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RESEARCH ARTICLE

Wolf reintroduction to Scotland could support substantial native woodland expansion and associated carbon sequestration

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Abstract

1. Large carnivores, including the grey wolf (*Canis lupus*), play an important role in the carbon cycle through modifying the behaviour and population of wild herbivores. Large carnivores have been eradicated from much of their former range and are now absent from the UK, contributing to increased herbivore populations, which can prevent natural regeneration of trees and woodland. A reintroduction of wolves to the UK could reduce deer populations and associated browsing of tree saplings, but the potential impacts on woodland expansion and carbon sequestration have not been assessed.
2. Here we estimate the impact of a wolf reintroduction in the Scottish Highlands on red deer populations, native woodland colonisation and carbon sequestration. We use a Markov predator–prey model to estimate that a reintroduction would lead to a population of 167 ± 23 wolves, sufficient to reduce red deer populations below 4 deer km^{-2}, the threshold at which we assume browsing to be sufficiently suppressed to enable natural colonisation of trees.
3. Using a model of potential new native woodlands we estimate the subsequent expansion of native woodland would result in an average annual carbon sequestration of 1.0 ± 0.1 Mt CO_2, with each wolf contributing an annual carbon sequestration of 6080 t CO_2.
4. *Practical Implication*. Our analysis demonstrates the ecosystem benefit that wolves can provide through control of red deer numbers, leading to native woodland expansion. Large-scale expansion of woodlands, facilitated through the return of wolves, can contribute to national climate targets and could provide potential economic benefits to landowners and communities through carbon finance.

KEYWORDS
carnivore restoration, native woodland, natural colonisation, trophic cascade, wolf reintroduction

1 | INTRODUCTION

Large carnivores play an important role in regulating ecosystems (Estes et al., 2011; Ripple et al., 2014). They alter the abundance and behaviour of their prey (Emerson et al., 2024; Manning et al., 2009), impacting vegetation structure (Beschta & Ripple, 2009), ecosystem function (Suraci et al., 2016), biogeochemical cycling and the carbon cycle (Leroux et al., 2020; Rizzuto et al., 2024; Schmitz et al., 2018; Schmitz & Leroux, 2020; Strickland et al., 2013). Recent work has suggested that the grey wolf (*Canis lupus*) enhances annual ecosystem carbon uptake by 260 Mt CO_2 across Northern Hemisphere forests through modifying herbivore populations and behaviour (Schmitz et al., 2023). Reintroducing wolves to parts of their natural range where they are no longer present could further increase carbon sequestration, contributing to the natural climate solutions that are needed to prevent climate warming exceeding 2°C (Griscom et al., 2017).

Large carnivores have experienced substantial population declines and range contractions (Ripple et al., 2014) and are now absent from the United Kingdom (UK). Lynx were eradicated from the UK around 700 AD (Hetherington et al., 2006) and the wolf was eradicated from Scotland about 250 years ago (Nilsen et al., 2007). The loss of natural predators, in particular the wolf, has contributed to increased population of Red deer (*Cervus elaphus*) across Scotland (Clutton-Brock et al., 2004). Despite ongoing management, red deer numbers in Scotland have increased over the last century (Edwards & Kenyon, 2013) with latest estimates of 360,000–400,000 (Pepper et al., 2020).

Deer abundance has important impacts on natural ecosystems including vegetation composition and dynamics, growth and survival of tree saplings, and nutrient cycling (Côté et al., 2004). Natural regeneration and colonisation of woodland in Scotland is limited by herbivore browsing (Gullett et al., 2023; Miller et al., 1998; Rao, 2017; Tanentzap et al., 2013). Increased deer populations also have widespread impact on woodland ecology (Fuller & Gill, 2001). The maximum density of deer under which regeneration and establishment of woodland can occur depends on the tree species, vegetation, soil fertility and herbivore distribution (Miller et al., 1998; Palmer et al., 2004). Palmer and Truscott (2003) found that less than 15% of saplings were browsed for deer densities below 2 km^{-2}, increasing to 30% for deer densities of 10 km^{-2} and to 80% for deer densities of 20 km^{-2}. Tanentzap et al. (2013) suggested that <10% of seedlings can be browsed to enable tree establishment, suggesting deer density exceeding 2 to 10 km^{-2} would suppress regeneration.

Deer, in combination with sheep in some areas, prevents tree regeneration across much of Scotland. The density of red deer on open-hill ground in the Highlands and Islands of Scotland in winter 2019 was estimated as 9.35 km^{-2} (Albon et al., 2019), too high to allow natural regeneration or colonisation. Lack of tree regeneration has contributed to a long term decline and loss of native woodland, with less than 4% of Scotland currently covered by native woodland (Native Woodland Survey of Scotland, 2014). At such high deer densities, natural regeneration and colonisation of woodland is largely restricted to areas where deer are excluded by fencing (Palmer et al., 2009). More intensive deer management in some locations has been shown to facilitate tree regeneration with increasing number of tree seedlings when red deer numbers were reduced below 3.5 km^{-2} (Rao, 2017). A reduction in deer numbers to less than 6 km^{-2} over a 60,000 ha landscape in the Cairngorms in eastern Scotland, facilitated natural colonisation and created about 164 ha of new woodland each year over a 30 year period (Gullett et al., 2023). If deer numbers were reduced more widely to levels that would permit natural colonisation, Fletcher et al. (2021) estimated that more than 39,000 km^2 of the Scottish Highlands would be suitable for establishment of native woodland.

In recent decades, large carnivores have started to re-establish across areas of mainland Europe (Chapron et al., 2014; Cimatti et al., 2021). Wolves now occupy 67% of their former European historical range (Ripple et al., 2014), including human-dominated landscapes in Central Europe, demonstrating an ability to co-exist close to humans (Chapron et al., 2014; Cretois et al., 2021). The wolf population in Western Europe now exceeds 12,000 (Hindrikson et al., 2017). Due to the natural barrier presented by the sea, reintroduction would be necessary to re-establish large carnivores in the UK (Seddon et al., 2014). Nilsen et al. (2007) suggested a wolf reintroduction to Scotland could result in 25 wolves per 1000 km^2. Gwynn and Symeonakis (2022) estimate a contiguous area of 10,139 to 18,857 km^2 of Scotland would be suitable for wolf and could support 200 to 376 individuals (50 to 94 wolf packs).

There is increasing acknowledgement that the climate and biodiversity crises cannot be managed in isolation (Pörtner et al., 2021), with greater interest in the potential role of natural processes, including restoring trophic cascades for ecosystem recovery (Cromsigt et al., 2018), to deliver co-benefits for climate, and nature recovery. Climate mitigation and adaptation will require large-scale changes in land management (Smith et al., 2019). Fletcher et al. (2021) estimated expansion of native woodlands across the Scottish uplands could remove nearly 700 million tons of CO_2 and make a sizeable contribution to national climate targets.

Discussions around potential large carnivore introductions to the UK (Convery et al., 2023; Wilson & Campera, 2024) and elsewhere (Gonzalez et al., 2024) are ongoing. The potential for a wolf reintroduction to reduce red deer populations in the Scottish

Highlands has already been demonstrated (Nilsen et al., 2007) but the impacts on woodland establishment and carbon sequestration have not been assessed. Here we combine a range of models to provide the first estimate of the impact of a reintroduction of wolves to Scotland on red deer population, natural colonisation of native woodlands and associated carbon sequestration. The expansion of wolves across their former range in western Europe has created substantial conflict, particularly with farmers and hunters (Martin et al., 2020). Substantial and wide-ranging stakeholder and public engagement would clearly be essential before any wolf reintroduction could be considered. Our aim is to provide new information to inform these ongoing and future discussions around human-wolf conflict and wolf reintroductions both in the UK and elsewhere.

2 | MATERIALS AND METHODS

2.1 | Wild Land Areas

We focused our analysis on the Scottish Wild Land Areas (WLAs), defined as the "most extensive areas of high wildness" in Scotland. WLAs were identified using a methodology based on the relative wildness of the landscape (NatureScot, 2014), taking into account perceived naturalness, rugged or challenging terrain, remoteness from public mechanised access, lack of built modern artefacts. WLAs are nationally important in Scottish Planning Policy, but are not a statutory designation.

