by the removal of coarse woody debris and stumps followed by planting of tree saplings (Angelstam et al., 1997; Matthews, 1991). Also, in areas where foresters prefer forests to regenerate naturally, they employ thinning to control naturally regenerating woody competitors and/or measures to control herbaceous vegetation, practices that are regarded as critical for achieving forest establishment (Ammer et al., 2011; McCarthy et al., 2011). All the aforementioned management activities interfere with natural processes associated with tree recruitment and prevent complete natural regeneration. Even management approaches that resemble natural processes, such as gap formation following selective cutting, change abiotic and biotic conditions more than natural gap formation (see Kuijper, 2011). This strongly influences the species composition and age class distribution of stands, regeneration process and resulting landscape structure.

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Forestry practices are generally aimed at wood production and hence promoting or planting commercially attractive, often fast-growing species. In many temperate areas, coniferous species are the most profitable, such as the Scots pine *Pinus* sylvestris, Norway spruce *Picea abies* and Silver fir *Abies alba*, or exotic species such as *Pseudotsuga menziesii*, *Abies grandis*, *Picea sitchensis and Larix kaempferi*. This borealization, the increasing share of coniferous species, is a well-documented phenomenon throughout temperate Europe (Jędrzejewska et al., 1994; Spencer & Kirby, 1992). It has resulted in coniferous species dominating forest stands that broadleaf species would naturally dominate (Jędrzejewska et al., 1994). In Europe, many forests have been converted to Norway spruce-dominated stands, which can only be maintained outside their natural range by silvicultural interventions that control interspecific competition and pests (Ammer et al., 2008). Plantation forests created or maintained under this system are characterized, among other features, by large homogeneous stands (often even aged and dominated by a single species). Nowadays throughout central Europe, many forestry management units aim to convert these pure coniferous stands into mixed stands with broadleaved species (Ammer et al., 2008; Knoke et al., 2008). Conifers generally show strong apical dominance, which makes them less tolerant towards ungulate browsing (i.e., their growth is more suppressed) than most deciduous species (e.g., see Churski et al., 2017). As a result, the impact of wolves on deer behaviour may shape managed tree stands differently than old-growth, mixed-species ones.

A second important consequence of forest management across Europe is that it has greatly changed the age and landscape structure of the forest. Managed forests, especially lack mature tree stands (>80 years), present in old-growth forests (Jędrzejewska et al., 1994). Although the sizes of clear cuts or gaps differ between European countries and regions, it creates a more coarse-grained mosaic of more or less homogeneous management units. This tree stand structure contrasts with the fine-scale, gap-phase dynamics that are characteristic of temperate old-growth forests (Bobiec et al., 2000; Kenderes et al., 2008). The larger gaps that forestry creates result in larger changes in microclimatic conditions, such as air and soil temperature, soil humidity and solar radiation, which all increase with increasing gap size (Latif & Blackburn, 2010). Moreover, forestry management increases landscape fragmentation (Mikusiński et al., 2018). For wolves, this affects the spatial distribution of their ungulate prey, which prefer to forage in gaps with abundant regeneration (Kuijper et al., 2009). Managed forests also have sharper contrasts between recently cut stands and older stands, which likely makes the presence of ungulate prey more predictable as they prefer the young, regenerating tree stands for wolves. The presence of more pronounced forest edges and more linear open elements in the landscape, resulting from forest roads and clear cuts, are two factors that enhance hunting success by wolves (Bojarska et al., 2017; Johnson-Bice et al., 2023).

Besides humans inducing changes in species composition, age structure and regeneration processes in forests, they can reduce or even exclude ungulate ecosystem impacts in a variety of ways. To reduce ungulate browsing damage and protect plantations, humans control ungulate numbers (as discussed under 'Section 2.3'), put up fences to protect forest plantations, or deter them by other means such as via chemical or physical deterrents. Forestry practices generally aim to reduce ungulate browsing rather than see ungulate impacts as a natural component of the tree regeneration process. In rare occasions in Europe where ungulate numbers are not controlled by hunting and co-occur with large carnivores over larger areas, such as in Białowieża Forest, ungulates are a selective agent determining regeneration levels, tree species composition (Churski et al., 2017; Kuijper, Cromsigt, et al., 2010; Kuijper, Jędrzejewska, et al., 2010) and even tree trait composition (Churski et al., 2022; Hedwall et al., 2018), engineering the ecosystem and function in a very different way than humans do. In most other managed systems, humans directly or indirectly shape the tree regeneration process and impacts of wolves on ungulate foraging behaviour may no longer impact woody plants, or will impact them in unexpected ways (Van Beeck Calkoen et al., 2018).