Because WLAs have been identified as Scotland's more natural and remote landscapes with low levels of human influence, they represent a potential target for any future wolf reintroduction. There are 42 WLAs in Scotland covering 14,537 km^2, nearly 20% of Scotland. We selected the four largest contiguous areas of wild land in the Scottish Highlands which we defined as WLAs separated by less than 5 km in distance and not intersected by major human infrastructure such as a dual-carriageway road. These four areas are: (i) Cairngorms (Cairngorms; Lochnagar–Mount Keen), (ii) South-west Highlands (Rannoch—Nevis—Mamores—Alder, Loch Etive mountains; Breadalbane—Schiehallion; Lyon–Lochay, Ben Lawers; Ben Lui, Ben More, Ben Ledi), (iii) Central Highlands (Kinlochhourn—Knoydart—Morar, Central Highlands Fisherfield—Letterewe—Fannichs; Moidart—Ardgour; Coulin and Ledgowan Forest, Flowerdale—Shieldaig—Torridon), (iv) North-west Highlands (Rhiddoroch—Beinn Dearg—Ben Wyvis, Inverpolly—Glencanisp, Quinag; Foinaven—Ben Hee, Ben Hope—Ben Loyal, Cape Wrath, Reay—Cassley, Ben Kilbreck—Armine Forest). These areas vary in size from 2100 km^2 to 4100 km^2 with a total area of 12,167 km^2 (Figure 1). Each area is individually larger than the minimum of 600 km^2 required for viable wolf populations (Sandom et al., 2012) and match the areas previously identified as the most suitable for wolf reintroduction in Scotland (Gwynn & Symeonakis, 2022). We assumed separate reintroductions within each area. As in previous work (Nilsen et al., 2007; Sandom et al., 2012) we assumed that wolves are confined to the introduction area and are not free to spread to surrounding regions as would be the case if the area was fenced. However, we acknowledge that securely fencing large areas would be challenging and unlikely to be feasible. Future work is needed to understand how wolves might be likely to spread if they were free to move across Scotland and how this would alter both equilibrium populations and temporal development of populations.

2.2 | Red deer—Wolf population modelling

We based our red deer and wolf population modelling using the models described in Nilsen et al. (2007). The red deer population model is a density-dependent, discrete-time, age- and sex structured Markov model parameterised based on a long-term individual-based study of red deer in Scotland (Clutton-Brock et al., 1982). The deer population dynamics include interactions between density dependence, climate and age structure (Clutton-Brock & Coulson, 2002; Clutton-Brock et al., 2002; Milner-Gulland et al., 2004). This model simulates the observed population dynamics of red deer in Scotland (Nilsen et al., 2007).

Survival and fecundity probabilities were fitted as logistic functions of hind density according to $R_{i,j} = 1 - \frac{1}{1+e^{-a+bD}}$, where $R_{i,j}$ is the deterministic vital rate for sex i in age class j, a and b are coefficients, and D is the density of adult hinds (≥3 years). The proportion of males at birth (m) is calculated as $m = 0.6438 – 0.00748D$.

The stochastic adult hind mortality for hinds in age class j was calculated as $\rho_j = R_j + z\sigma_j$, where z is a standardised normal deviate with a standard deviation of σ_j. The model assumes fecundity and other class-specific mortality rates are correlated with adult hind mortality such that $\rho_{i,j} = R_{i,j} + \sigma_{i,j} z \sqrt{1 - r^2} + r\sigma_{i,j} A$, where $\rho_{i',j}$ is the stochastic rate for sex i and age j, r is the correlation between the rate and adult hind mortality, and A is the average of the z-values for adult hind mortality (Clutton-Brock et al., 2002; Milner-Gulland et al. 2004). We assume $r = 0.522$ for stag mortality and $r = -0.452$ for all other rates.

The wolf population was simulated using an individual based model. The wolf population was characterised as the number of packs, the number of wolves in each pack, and the age, sex and social status of each wolf classified as juvenile (J; 6–18 months), sub-adult (Sa; 18–30 months), sub-dominant adult (A; >30 months) or dominant adult (Do). All packs that include an alpha pair are assumed to produce a litter. The discrete probability distribution for litter size had a mean of 3.5 pups and a range from zero to six. The sex of each recruit was determined as a result of a Bernoulli trial with mean 0.5. Individuals are recruited into the population at 6 months. We assume different wolf survival rates for juveniles, wolves aged 1–6 years, and older wolves (>6 years). If the pack includes one or more alpha individuals, dispersal of the rest of the pack was calculated as a binomially distributed random variable, assumed to be age-dependent, with older individuals more likely to disperse. Alpha individuals are assumed not to disperse. If both alpha individuals died, all remaining members of the pack

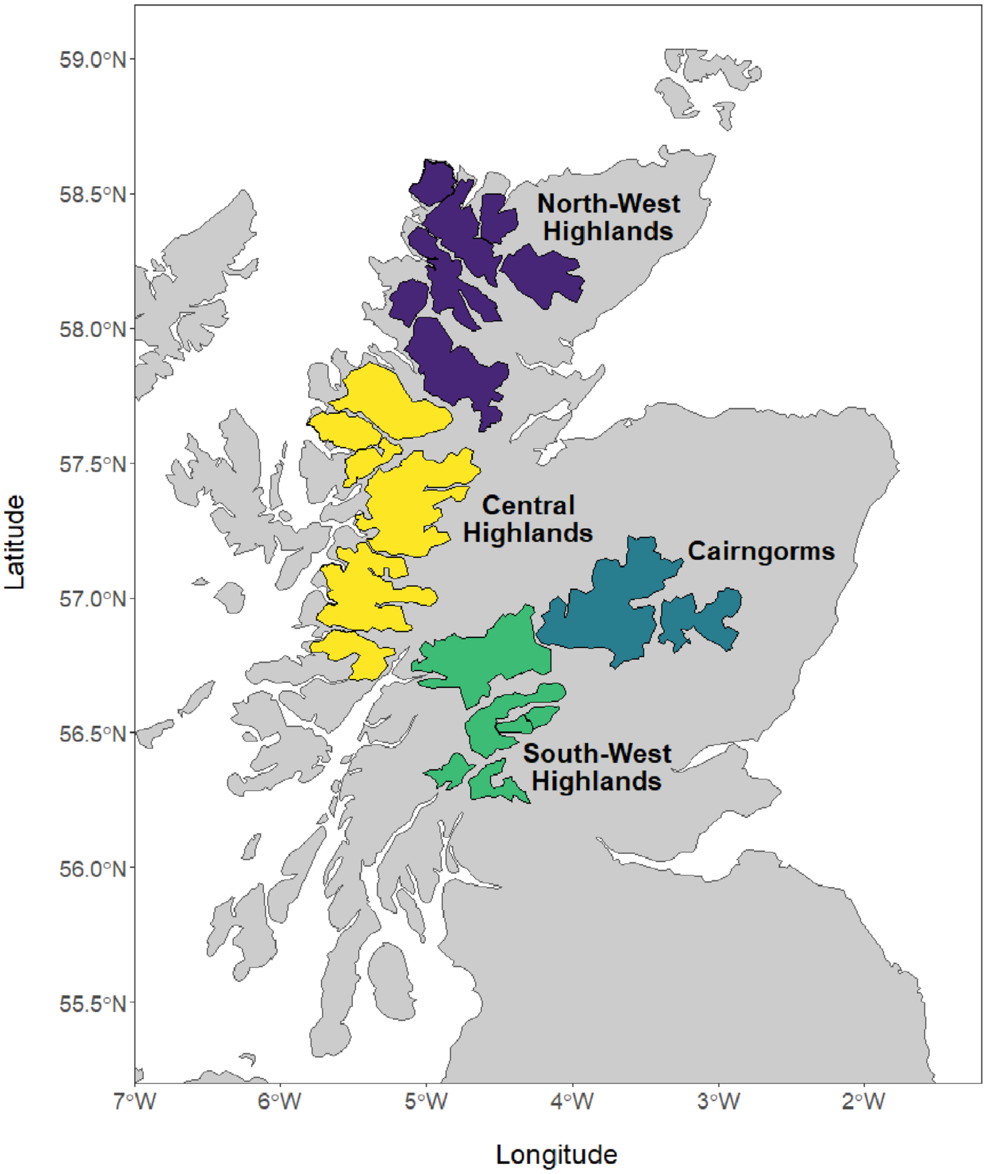

FIGURE 1 Location of the four areas where wolf reintroductions are simulated: Cairngorms, South-West Highlands, Central Highlands and North-West Highlands.

dispersed. If only one dominant individual was alive, the pack continued to occupy the territory but did not breed until a dispersing adult joined the pack.

We assume dispersing individuals can become breeders either by occupying a vacant territory that an individual of the opposite sex also dispersed into or by joining widowed alpha individuals of the opposite sex. Juvenile wolves can only breed after 1 year after dispersal, consequently the minimum age of first reproduction was 24 months. Dispersing wolves that were not successful in establishing a territory were assumed to die. We assume that dispersing wolves cannot join packs with an alpha pair.

Dispersal probabilities for juveniles, sub-adults and adults when one or both breeders were present were 0.3, 0.5 and 0.9, respectively. Dispersing wolves were assumed to actively seek a territory in which to become breeders. We assumed that 30% of the dispersing wolves were not successful in occupying a territory when vacant territories were available.

The mean density of red deer in the Highlands and Islands of Scotland has recently been estimated as 9.35 (8.01–10.69, 95% CI) deer km^{-2} (Albon et al., 2019). For each simulation, we ran the red deer model for 50 years before a wolf reintroduction. For each of the four regions simulated, we applied a hind harvest rate of 10% that results in a red deer density prior to wolf reintroduction of ~9 deer km^{-2}. We tested the sensitivity of using initial red deer density of 8–11 deer km^{-2}, and found that this did not alter our results. Nilsen et al. (2007) found that red deer populations could not support a hind harvest greater than 4%–5% as well as a viable wolf population. We assumed that hind harvest continues at 10% after wolf introduction, but reduced the hind harvest rate to 5% if deer populations are less than 8 deer km^{-2} and to 1.5% if numbers are less than 6 deer km^{-2}.

In each region simulated, we assumed a reintroduction of three wolf packs, each consisting of three wolves. For each area, we ran the model 100 times.

In our simulations, we updated the deer and wolf population annually within each of the four regions for 100 years after wolf reintroduction, based on the underlying model parameters. We calculated the mean and standard deviation of wolf and red deer density across the 100 simulations.

We tested the sensitivity of our results to uncertainty in the parameters in the wolf population model. We selected the parameters that were identified by Nilsen et al. (2007) as being the most important: the rate at which wolves kill deer when deer are abundant (a), adult wolf survival rates (s_{adult}) and the probability that a dispersing wolf is successful in establishing a territory (p_{settle}). For each parameter we completed 10 sensitivity simulations varying the parameter by up ±10% in increments of 2 percentage points. For each parameter, we calculated the standard deviation of wolf density calculated by the model across the 10 simulations. We combined the standard deviations in quadrature to estimate an uncertainty in wolf population.

2.3 | Potential for native woodland

We used the potential for native woodland model (NWM; Towers et al., 2004) to predict potential national vegetation classification (NVC) woodland types across the four areas selected in this study. The model predicts the woodland types that would be expected under current soil and vegetation conditions with no or minimal ground intervention, including fertilisation, ground preparation and drainage. The model uses information on soils from the national soils survey and the national land cover map (Towers et al., 2004).

The outputs of the model are categorised into 58 woodland types, which may be single, interchangeable or mosaics of different NVC classes. A comparison of the woodland types simulated by the NWM with on-the-ground NVC surveys, suggest that the NWM accurately predicts site suitability for a range of NVC classes spanning oakwoods, ashwoods and pinewoods (Towers et al., 2004) that are the dominant NVC classes across the areas in our study.

Previous studies have suggested that deer numbers less than 5–10 km^{-2} are required to allow tree establishment (Beaumont et al., 1995; Miller et al., 1998; Mitchell et al., 1977; Rao, 2017; Staines, 1995). We assumed that natural colonisation and tree establishment occur if deer numbers are reduced to less than 4 km^{-2}. In a sensitivity study, we assumed natural colonisation occurs below deer numbers of 7 km^{-2}.

2.4 | Carbon sequestration

We assumed carbon sequestration for mature native woodland (80% canopy cover) of 84 tonnes of carbon per hectare ($tC\,ha^{-1}$) based on data from 12 native woodland sites across Scotland (Perks et al., 2010). These were predominantly upland sites with nutrient poor soils with similar conditions and NVC types to those simulated by the NWM across the WLA that were the focus on this study including W17 (upland oak/birch with bilberry), W18 (Scots pine with heather), W11 (upland oak/birch with bluebell/wild hyacinth), W7 (alder/ash with yellow pimpernel), W9b (upland ash with birch/rowan/aspen) and W4 (birch with purple moor grass).

To provide carbon sequestration for different woodland types predicted by the NWM, we scaled carbon sequestration by the canopy cover for each woodland type. To determine the percentage canopy cover for the woodland types predicted by the NWM, each component part of the woodland types was assigned a canopy cover value based on the values in Fletcher et al. (2021): Types W4a, W6-W11 and W16-W19 were assigned 80% canopy cover; W4 (with open ground) and Sc1, Sc3, Sc6 and Sc7 were assigned 30% canopy cover; and Sc2, Sc4, Sc5 and Sc8 were assigned 10% canopy cover.

As in Fletcher et al. (2021), we assumed new woodlands take 100 years to reach maturity. We assumed carbon sequestration begins when deer numbers reduce below the threshold for natural colonisation. We calculated cumulative carbon sequestration over a 100 year period and assumed that carbon sequestration is linear across this period from the year when natural colonisation begins, which is reasonable when calculating the cumulative impact over 100 years. We did not account for potential changes in below-ground and soil carbon (Tanentzap & Coomes, 2012) and so total carbon sequestration is likely to be higher than presented here.

We calculated sensitivity of our carbon sequestration estimates to parameters in the wolf population model. For each of the parameters tested we calculated the year deer populations fall below the threshold for natural colonisation and then calculated the resulting carbon sequestration for that scenario. We report the standard deviation across all the parameter combinations.

We calculated an annual financial benefit associated with carbon sequestration assuming £25.36 per tonne of CO_2 based on UK Woodland Carbon Code prices in 2023 (Woodland Carbon Code, 2023) ($31.95 per tonne CO_2 assuming GBP £1 = US $1.26). We did not apply inflation to our estimated financial benefits. We calculated a nominal value per wolf by dividing the annual financial benefit by the average wolf population. We estimated an uncertainty by combining our uncertainty in the wolf population and the uncertainty in carbon sequestered.

2.5 | Model framework

Figure 2 shows the model framework used for our study. The Wild Land Area mapping (Section 2.1) was used to determine the spatial extent of the area. We then applied a red deer–wolf model (Section 2.2) to simulate the annual dynamics of red deer and wolf populations. The annual population of red deer was used along with the native woodland model (Section 2.3) to simulate the potential expansion of native woodland. Finally, information on the carbon sequestration of new native woodlands (Section 2.4) was used to estimate the annual carbon sequestration.

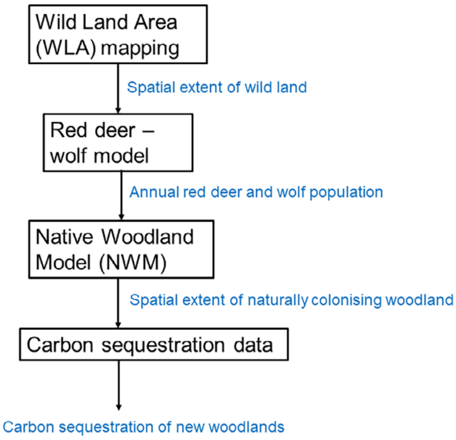

FIGURE 2 Model framework for simulating the impacts of grey wolves on red deer populations, native woodlands and carbon sequestration.

The models were coupled at an annual time-scale. Each year the red deer and wolf population was used to assess the potential for woodland expansion and the annual carbon sequestration was calculated. A simplification of our approach is that the expansion of woodland does not alter red deer–wolf population dynamics.

3 | RESULTS AND DISCUSSION

Table 1 reports the results of our simulations. Average wolf populations after reintroduction are 13–14 wolves per 1000 km^2, somewhat lower than the 20–49 wolves per 1000 km^2 recorded in unmanaged wolf populations in the Bialowieza Forest, Poland (Jedrzejewski et al., 2002) or 25–100 wolves per 1000 km^2 in the Yellowstone National Park, USA (Hobbs et al., 2024). The lower estimated carrying capacity in our study may be because we assume that wolves only predate red deer, whereas in reality there are multiple prey species. Total wolf populations vary from 27 wolves in the Cairngorms to 56 wolves in the Central Highlands. The total population across the four areas of the Scottish Highlands is estimated to be 167 ± 23 wolves, similar to previous estimates (Gwynn & Symeonakis, 2022; Nilsen et al., 2007). Our estimated total population is also similar to the viable population of 200 wolves estimated for the recent reintroduction to Colorado, USA (Hoag et al., 2023).

Deer populations decline after a wolf reintroduction (Figure 3). In our simulations, it takes 20–23 years after wolf reintroduction for deer populations to decline below 4 km^{-2} (Table 1; 11–12 years for deer populations to decline below 7 km^{-2}). Our results on wolf–deer dynamics are similar to those reported in Nilsen et al. (2007). Passoni et al. (2024) used a wolf-elk model to simulate that a population of 99 wolves was sufficient to reduce elk numbers by 61% in the Yellowstone ecosystem. In the western European Alps, a wolf density of 17–29 wolves per 1000 km^2 caused 19%–51% of annual red deer mortality sufficient to have a limiting effect on populations (Gazzola et al., 2007). In the Bialowieza Forest in Poland, wolves took 12% of red deer each year which was equivalent to 40% of annual red deer mortality (Jedrzejewski et al., 2002). In more productive habitats, where ungulates can have a very high reproduction rate the impacts of wolf predation on ungulate populations can be lower (Meriggi et al., 2011). In the Northern Apennines, Italy, wolf range expansion has followed the expansion of roe deer (Torretta et al., 2024). The high deer densities in Scotland contrast with some parts of Europe where scarcity of wild prey can be a limiting factor for large carnivores such as wolves (Rossa et al., 2023). The potential for wolves to mediate trophic cascades in human-dominated landscapes is heavily influenced by humans and their effects on the behaviour of both predator and prey (Kuijper et al., 2016). We simulated continued hind deer cull after a potential wolf reintroduction to capture such interactions. However, we did not simulate potential impacts of humans on wolf populations via legal hunting or poaching. In parts of Europe, poaching may supress wolf populations by a factor of 4 (Liberg et al., 2012) reducing the potential for wolves to regulate prey species. In forested regions of Scandinavia with intensive forestry and where deer are hunted by humans, wolves were not associated with either reduced herbivore populations or reduced browsing pressure (Ausilio et al., 2021). Future research is needed to better understand the potential for carnivores to initiate trophic cascades in human dominated landscapes. In addition to altering herbivore populations, wolves can also alter herbivore behaviour and browsing pressure (Manning et al., 2009). We did not simulate such interactions, which might further enhance the potential for wolves to increase woodland regeneration.