2.5 | Novel playing field for predator–prey interactions

In addition to changes in woody plant communities, the modifications that occurred in agricultural landscapes largely affect predator–prey interactions. First, because it transformed food availability ('foodscape') for ungulates that receive food subsidies to varying extent of agricultural crops in their diet (Spitzer et al., 2020). Second, the agricultural landscape led to a higher fragmentation and modified landscape structure. We argue that this is the last key aspect in which novel European ecosystems differ from areas with a lower human impact in their landscape structure and their spatio-temporal dynamics in human activities. Especially in its highly fragmented and multi-use landscapes, Europe generally lacks large continuous blocks of wild lands (in contrast to the US, see Mech, 2017) because they are interspersed with agricultural areas, urban areas or infrastructure. Besides this variation in land-use practices, the intensity that different parts of landscapes are used can also vary, such as spatial patterns of logging in forest systems (Mikusiński et al., 2018), which can also increase landscape fragmentation.

Why are continuous blocks of wild lands (following Mech, 2017) relevant for wolf-prey interactions? Large carnivores generally avoid humans to a larger extent than their ungulate prey (Rogala et al., 2011). Because ungulates are less sensitive to human activity than their predators, they can reduce predation risk by increasing their use of areas with higher human activity via the well-known 'human-shield effect' (Berger, 2007; Kuijper et al., 2015; Muhly et al., 2011). In areas with relatively low human pressure, such as Banff National Park (Canada) and Białowieża Forest (Poland), studies have found that human activity modifies predator–prey interactions leading to impacts measurable at the (woody) vegetation level (Bubnicki et al., 2019; Hebblewhite et al., 2005). As a result, deer presence (Kuijper et al., 2015) and browsing intensity (Kuijper et al., 2013; Van Ginkel et al., 2019) are most reduced and tree regeneration most enhanced (Kuijper et al., 2013) in areas with the lowest human pressure. Human presence may thus shift predator–prey interactions to parts of landscapes farthest away from human activities. The question is whether and in what form such

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trophic cascading effects occur in more fragmented landscapes with a restricted playing field where predator–prey interactions can occur (Kuijper et al., 2016). In these landscapes, prey species face different (either overlapping or opposing) risk landscapes imposed by humans and large carnivores. This could cause ungulate prey species to be 'squeezed' between two risk landscapes (Lone et al., 2014). On the other hand, the impact of humans may be so dominant that they override the potential ecosystem impacts of large carnivores (Van Beeck Calkoen et al., 2022). However, if wolves become more tolerant towards humans in these landscapes, the playing field for predator–prey interactions could be further modified as ungulate prey may no longer be able to use humans to win the predator–prey arms race (Muhly et al., 2011). If the predation pressure of wolves close to humans increases, then the availability of refugia for deer will diminish.

Studies have shown that linear anthropogenic elements in the landscape, even inside large blocks of wildland, can largely modify predator–prey interactions (Johnson-Bice et al., 2023). For example, oil pipelines increase the movement speed of wolves, increasing the predation pressure on woodland caribou (Dickie et al., 2017). Wolves (Bojarska et al., 2017) and other large carnivores can also use fences to facilitate killing prey (Davies-Mostert et al., 2013). Recent studies have also shown that artificial nightlight has the potential to alter predator–prey dynamics including in apex carnivores (Ditmer et al., 2021). The existing and increasing penetration of the landscape with anthropogenic light (and sounds and scents), infrastructure, forest plantation fences and border fences is another important pathway that could modify wolf impacts and change the playing field in which wolf-prey interactions take place.