Figure 4 shows the potential carbon sequestration from native woodland expansion across the four areas over a 100-year period after a wolf reintroduction. Over this period, individual areas sequester between 17 and 38 Mt CO_2. On average wolf reintroduction increases carbon sequestration by 18–26 g C m^{-2} $year^{-1}$ (Table 1) at the lower end of the 24–52 g C m^{-2} $year^{-1}$ estimated for wolf-deer interactions in North America (Wilmers & Schmitz, 2016) or 37 ± 13 g C m^{-2} $year^{-1}$ estimated for wolf across the boreal forest (Schmitz et al., 2023). Estimated sequestration rates in the North West Highlands and Cairngorms are lower than in the SW and Central Highlands due to higher elevations and less favourable conditions for woodland establishment. Our sequestration rates are also similar to the estimated biomass offtake by herbivore grazing at UK oak woodland sites of up to 16 g m^{-2} $year^{-1}$ (Palmer et al., 2004).

Total carbon sequestration across the four areas after 100 years is 102 ± 10 Mt CO_2, equivalent to an annual sequestration of 1.0 ± 0.1 Mt CO_2 $year^{-1}$. This is equivalent to approximately 5% of the carbon removal target for UK woodlands that has been suggested by the UK's Climate Change Committee (UKCCC) as being necessary to reach net-zero by 2050. While much of the carbon sequestration considered here would occur post-2050, natural colonisation could play an important role in the maintenance of a longer term carbon sink on UK land. Based on the total carbon sequestration and the total wold population, the average annual carbon sequestration per wolf is 6080 ± 980 t CO_2.

Assuming a carbon price of £25.36 per tonne of CO_2, the carbon sequestration from native woodland establishment due to wolf

TABLE 1 Summary of the wolf population, number of years after wolf reintroduction before tree regeneration begins, carbon sequestration and financial value following a wolf reintroduction to four areas of the Scottish Highlands (location indicated in Figure 1).

Area	Area (km^2)	Start year	Wolf population density, mean (per 1000 km^2)	Total sequestration (Mt CO_2)	Sequestration (g C m^{-2} $year^{-1}$)	Value of carbon sequestration (£Million)	Total wolf population	Annual sequestration per wolf (t CO_2 $year^{-1}$)	Annual value per wolf (£)
Cairngorms	2108	20 ± 8	13.0 ± 1.2	17.2 ± 1.8	22.3 ± 2.2	437.4 ± 44	27 ± 2	6280 ± 880	£159,400 ± 22,000
SW Highlands	2674	21 ± 5.6	14.1 ± 1.8	23.8 ± 1.7	24.6 ± 1.7	604.6 ± 42	37 ± 6	6390 ± 890	£162,000 ± 23,000
Central Highlands	4097	21 ± 8	13.9 ± 2.2	36.6 ± 4.1	25.7 ± 2.5	979.9 ± 98	56 ± 9	6800 ± 1300	£172,300 ± 34,000
NW Highlands	3316	23 ± 7	13.7 ± 2.1	21.8 ± 1.9	17.8 ± 1.4	633.4 ± 46	45 ± 7	4800 ± 820	£122,000 ± 21,000
Total	12,167	–	–	101.6 ± 9.5		2580 ± 230	167	6080 ± 980	£154,000 ± 25,000

Note: The start year of tree regeneration is determined as the number of years after wolf reintroduction before red deer populations fall below the assumed threshold for regeneration (see Section 2). Average wolf populations and total carbon sequestration are reported for the 100 years following a wolf reintroduction. The value of carbon sequestration is calculated based on GBP £25.36 per tonne of CO_2.

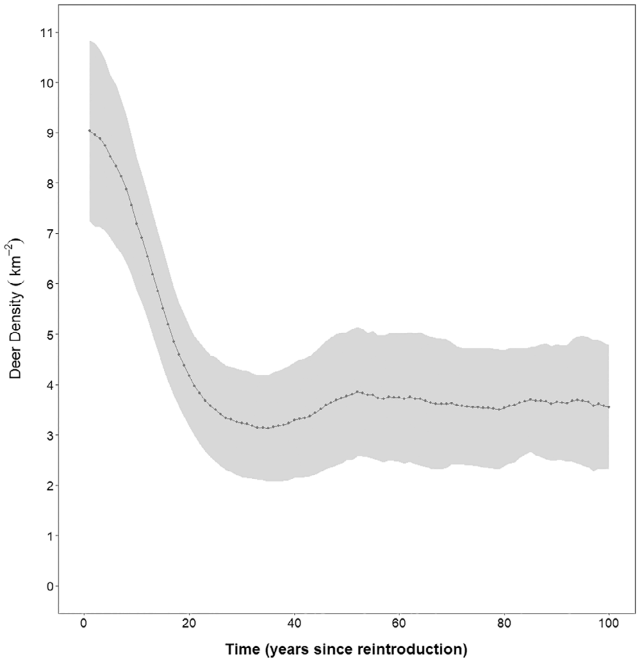

FIGURE 3 Predicted deer dynamics in the Central Highlands after a wolf reintroduction. Mean red deer density (black line) and ±1 standard deviation (grey shading).

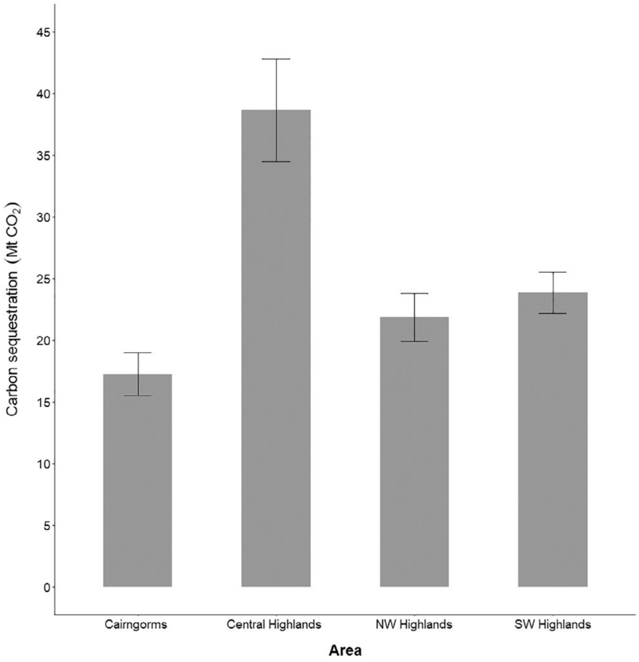

FIGURE 4 Potential carbon sequestration from native woodland expansion over a 100 year period after wolf reintroduction. Error bars show the estimated uncertainty (see Section 2).

reintroduction has an estimated value of £2580 million ± £230 million over a 100 year period (US $3250 million ± $290 million). At the annual scale, wolf reintroduction would be worth an average of £25.8 million ± £2.3 million per year (US $32.5 million ± $3 million). Assuming a population of 167 wolves, this means that each wolf would be worth an average of £154,000 ± £25,000 per year

(\$194,000 ± \$32,000) over the 100 year period. Hoag et al. (2023) used a willingness-to-pay method to estimate an annual benefit of US\$115 million for a population of 200 wolves in Colorado following a recent reintroduction, equivalent to an annual benefit of \$575,000 for each wolf. We acknowledge that our financial analysis is simplistic and merely represents the potential value from carbon sequestration. As such our estimate undervalues the functional role that wolves play in sustaining the ecosystem and the wide range of resulting ecosystem services. Furthermore, our estimate does not include the upfront costs of establishing wolves in the environment, any ongoing management costs to maintain wolves in a human dominated landscape or any opportunity costs associated with the presence of wolves. Furthermore, the costs of tree planting in places without an adequate seed source for natural colonisation are not included. Future work is needed to complete a full economic valuation.

We explored the sensitivity of our analysis to several key variables. The reported uncertainty in our estimates (see Table 1) includes the key uncertainties in the wolf model as identified by Nilsen et al. (2007). Together these result in an estimated uncertainty in carbon sequestration values of approximately ±10%. We also explore uncertainties in the threshold deer population below which natural regeneration is not suppressed by browsing. If deer numbers need to be below 7 km^{-2} to facilitate natural regeneration of trees, wolves reduce deer numbers below this threshold more rapidly and the total carbon sequestration is increased by ~14% to 1.14 Mt CO_2 per year over a 100 year period. This increases the financial benefit to £29 million per year meaning each wolf would deliver an annual financial benefit of £173,000. Our financial benefits use 2023 Woodland Carbon Code Prices, but carbon prices are likely to rise in the future.

Our analysis quantifies the impacts of a potential wolf reintroduction on red deer and the subsequent impacts on vegetation, woodland regeneration and carbon storage. We note that an increased culling of red deer and improved deer management would also lead to some of the benefits outlined here (Gullett et al., 2023; Kirkland et al., 2021; Rao, 2017). However, the full functional role that wolves play in a landscape and the wide suite of benefits they provide is difficult to fully replicate through management alone (Martin et al., 2020).

The financial benefit associated with carbon would be in addition to other well documented economic and ecological impacts from wolf reintroduction, which include, ecotourism (Duffield, 2019), a reduction in deer-related road traffic accidents (Gilbert et al., 2017; Raynor et al., 2021), a reduction in Lyme disease associated with deer (Levi et al., 2014) and a broad spectrum of ecological benefits relating from the reestablishment of reduced herbivory and modified herbivore behaviour (Martin et al., 2020). A wolf reintroduction could reduce the costs of a deer culls (Nilsen et al., 2007). In this work we reduce the rate of hind harvest rate if deer populations fall below 8 km^{-2}. In Scotland, a reduction in hind harvest rate would result in reduced costs to the land owner or land manager but we do not attempt to quantify these savings. We note that this is context specific: in other regions of Europe hunters pay a fee to hunt and a reduction in hunting opportunities associated with reduced hind harvest rate would be an economic loss. A reduction in wild herbivores could improve availability of vegetation for livestock (Prowse et al., 2015). Expansion of woodland would have a range of other benefits beyond carbon sequestration, including natural flood management (Monger et al., 2022, 2024; Harvey & Henshaw, 2023) and enhanced biodiversity (Burton et al., 2018). Herbivore pressure has resulted in mountain woodland being a particularly scarce habitat in the Scottish Highlands; expansion of this habitat will bring a wide range of benefits (Watts & Jump, 2022).

Conflict between humans and wolves is substantial and there are major challenges to coexistence (Martin et al., 2020). Substantial and widespread stakeholder and public engagement would be needed prior to any wolf reintroduction to identify potentially affected groups including farmers, foresters, gamekeepers and hunters (Niemiec et al., 2020; Wilson & Campera, 2024). Human-wildlife conflicts involving carnivores are common and must be addressed, through public policies that account for people's attitudes (Huber et al., 2008), for a reintroduction to be successful. One major source of conflict is predation of livestock (Treves et al., 2004) and the impacts on farmers (Zahl-Thanem et al., 2020). Where wolves have expanded their range in Europe, farmers and hunters have particularly negative attitudes (Dressel et al., 2014). In Scotland, there would be important concerns around loss of livestock, particularly sheep (Nilsen et al., 2007). Sheep stocks have declined across much of the Scottish Highlands in the last few decades (Albon et al., 2019), but concerns are still likely to be substantial. In southern Europe the presence of wild ungulates was found to reduce wolf predation on livestock (Meriggi et al., 2011; Meriggi & Lovari, 1996). In contrast to some parts of Europe (Rossa et al., 2023), deer are abundant and widespread in Scotland which may reduce the potential for livestock-wolf conflict. Developing effective methods to reduce livestock losses might help reduce wolf-human conflicts and safeguard human livelihoods (van Eeden et al., 2018). Fear of wolves is another reason for human-wolf conflict.

Across Europe, recolonization of wolves to human dominated landscapes has caused challenges (Pettersson et al., 2021) and lessons can be learned from these experiences. Likewise understanding can be gained from wolf reintroductions that have been conducted in the USA. There are ongoing debates around wolf reintroduction in other countries that could also inform discussions in the UK. For example, there are proposals to reintroduce wolves to Japan to help control increasing deer populations and reduce forest and agricultural damage (Sakurai et al., 2023). Substantial gaps in our understanding of the ecological effects of large carnivores especially in human dominated landscapes also need to be addressed (Ausilio et al., 2021; Kuijper et al., 2016).

The financial benefits associated with expansion of native woodland and subsequent carbon sequestration following a wolf reintroduction may influence landowner and land manager opinions around large carnivores, though economic motivations are only one aspect of decision making (Thomas et al., 2015). Carefully designed benefit sharing mechanisms would be needed to ensure that financial benefits were distributed in an equitable way and that any livelihoods negatively impacted by wolves were adequately compensated. The design of these compensation schemes could be informed by policies and practices in countries where wolf populations have already recovered or where recent reintroductions have occurred (Hoag et al., 2023).

There are ongoing discussions around the interactions between predators and prey and the extent to which prey populations are controlled by predators and vice-versa. There is evidence of ecological change in landscapes that have lost or gained large carnivores (Atkins et al., 2019; Ripple et al., 2014) that demonstrates the role played by large carnivores. Long-term monitoring of wolves in Italy spanning more than four decades provides important information on the expansion of wolves and the interaction with prey species in a human-dominated landscape (Dondina et al., 2015; Meriggi et al., 1991, 1996, 2015; Torretta et al., 2024). Where deer numbers have increased they become an increasing component of wolf diet (Torretta et al., 2024).

Our work does not account for changes in nutrient cycling (le Roux et al., 2018) or behavioural adaptations of prey to the return of predators (Gerber et al., 2024) which can result in additional impacts on plant communities (Fortin et al., 2005). Predators have been shown to impact prey behaviour even when predators are at low densities (Laundré et al., 2001). This means we may underestimate the impacts of a potential return of wolves on vegetation and nutrient cycling. However, in some studies in Europe, wolves and roe deer show low spatial avoidance at a landscape scale although changes in activity patterns were documented (Torretta et al., 2016). Future work is needed to further understand behavioural adaptations of prey, particularly in human dominated landscapes (Gerber et al., 2024). Future modelling studies will then be need that include these interactions. The presence and abundance of seed sources or the impact of ground cover composition in the rate of natural colonisation was not accounted for in our analysis. The density of new saplings is typically greatest close to adult seed sources (Murphy et al., 2022), though natural colonisation is recorded at substantial distances from a seed source (Bauld et al., 2023; Spracklen et al., 2013). It is likely that in some areas, lack of suitable seed source will limit the rate of natural regeneration (Bunce et al., 2014). Ground cover composition can also hinder seedling establishment (Tanentzap et al., 2013) and some selective disturbance may be necessary for tree colonisation (Sandom et al., 2013). Tree planting or direct seeding (Willoughby et al., 2019) will be required to establish woodlands in some areas. Targeted tree planting to establish seed sources for subsequent natural colonisation and regeneration may be a way to accelerate woodland creation through natural colonisation (Williams et al., 2024). We also recognise that other conditions need to be met to facilitate natural colonisation such as the absence of prescribed moorland burning which is widespread in some parts of Scotland (Spracklen & Spracklen, 2023).

Our analysis does not consider the impacts of changing herbivore dynamics and woodland expansion on soil carbon. Total carbon stocks to 1 m depth in Scotland are estimated to be 3056 Mt (Rees et al., 2018), making it a significant national carbon store and important to consider in the context of land use change. In temperate forests the presence of ungulate herbivores has been shown to negatively affect inputs to soil C through plant litter, subsequently impacting below-ground C stocks, however responses are highly dependent on the type of vegetation and herbivores, making it difficult to generalise (Mayer et al., 2020; Tanentzap & Coomes, 2012). In contrast, soil disturbance associated with tree planting can potentially lead to soil carbon losses particularly on high carbon content soils such as those which cover much of upland Scotland (Friggens et al., 2020; Warner et al., 2022). Consequently, woodland expansion as a consequence of a wolf reintroduction may reduce the potential for loss of soil organic carbon both through a reduction in herbivore density increasing litter inputs combined with the lower soil disturbance associated with natural colonisation. A better understanding of soil carbon dynamics is critical to future projections of carbon sequestration potential from native woodland expansion, either through tree planting or natural colonisation, which are both currently constrained by a lack of UK-based evidence.

4 | CONCLUSIONS

Our analysis shows that a wolf reintroduction to the Scottish Highlands could reduce red deer numbers sufficiently to lead to natural colonisation of trees and expansion of native woodlands with associated carbon sequestration benefits. We used a model of wolf–red deer dynamics to estimate a wolf reintroduction to four areas of the Scottish Highlands covering 12,167 km^2 would lead to a total wolf population of 167 ± 23 individuals. Our modelling approach included a number of important simplifications: we assumed that wolves could not leave the reintroduction area, we did not account for alterations in behaviour of prey, changes in nutrient cycling or human-wolf conflicts. Future work is needed to address these simplifications. Wolves reduce simulated average red deer populations to less than 4 km^{-2} within 20 to 23 years after reintroduction. We used a model of native woodland potential to estimate expansion of native woodlands would sequester 100 Mt CO_2 over a 100 year period (average annual carbon sequestration of 1.0 ± 0.1 Mt CO_2) sufficient to make an important contribution to national climate targets. This substantial carbon sequestration and the potential financial benefit related to wolf reintroduction may influence landowner and land manager perspectives around large carnivores. Carefully designed benefit sharing mechanisms would be needed to ensure any financial benefits are shared equitably across landowners, land managers and local communities. Comprehensive stakeholder engagement would be needed well in advance of any proposed reintroduction to identify potentially affected groups and address challenges of co-existing with large carnivores. Our work provides further evidence of the role of large carnivores in assisting ecosystem recovery and delivering the nature-based solutions required to address the climate emergency.