Next to this more static fragmentation of the landscape, the actual presence and activities of humans in human-dominated systems can be highly dynamic, fragmenting the landscape even further. Daytime peaks in human activity increase the nocturnality of mammals across different taxa (Gaynor et al., 2018). Such avoidance of human disturbances could result in marked shifts away from natural activity patterns, modifying the interactions between species (Gaynor et al., 2018). A recent study shows that wolves take both prey availability and avoidance of human activities into account while hunting, which determines the distribution of prey kill sites (Barker et al., 2023). In systems where both humans and wolves occur, the predation risk perceived by ungulate prey may therefore also vary between day and night in relation to long-term spatial patterns of risk (Proudman et al., 2021). Human activities can make parts of landscapes temporally unattractive or unavailable for either the wolf or its ungulate prey species, illustrating that it is essential to consider these spatio-temporal dynamics of human activities when attempting to understand predator–prey interactions (Kuijper et al., 2019; Moleón & Sánchez-Zapata, 2022; Palmer et al., 2023). These human impacts resemble the spatio-temporally dynamic landscapes of fear that wolves impose on their prey species (Kohl et al., 2018) that allow prey to use high predation risk areas during times wolves are inactive (Kohl et al., 2019). A crucial difference between these more natural landscapes with human-dominated ones is that human activities modify the playing field for both the wolf and their prey and greatly modifying the spatio-temporal distribution of a range of species at the landscape scale (Suraci et al., 2019).

A further complexity is that in response to the re-appearance of wolves, humans tend to change their behaviour or policies (see Box 1). This can affect the way ungulate prey species or wolves

BOX 1 Feedbacks between wolf presence and human behaviour and policy.

With our often overriding ecosystem impacts, humans have been classified to act as 'human super predators' affecting all trophic levels including apex predators (Darimont et al., 2015). Recent studies have stressed the need to integrate human impacts as an integral part of ecosystem functioning (Kuijper et al., 2016; Moleón & Sánchez-Zapata, 2022; Palmer et al., 2023). While recent studies have shown how human factors modify wolf impacts (Bubnicki et al., 2019) or create contrasting risk landscapes (Lone et al., 2014), we did not integrate the feedback mechanisms of wolf presence on human behaviour. The recolonization of wolves, as a highly conflict-prone species, leads to emotions and discussions in society. In response to the reappearance of wolves, humans tend to change their behaviour or policy. For example, in areas in Sweden where wolves appeared hunters reduced their ungulate hunting bags to compensate for wolf-induced reductions in ungulate numbers. However, the overestimated impact of wolves leads to over-compensation by hunters and increasing ungulate numbers in areas with wolves (Wikenros et al., 2015). Other examples of changing human behaviour in response to wolf recolonization include the placement of fences to protect livestock or recommended changes in recreational activities (e.g., keep dogs leashed and prevent night activities, see Penteriani et al., 2016). These changes in human behaviour can modify wolf impacts on wildlife in general, but changes in wolf protection policy can largely influence wolves themselves. Whereas wolves have a high protective status in most European countries (Kuijper et al., 2019) changing the protective status and re-opening wolf population control are again being discussed at the European Commission level. Moreover, there are clear regional differences in attitudes towards large carnivores and people from urbanized areas tend to have a more positive attitude towards large carnivores (Williams et al., 2002). These attitudes can change dramatically when conflicts with recolonizing carnivores emerge leading to increasing anti-wolf sentiment in some areas where wolves have recovered (Williams et al., 2002). As humans are often dominant in determining ecosystem functioning and are highly reactive to changes, there is an urgent need to consider the drivers and ways how changes in human behaviour in response to increasing wolf numbers create feedback loops to ecosystem processes.

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themselves are managed. But it can also lead to people changing their outdoor activities in areas where wolves are present to minimize the risk of meeting large carnivores (e.g., avoidance of night activities or keeping dogs leashed; Penteriani et al., 2016). These reactive changes in human behaviour, including to management or conservation policies, as a response to wolf numbers increasing can create feedback loops within ecosystem processes (Box 1). This calls for increased awareness when evaluating ecological processes in which humans play intrinsic prominent role, that is, are part of the ecological system.