AUTHOR CONTRIBUTIONS

Dominick V. Spracklen conceived the analysis; Dominick V. Spracklen and Jude V. Lane conducted the wolf–deer modelling; Tasmin

Fletcher completed the native woodland analysis; Erlend B. Nilsen advised on the wolf model; all authors contributed to discussions and commented on the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The Native Woodland Model data are available at https://openscience.hutton.ac.uk/dataset/native-woodland-model-2004 (Donnelly, 2004). The Wild Land Area data are available at https://gis-downloads.nature.scot/WLA_SCOTLAND_SHP_27700.zip (NatureScot Chapron et al., 2014).

RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources Natural colonisation, Native woodland, Reintroduction.

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REFERENCES

Albon, S. D., McLeod, J., Potts, J., Irvine, J., Fraser, D., & Newey, S. (2019). Updating the estimates of national trends and regional differences in red deer densities on open-hill ground in Scotland. Scottish Natural Heritage Research Report No. 1149.

Atkins, J. L., Long, R. A., Pansu, J., Daskin, J. H., Potter, A. B., Stalmans, M. E., Tarnita, C. E., & Pringel, R. M. (2019). Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science*, *364*, 173–177. https://doi.org/10.1126/science.aau3561

Ausilio, G., Sand, H., Månsson, J., Mathisen, K. M., & Wikenros, C. (2021). Ecological effects of wolves in anthropogenic landscapes: The potential for trophic cascades is context-dependent. *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/fevo.2020.577963

Bauld, J., Guy, M., Hughes, S., Forster, J., & Watts, K. (2023). Assessing the use of natural colonization to create new forests within temperate agriculturally dominated landscapes. *Restoration Ecology*, *30*(8), e14004. https://doi.org/10.1111/rec.14004

Beaumont, D., Dugan, D., Evans, G., & Taylor, S. (1995). Deer management and tree regeneration in the RSPB Reserve at Abernethy Forest. *Scottish Forestry*, *49*, 155–161.

Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, *142*(11), 2401–2414. https://doi.org/10.1016/j.biocon.2009.06.015

Bunce, R. G. H., Wood, C. M., Smart, S. M., Oakley, R., Browning, G., Daniels, M. J., Ashmole, P., & Cresswell, J. (2014). The landscape ecological impacts of afforestation in the British uplands and some initiatives to restore native woodland cover. *Journal of Landscape Ecology*, *7*, 5–24. https://doi.org/10.2478/jlecol-2014-0013

Burton, V., Moseley, D., Brown, C., Metzger, M. J., & Bellamy, P. (2018). Reviewing the evidence base for the effects of woodland expansion on biodiversity and ecosystem services in the United Kingdom. *Forest Ecology and Management*, *430*, 366–379. https://doi.org/10.1016/j.foreco.2018.08.003

Chapron, G., Kaczensky, P., Linnell, J. D., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., … Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*(6216), 1517–1519. https://doi.org/10.1126/science.1257553

Cimatti, M., Ranc, N., Benítez-lópez, A., Maiorano, L., Boitani, L., Cagnacci, F., Čengić, M., Ciucci, P., Huijbregts, M. A. J., Krofel, M., López-Bao, J. V., Selva, N., Andren, H., Bautista, C., Ćirović, D., Hemmingmoore, H., Reinhardt, I., Marenče, M., … Santini, L. (2021). Large carnivore expansion in Europe is associated with human population density and land cover changes. *Diversity and Distributions*, *27*, 602–617. https://doi.org/10.1111/ddi.13219

Clutton-Brock, T. H., Coulson, T., & Milner, J. M. (2004). Red deer stocks in the highlands of Scotland. *Nature*, *429*, 261–262. https://doi.org/10.1038/429261a

Clutton-Brock, T. H., Coulson, T., Milner-Gulland, E. J., Armstrong, H. M., & Thomson, D. (2002). Sex differences in emigration and mortality affect optimal management of deer populations. *Nature*, *415*, 633–637. https://doi.org/10.1038/415633a

Clutton-Brock, T. H., & Coulson, T. N. (2002). Ungulate population dynamics: The devil is in the detail. *Philosophical Transactions of the Royal Society*, *357*, 1299–1306. https://doi.org/10.1098/rstb.2002.1128

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red Deer: Behaviour and ecology of two sexes*. University of Chicago Press.

Convery, I., Nevin, O., Blackshaw-Crosby, E., Brady, D., & Fisher, M. (2023). The case for wolves in the UK. In *The Wolf*. Boydell and Brewer. https://doi.org/10.1515/9781805430551-031

Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Cretois, B., Linnell, J. D. C., Van Moorter, B., Kaczensky, P., Nilsen, E. B., Parada, J., & Rød, J. K. (2021). Coexistence of large mammals and humans is possible in Europe's anthropogenic landscapes. *iScience*, *24*(9), 103083. https://doi.org/10.1016/j.isci.2021.103083

Cromsigt, J. P. G. M., te Beest, M., Kerley, G. I. H., Landman, M., le Roux, E., & Smith, F. A. (2018). Trophic rewilding as a climate change mitigation strategy? *Philosophical Transactions of the Royal Society B*, *373*, 20170440. https://doi.org/10.1098/rstb.2017.0440

Dondina, O., Meriggi, A., Dagradi, V., Perversi, M., & Milanesi, P. (2015). Wolf predation on livestock in an area of northern Italy and prediction of damage risk. *Ethology Ecology and Evolution*, *2015*(27), 200–219. https://doi.org/10.1080/03949370.2014.916352

Donnelly, D. (2004). The James Hutton Institute. Data from: Native Woodland Model 2004. https://openscience.hutton.ac.uk/dataset/native-woodland-model-2004

Dressel, S., Sandström, C., & Ericsson, G. (2014). A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. *Conservation Biology*, *29*(2), 565–574. https://doi.org/10.1111/cobi.12420

Duffield, J. (2019). Shopping for wolves: Using nonmarket valuation for informing conservation districts. In R. Rasker (Ed.), *People and public lands*. Headwaters Economics.

Edwards, T., & Kenyon, W. (2013). Scottish parliament information centre: wild deer in Scotland. [cited 2014 January 8]. Available from: http://www.scottish.parliament.uk/ResearchBriefingsAndFactsheets/S4/SB_13-74.

Emerson, L. D., Wittmer, H. U., Elbroch, M., Kostoglou, K., Bannister, K. J., Psaila, J. J., Whisson, D., & Ritchie, E. G. (2024). A global assessment of large terrestrial carnivore kill rates. *Biological Reviews*, *100*(1), 327–350. https://doi.org/10.1111/brv.13143

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fletcher, T. I., Scott, C. E., Hall, J., & Spracklen, D. V. (2021). The carbon sequestration potential of Scottish native woodland. *Environmental Research Communications*, *3*, 041003. https://doi.org/10.1088/2515-7620/abf467

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*, 1320–1330. https://doi.org/10.1890/04-0953

Friggens, N. L., Hester, A. J., Mitchell, R. J., Parker, T. C., Subke, J. A., & Wookey, P. A. (2020). Tree planting in organic soils does not result in net carbon sequestration on decadal timescales. *Global Change Biology*, *26*(9), 5178–5188. https://doi.org/10.1111/gcb.15229

Fuller, R. J., & Gill, R. M. (2001). Ecological impacts of increasing numbers of deer in British woodland. *Forestry*, *74*, 193–199. https://doi.org/10.1093/forestry/74.3.193

Gazzola, A., Avanzinelli, E., Bertelli, I., Tolosano, A., Bertotto, P., Musso, R., & Apollonio, M. (2007). The role of the wolf in shaping a multi-species ungulate community in the Italian western Alps. *The Italian Journal of Zoology*, *74*(3), 297–307. https://doi.org/10.1080/11250000701447074

Gerber, N., Riesch, F., Bojarska, K., Zetsche, M., Rohwer, N.-K., Signer, J., Isselstein, J., Herzog, S., Okarma, H., Kuijper, D. P. J., & Balkenhol, N. (2024). Do recolonising wolves trigger non-consumptive effects in European ecosystems? A review of evidence. *Wildlife Biology*, *2024*(6), e01229. https://doi.org/10.1002/wlb3.01229

Gilbert, S. L., Sivy, K. J., Pozzanghera, C. B., DuBour, A., Overduijn, K., Smith, M. M., Zhou, J., Little, J. M., & Prugh, L. R. (2017). Socioeconomic benefits of large carnivore recolonization through reduced wildlife-vehicle collisions. *Conservation Letters*, *10*, 431–439. https://doi.org/10.1111/conl.12280

Gonzalez, M. N., Berl, R. E. W., Teel, T. L., & Niemiec, R. (2024). The impact of social norms on intended individual and collective civic actions related to wolf reintroduction. *Society & Natural Resources*, *37*(8), 1–17. https://doi.org/10.1080/08941920.2024.2335400

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., … Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(44), 11645–11650. https://doi.org/10.1073/pnas.1710465114

Gullett, P. R., Leslie, C., Mason, R., Ratcliffe, P., Sargent, I., Beck, A., Cameron, T., Cowie, N. R., Hetherington, D., MacDonell, T., Moat, T., Moore, P., Teuten, E., & Hancock, M. H. (2023). Woodland expansion in the presence of deer: 30 years of evidence from the Cairngorms Connect landscape restoration partnership. *Journal of Applied Ecology*, *60*(11), 2298–2308. https://doi.org/10.1111/1365-2664.14501

Gwynn, V., & Symeonakis, E. (2022). Rule-based habitat suitability modelling for the reintroduction of the grey wolf (*Canis lupus*) in Scotland. *PLoS One*, *17*(10), e0265293. https://doi.org/10.1371/journal.pone.0265293

Harvey, G. L., & Henshaw, A. J. (2023). Rewilding and the water cycle. *Wiley Interdisciplinary Reviews: Water*, *10*, e1686. https://doi.org/10.1002/wat2.1686

Hetherington, D. A., Lord, T. C., & Jacobi, R. M. (2006). New evidence for the occurrence of the Eurasian lynx (*Lynx lynx*) in medieval Britain. *Journal of Quaternary Science*, *21*(1), 3–8. https://doi.org/10.1002/jqs.960

Hindrikson, M., Remm, J., Pilot, M., Godinho, R., Vik Stronen, A., Baltrunaité, L., Czarnomska, S. D., Leonard, J. A., Randi, E., Nowak, C., Akesson, M., Lopez-Bao, J. V., Alvares, F., Llaneza, L., Echegaray, J., Vilà, C., Ozolins, J., Rungis, D., Aspi, J., … Saarma, U. (2017). Wolf population genetics in Europe: A systematic review, meta-analysis and suggestions for conservation and management. *Biological Reviews*, *72*, 248–270. https://doi.org/10.1111/brv.12298

Hoag, D. L. K., Burkhardt, J., Ghasemi, B., Breck, S., Niemiec, R., & Crooks, K. (2023). Willingness to pay for reintroducing wolves in a divided voting base. *Global Ecology and Conservation*, *46*, e02576. https://doi.org/10.1016/j.gecco.2023.e02576

Hobbs, N. T., Johnston, D. B., Marshall, K. N., Wolf, E. C., & Cooper, D. J. (2024). Does restoring apex predators to food webs restore ecosystems? Large carnivores in Yellowstone as a model system. *Ecological Monographs*, *94*(2), e1598. https://doi.org/10.1002/ecm.1598

Huber, D., Kusak, J., Majić-Skrbinšek, A., Majnarić, D., & Sindičić, M. (2008). A multidimensional approach to managing the European brown bear in Croatia. *Ursus*, *19*, 22–32.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., Selva, N., Zub, K., & Szymura, L. (2002). Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). *Ecology*, *83*, 1341–1356. https://doi.org/10.1890/0012-9658(2002)083[1341:KRAPBW]2.0.CO;2

Kirkland, H., Hare, D., Daniels, M., Krofel, M., Rao, S., Chapman, T., & Blossey, B. (2021). Successful deer management in Scotland requires less conflict not more. *Frontiers in Conservation Science*, *2*, 770303. https://doi.org/10.3389/fcosc.2021.770303

Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., & Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 1841. https://doi.org/10.1098/rspb.2016.1625

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Canadian Journal of Zoology*, *79*, 1401–1409. https://doi.org/10.1139/z01-094

le Roux, E., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2018). Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Current Biology*, *28*, 2493–2499. https://doi.org/10.1016/j.cub.2018.05.088

Leroux, S. J., Wiersma, Y. F., & Vander Wal, E. (2020). Herbivore impacts on carbon cycling in boreal forests. *Trends in Ecology & Evolution*, *35*(11), 1001–1010. https://doi.org/10.1016/j.tree.2020.07.009

Levi, T., Kilpatrick, A. M., & Wilmers, C. C. (2014). Deer, predators, and the emergence of Lyme disease. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(27), 10942–10947. https://doi.org/10.1073/pnas.1204536109

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H. C., Hobbs, N. T., & Sand, H. (2012). Shoot, shovel and shut up: Cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 910–915. https://doi.org/10.1098/rspb.2011.1275

Manning, A. D., Gordon, I. J., & Ripple, W. J. (2009). Restoring landscapes of fear with wolves in the Scottish Highlands. *Biological Conservation*, *142*(10), 2314–2321. https://doi.org/10.1016/j.biocon.2009.05.007

Martin, J.-L., Chamaillé-Jammes, S., & Waller, D. M. (2020). Deer, wolves, and people: Costs, benefits and challenges of living together.

Biological Reviews, *95*(3), 782–801. https://doi.org/10.1111/brv.12587

Mayer, M., Prescott, C. E., Abaker, W. E. A., Augusto, L., Cécillon, L., Ferreira, G. W. D., James, J., Jandl, R., Katzensteiner, K., Laclau, J.-P., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J. A., Vanguelova, E. I., & Vesterdal, L. (2020). Influence of forest management activities on soil organic carbon stocks: A knowledge synthesis. *Forest Ecology and Management*, *466*, 118127. https://doi.org/10.1016/j.foreco.2020.118127

Meriggi, A., Brangi, A., Matteucci, C., & Sacchi, O. (1996). The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography*, *19*, 287–295.

Meriggi, A., Brangi, A., Schenone, L., Signorelli, D., & Milanesi, P. (2011). Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethology Ecology & Evolution*, *23*(3), 195–210. https://doi.org/10.1080/03949370.2011.577814

Meriggi, A., Dagradi, V., Dondina, O., Perversi, M., Milanesi, P., Lombardini, M., Raviglione, S., & Repossi, A. (2015). Short-term responses of wolf feeding habits to changes of wild and domestic ungulate abundance in northern Italy. *Ethology Ecology and Evolution*, *27*, 389–411. https://doi.org/10.1080/03949370.2014.986768

Meriggi, A., & Lovari, S. (1996). A review of wolf predation in southern Europe: Does the wolf prefer wild prey to livestock? *Journal of Applied Ecology*, *33*(6), 1561–1571. https://doi.org/10.2307/2404794

Meriggi, A., Rosa, P., Brangi, A., & Matteucci, C. (1991). Habitat use and diet of the wolf in northern Italy. *Acta Theriologica*, *36*, 141–151. https://doi.org/10.4098/AT.arch.91-11

Miller, G., Cummings, R., & Hester, A. (1998). *Scottish forestry*. Royal Scottish Forestry Society.

Milner-Gulland, E. J., Coulson, T., & Clutton-Brock, T. H. (2004). Sex differences and data quality as determinants of income from hunting red deer *Cervus elaphus*. *Wildlife Biology*, *10*(3), 187–201. https://doi.org/10.2981/wlb.2004.025

Mitchell, B., Staines, B. W., & Welch, D. (1977). *Ecology of Red Deer*. Institute of Terrestrial Ecology.

Monger, F., Spracklen, D. V., Kirkby, M. J., & Schofield, L. (2022). The impact of semi-natural broadleaf woodland and pasture on soil properties and flood discharge. *Hydrological Processes*, *36*(1), e14453. https://doi.org/10.1002/hyp.14453

Monger, F., Spracklen, D. V., Kirkby, M. J., & Willis, T. (2024). Investigating the impact of woodland placement and percentage cover on flood peaks in an upland catchment using spatially distributed TOPMODEL. *Journal of Flood Risk Management*, *17*, e12977. https://doi.org/10.1111/jfr3.12977

Murphy, T. R., Hanley, M. E., Ellis, J. S., & Lunt, P. H. (2022). Optimizing opportunities for oak woodland expansion into upland pastures. *Ecological Solutions and Evidence*, *3*(1), e12126. https://doi.org/10.1002/2688-8319.12126

Native Woodland Survey of Scotland. (2014). Forestry Commission Scotland. 978 0 85538 899 7.