3 | WOLVES IN NOVEL ECOSYSTEMS CREATE NOVEL INTERACTIONS

When we acknowledge that ecosystems have been transformed across all trophic levels during the decades or centuries that wolves were absent, it implies that wolves are currently recolonizing human-modified landscapes (Chapron et al., 2014; Kuijper et al., 2016) that should be regarded as novel ecosystems. As such, we should also expect the wolf to have different ecological impacts and services in the areas it is recolonizing compared with areas less disturbed by humans (e.g., Bubnicki et al., 2019; Ripple et al., 2014). Wolves in human-modified ecosystems will engage in an array of novel interactions that do not occur in more complete ecosystems with lower human impact (Figure 1). The new aspects of these novel ecosystems include changes to prey communities, (meso)carnivore communities, wolves themselves (genetics, behaviour), woody plant communities and the playing field for predator–prey interactions, all of which have the potential to greatly modify the wolf's ecosystem impacts on prey species, (meso)carnivores and plants (Figure 2). These novel ecosystem aspects logically also raise the potential for novel interactions with cascading impacts on lower trophic levels. We not only listed some plausible novel interactions to exemplify this thinking (see Box 2), but also realize that many more (unexpected) impacts will likely become apparent in the years to come after wolves are present in human-dominated landscapes long-term.

Returning to the question raised in the introduction of whether wolves can re-establish their ecosystem impacts in novel ecosystems, the answer is 'yes, they can', looking at the evidence for behavioural impacts on prey species from European systems (e.g., Bubnicki et al., 2019; Kuijper et al., 2013, 2015; Sahlén et al., 2016). But in many respects, these impacts will differ from those recorded in areas with lower human impacts and wolf presence (Figure 2). On the one hand, the potential for trophic cascades as we know them from areas with low human impact may in many cases be strongly limited by overriding human factors or other changes in ecosystem structure. On the other hand, there is also great potential for new interactions and new pathways that can lead to trophic cascading impacts in these novel, human-modified systems (see Box 2). This calls in our opinion for re-evaluation of the hypotheses to be tested in future studies on wolf impacts in novel ecosystems.

4 | FUTURE DIRECTIONS: LOOKING FOR NOVEL INTERACTIONS

We should not have blinkers on and expect to find only the wolf-induced ecosystem impacts observed in areas relatively undisturbed by humans in Europe (Bubnicki et al., 2019) or even North America (Ripple et al., 2014). Rather, we should keep our eyes open for novel interactions (see Box 2). This means for example that large-scale changes in patterns if ungulate prey space use (Kohl et al., 2018, 2019) or impacts on ungulate densities (Van Beeck Calkoen et al., 2023) may not occur. Instead, it is more likely that changes in behaviour or community structure of prey or mesocarnivores will occur at much finer spatio-temporal scales. The novelty of human-modified ecosystems could lead to wolves exerting their ecosystem impacts in unexpected ways. Maybe they change feral cat behaviour, and in this way reduce the impacts of cats on bird communities? Or perhaps they affect crop damage by altering deer or wild boar behaviour (see Widén et al., 2022)? Looking for these novel interactions from a fresh perspective (Box 2) is the real added value of studies in European human-modified systems recently recolonized by wolves, in addition to studies documenting their impacts in areas with low human impact as a reference.

A variety of human activities characterize the human-dominated landscapes that wolves are currently recolonizing. We argue that understanding how they modify wolf behaviour and influence the ecological impacts that wolves can exert should be a crucial part of future studies (see Box 1). Especially the spatio-temporal patterns of human activities and the dynamic nature of the perceived risk they impose on wolves and their ungulate prey species should be integrated into these studies. We endorse recent pleas to integrate humans into ecological studies (Kuijper et al., 2016; Moleón & Sánchez-Zapata, 2022; Palmer et al., 2023; Suraci et al., 2019) but further add that changes in behavioural responses of wolves towards humans should be a crucial additional consideration. Studies have implicated habituation or increased tolerance of wolves to humans as a major factor in increasing the probability of wolf attacks on humans (Linnell et al., 2021; McNay, 2002) and likely also facilitating livestock predation (Meuret et al., 2020), so this potential for wolves to lose their fear of humans deserves serious attention. Preventing habituation is one of the major challenges for wolf conservation in Europe in areas where humans are widespread (Kuijper et al., 2019). Besides being relevant for wolf management, changes in the wolf's tolerance of humans have the potential to significantly modify its ecological impacts making it an important research topic (Kuijper et al., 2016).

Finally, we would be better able to predict wolf impacts in novel European systems if we studied under what context the wolf's ecological impacts occur in human-modified landscapes. For example, we could pose the following questions: do they only occur in

BOX 2 Directions for future research: potential novel interactions.

Listed below are seven plausible interactions that can occur in human-modified ecosystems leading to novel pathways for how wolves affect ecosystem processes.

1. Wolves indirectly affecting ungulate crop damage

Looking at the preference of wolves to hunt in open landscape, documented in less human-disturbed areas (Creel et al., 2005), they may likewise adapt to hunt abundant ungulates in open agricultural areas in human-dominated landscapes. Anti-predator behavioural response of ungulate prey (e.g., avoidance of high-risk open areas) may lead to reduced crop damage by ungulates (Widén et al., 2022). Alternatively, when wolves keep on avoiding open habitats and only selectively use forested parts of the landscape (Nowak et al., 2017), the opposite may occur with increasing herbivore use of open, safer, habitats leading to potential increase in crop damage by ungulates. The reduction or increase in crop damage by ungulates may be dependent on landscape configuration. How wolves will affect patterns of ungulate space use could likewise modify the spread of zoonotic diseases.

2. Wolves profiting from anthropogenic linear landscape elements

That wolves profit from human infrastructure such as pipelines has been documented for North American systems, with feedbacks to prey impact (Dickie et al., 2017). Wolves are also known to profit from (forest) roads (Zimmermann et al., 2014). As human-dominated landscapes are full of anthropogenic linear elements (e.g., roads, channels and bare strips under electricity lines) wolves may increasingly adapt to profit from these elements to facilitate their movement and hunting success. Besides, fences are known to increase hunting success or large carnivores (Davies-Mostert et al., 2013) and also for wolves this has been shown (Bojarska et al., 2017). The presence of fences and the increasing occurrence of border fences (Linnell et al., 2016) may facilitate the hunting success of wolves and increase their impact on ungulate prey.

3. Wolves mediating impacts of feral cats and dogs

The enormous impacts on small mammals and birds of feral cats and dogs have been well-documented (Hughes & Macdonald, 2013; Loss et al., 2022). Large carnivores, such as wolves, interact with mesocarnivores in several ways ranging from predation, facilitation and competition (Prugh & Sivy, 2020). Intra-guild suppression on both felids and canids occurs, especially with felid apex predators (as wolf). In this way, wolf presence could modify the behaviour of cats and dogs (potentially induced by changed human behaviour, see Box 1) by creating a risky landscape or suppressing population density of feral cats and dogs. If so, wolves potentially reduce deleterious impact of cats on bird communities (Loss et al., 2022) or the impact of dogs on wildlife communities (Hughes & Macdonald, 2013).

4. Different human activities create different fear effects on wolves

Wolves are smart animals and learn fast. Especially after frequent exposure to certain types of human activities, they may quickly learn to associate some human activities with more risk than others. For example, recreation might be perceived as less fearful and hunters (even when targeting ungulates) as more. Different human activities may therefore lead to largely different impacts on wolves or modify in a bottom-up fashion other wildlife including ungulate prey.

5. More benign response to humans alters human-shield effects for prey

When wolves become more tolerant to human presence in human-dominated landscapes or bolder individuals are more likely to settle or survive, this impacts their patterns of space use. Large carnivores generally more strongly avoid human presence than their ungulate prey, leading to 'human-shield' effects. Prey can profit from human presence by providing relatively safe areas. These processes have been well-documented in less human-disturbed areas but could work differently in human-dominated systems. A higher tolerance of wolves towards humans would reduce or diminish these human-shield effects leading to modified spatial interactions between wolf and their prey.

6. Positive feedback of livestock presence on wolf impacts on wild prey

In several regions in Europe, wolves rely on livestock as an important additional or alternative food source. When livestock protection measures are not adequate this can lead to an important human-derived food source leading to an array of possible impacts on the

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BOX 2 (Continued)

apex predator (Newsome et al., 2017). It could facilitate higher wolf numbers than when they would rely on natural prey alone leading to increasing wolf numbers exerting stronger impacts on natural prey (Newsome et al., 2015).

7. Wolf recolonization leading to changes in livestock husbandry practices

In some regions in Europe, the practices for livestock husbandry have been developed in the absence of wolves during the last one to two centuries. Some of these practices, like keeping sheep in large herds and leaving them unattended roaming large areas (e.g., in France and cattle in alpine meadows), may become unattractive or economically unfeasible to maintain. As these livestock husbandry practices have shaped the landscape, abandonment or changes in these practices can lead to the transformation of these pastoral landscapes.

non-hunted ungulate populations, or only in parts of the landscape with low human presence, or how does wolf hunting affect their ecological role? We argue that future research should focus on this context-dependence of wolf impacts on prey or mesocarnivore species (see also Wirsing et al., 2021).

5 | IMPLICATIONS

Several recent studies failed to find the effects of wolves in human-dominated systems that they initially predicted (e.g., Nicholson et al., 2014; Sand et al., 2021; Van Beeck Calkoen et al., 2018, 2023). The results of these studies contrast with those from the least human-impacted areas in Europe, which did find trophic cascading impacts of wolves, albeit being strongly modified by human activities (Bubnicki et al., 2019; Van Ginkel et al., 2019). This implies that the ecosystem impacts of wolves can be redundant compared with the overriding human impacts (e.g., recreation, hunting and traffic) on ungulate prey and mesocarnivore species or other trophic levels (Kuijper et al., 2016). We argue that it is not so much that wolves will have no ecosystem impacts in European human-dominated landscapes, but rather that these impacts (including novel interactions) can occur but will be highly context-dependent. This has important implications for the management of wolves in human-dominated landscapes. Understanding the context dependence could guide us to act to improve habitat conditions to enable wolves to exert their ecosystem impacts again. In other words, in some areas we could reduce human impacts and allow wolves to do part of the jobs that we have taken over from them (i.e., impacting prey densities & their behaviour). In fact, the EU Habitats Directive requires member states to maintain the wolf at favourable conservation status, which not only refers to numbers and population connectivity, but also requires the wolf to be a 'viable component of its natural habitat'. This sentence is often interpreted as meaning that the ecological functionality of the wolf should be preserved (Epstein, 2016; Trouwborst, Fleurke, et al., 2017). The need to allow more natural processes in nature management fits with recent findings that less than 28% of European national parks follow the IUCN recommendation to have at least 75% of the area protected as a non-intervention zone (van Beeck Calkoen et al., 2020). If we want to maximize the wolf's ecosystem services, we should start reducing human impacts and allow more space for wolves to exert their ecosystem impacts again to restore processes we have lost in their absence. We conclude that rather than be disappointed with not finding re-established ecosystem impacts after wolves recolonize human-modified landscapes, we should look with a fresh view and not necessarily expect to find impacts similar to those observed in low human-impacted areas. This also should encourage us to re-assess the questions we ask about wolf impacts in novel systems by evaluating the degree of changes across trophic levels (Figures 1 and 2; Box 2). Wolves entering novel, human-modified ecosystems imply that expected wolf impacts also differ from documented impacts in less human-impacted areas. A more promising direction for future studies is exploring what new interactions establish in the novel ecosystems wolves are colonizing. These novel interactions may be the true ecological and societal value of having wolves return to landscapes now dominated by humans.

AUTHOR CONTRIBUTIONS

Dries P. J. Kuijper: Conceptualization; funding acquisition; project administration; supervision; visualization; writing—original draft; writing—review and editing. Tom A. Diserens: Writing—original draft; writing—review and editing. Elise Say-Sallaz: Visualization; writing—review and editing. Katharina Kasper, Paulina A. Szafrańska, Maciej Szewczyk and Kinga M. Stępniak: Writing—review and editing. Marcin Churski: Conceptualization; funding acquisition; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

We declare that there were no potential sources of conflict of interest.

DATA AVAILABILITY STATEMENT

No data were used for this study.

ORCID

D. P. J. Kuijper https://orcid.org/0000-0002-0324-5893
E. Say-Sallaz https://orcid.org/0000-0002-5106-566X
K. Kasper https://orcid.org/0000-0001-9948-2377
M. Szewczyk https://orcid.org/0000-0001-7424-1120
K. M. Stępniak https://orcid.org/0000-0002-4506-2542
M. Churski https://orcid.org/0000-0001-8727-0203

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