NatureScot. (2014). Wild land areas 2014. Data from: NatureScot GIS Downloads. https://gis-downloads.nature.scot/WLA_SCOTLAND_SHP_27700.zip

Niemiec, R., Berl, R. E. W., Gonzalez, M., Teel, T., Camara, C., Collins, M., Salerno, J., Crooks, K., Schultz, C., Breck, S., & Hoag, D. (2020). Public perspectives and media reporting of wolf reintroduction in Colorado. *PeerJ*, *8*, e9074. https://doi.org/10.7717/peerj.9074

Nilsen, E. B., Milner-Gulland, E. J., Schofield, L., Mysterud, A., Stenseth, N. C., & Coulson, T. (2007). Wolf reintroduction to Scotland: Public attitudes and consequences for red deer management. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 995–1003. https://doi.org/10.1098/rspb.2006.0369

Palmer, S. C. F., Mitchell, R. J., Truscott, A.-M., & Welch, D. (2004). Regeneration failure in Atlantic oakwoods: The roles of ungulate grazing and invertebrates. *Forest Ecology and Management*, *192*(2–3), 251–265. https://doi.org/10.1016/j.foreco.2004.01.038

Palmer, S. C. F., & Truscott, A.-M. (2003). Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris* L.) and its effects on sapling growth. *Forest Ecology and Management*, *182*(1–3), 31–47. https://doi.org/10.1016/S0378-1127(03)00026-4

Palmer, S. C. F., Truscott, A.-M., Mitchell, R. J., & Welch, D. (2009). Regeneration in Atlantic oakwoods: Has deer management had a beneficial effect? *Botanical Journal of Scotland*, *57*(1–2), 167–178. https://doi.org/10.1080/03746600508685095

Passoni, G., Coulson, T., Cagnacci, F., Hudson, P., Stahler, D. R., Smith, D. W., & Lachish, S. (2024). Investigating tritrophic interactions using bioenergetic demographic models. *Ecology*, *105*(1), e4197. https://doi.org/10.1002/ecy.4197

Pepper, S., Barbour, A., & Glass, J. (2020). *The management of wild deer in Scotland*, Report of the Deer Working Group, ISBN: 978–1–83960-525-3. The Scottish Government.

Perks, M. P., Nagy, L., Meir, P., Auld, M., Wood, M., Atkinson, N., Staples-Scott, L., Harvey, G., McGhee, W., & Tipper, R. (2010). *Carbon sequestration benefits of new native woodland expansion in Scotland*. Scottish Forest Alliance.

Pettersson, H. L., Quinn, C. H., Holmes, G., Sait, S. M., & López-Bao, J. V. (2021). Welcoming wolves? Governing the return of large carnivores in traditional pastoral landscapes. *Frontiers in Conservation Science*, *2*, 710218. https://doi.org/10.3389/fcosc.2021.710218

Pörtner, H.-. O., Pörtner, H.-O., Scholes, R. J., Agard, J., Archer, E., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W. L., Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M. A., Handa, C., Hickler, T., Hoegh-Guldberg, O., … Ngo, H. (2021). *Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change*. (p. 252).

Prowse, T. A. A., Johnson, C. N., Cassey, P., Bradshaw, C. J. A., & Brook, B. W. (2015). Ecological and economic benefits to cattle rangelands of restoring an apex predator. *Journal of Applied Ecology*, *52*, 455–466. https://doi.org/10.1111/1365-2664.12378

Rao, S. J. (2017). Effect of reducing red deer *Cervus elaphus* density on browsing impact and growth of scots pine *Pinus sylvestris* seedlings in semi-natural woodland in the Cairngorms, UK. *Conservation Evidence*, *14*, 22–26.

Raynor, J. L., Grainger, C. A., & Parker, D. P. (2021). Wolves make roadways safer, generating large economic returns to predator conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(22), e2023251118. https://doi.org/10.1073/pnas.2023251118

Rees, R. M., Buckingham, S., Chapman, S. J., Jones, S., Lilly, A., Matthews, R. B., Morison, J. I. L., Perks, M., Vanguelova, E., Yamulki, S., & Yeluripati, J. (2018). Soil carbon and land use in Scotland. https://www.climatexchange.org.uk/media/3046/soil-carbon-and-land-use-in-scotland.pdf

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Rizzuto, M., Leroux, S. J., & Schmitz, O. J. (2024). Rewiring the carbon cycle: A theoretical framework for animal-driven ecosystem carbon sequestration. *JGR Biogeosciences*, *129*(4), e2024JG008026. https://doi.org/10.1029/2024JG008026

Rossa, M., Torres, R. T., Linck, P., Martins, R., Couto, A., Aliácar, S., Hipólito, D., Brotas, G., Fonseca, C., & Carvalho, J. (2023). Environmental favorability models as a tool to support trophic rewilding initiatives. *Restoration Ecology*, *32*(3), e14048. https://doi.org/10.1111/rec.14048

Sakurai, R., Tsunoda, H., Enari, H., & Stedman, R. C. (2023). Public attitudes and intentions toward engaging in reintroduction of wolves to Japan. *Conservation Biology*, *37*(6), e14130. https://doi.org/10.1111/cobi.14130

Sandom, C., Bull, J., Canney, S., & Macdonald, D. W. (2012). Exploring the value of wolves (*Canis lupus*) in landscape-scale fenced reserves for ecological restoration in the Scottish Highlands. In M. J. Somers & M. Hayward (Eds.), *Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes?* (pp. 245–276). Springer New York. https://doi.org/10.1007/978-1-4614-0902-1_14

Sandom, C. J., Hughes, J., & Macdonald, D. W. (2013). Rooting for rewilding: Quantifying wild boar's sus scrofa rooting rate in the Scottish Highlands. *Restoration Ecology*, *21*(3), 329–335. https://doi.org/10.1111/j.1526-100X.2012.00904.x

Schmitz, O. J., & Leroux, S. J. (2020). Food webs and ecosystems: Linking species interactions to the carbon cycle. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1), 271–295. https://doi.org/10.1146/annurev-ecolsys-011720-104730

Schmitz, O. J., Sylvén, M., Atwood, T. B., Bakker, E. S., Berzaghi, F., Brodie, J. F., Cromsigt, J. P. G. M., Davies, A. B., Leroux, S. J., Schepers, F. J., Smith, F. A., Stark, S., Svenning, J. C., Tilker, A., & Ylänne, H. (2023). Trophic rewilding can expand natural climate solutions. *Nature Climate Change*, *13*, 324–333. https://doi.org/10.1038/s41558-023-01631-6

Schmitz, O. J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T. B., Galetti, M., Davies, A. B., Goetz, S. J. (2018). Animals and the zoogeochemistry of the carbon cycle. *Science*, *362*(6419), eaar3213. https://doi.org/10.1126/science.aar3213

Seddon, P., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, *345*(6195), 406–412. https://doi.org/10.1126/science.1251818

Smith, P., Calvin, K., Nkem, J., Campbell, D., Cherubini, F., Grassi, G., Korotkov, A., Hoang, L., Lwasa, S., McElwee, P., Nkonya, E., Saigusa, N., Soussana, J.-F., Taboada, M. A., Manning, F. C., Nampanzira, D., Arias-Navarro, C., Vizzarri, M., House, J., … Arneth, A. (2019). Which practices co-deliver food security, climate change mitigation and adaptation, and combat land degradation and desertification? *Global Change Biology*, *26*(3), 1532–1575. https://doi.org/10.1111/gcb.14878

Spracklen, B. D., Lane, J. V., Spracklen, D. V., Williams, N., & Kunin, W. E. (2013). Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain. *Forest Ecology and Management*, *310*(15), 204–212. https://doi.org/10.1016/j.foreco.2013.08.001

Spracklen, B. D., & Spracklen, D. V. (2023). Assessment of peatland burning in Scotland during 1985–2022 using Landsat imagery. *Ecological Solutions and Evidence*, *4*(4), e12296. https://doi.org/10.1002/2688-8319.12296

Staines, B. W. (1995). The impact of red deer on the regeneration of native pinewoods. In J. R. Aldhous (Ed.), *Our Pinewood Heritage* (pp. 107–114). Forestry Commission.

Strickland, M. S., Hawlena, D., Reese, A., & Schmitz, O. J. (2013). Trophic cascade alters ecosystem carbon exchange. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(27), 11035–11038. https://doi.org/10.1073/pnas.1305191110

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D., & Zanette, L. Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, *7*, 10698. https://doi.org/10.1038/ncomms10698

Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: Do browsing and grazing herbivores matter? *Biological Reviews*, *87*(1), 72–94. https://doi.org/10.1111/j.1469-185X.2011.00185.x

Tanentzap, A. J., Zou, J., & Coomes, D. A. (2013). Getting the biggest birch for the bang: Restoring and expanding upland birchwoods in the Scottish Highlands by managing red deer. *Ecology and Evolution*, *3*(7), 1890–1901. https://doi.org/10.1002/ece3.548

Thomas, H. J. D., Paterson, J. S., Metzger, M. J., & Sing, L. (2015). Towards a research agenda for woodland expansion in Scotland. *Forest Ecology and Management*, *349*, 149–161. https://doi.org/10.1016/j.foreco.2015.04.003

Torretta, E., Brangi, A., & Meriggi, A. (2024). Changes in wolf occupancy and feeding habits in the northern Apennines: Results of Long-term predator–prey monitoring. *Animals*, *14*(5), 735. https://doi.org/10.3390/ani14050735

Torretta, E., Serafini, M., Imbert, C., Milanesi, P., & Meriggi, A. (2016). Wolves and wild ungulates in the Ligurian Alps (western Italy): Prey selection and spatial-temporal interactions. *Mammalia*, *81*, 537–551.

Towers, W., Hall, J., Hester, A., Malcolm, A., & Stone, D. (2004). *The potential for native woodland in Scotland: The native woodland model*. Scottish Natural Heritage.

Treves, A., Naughton-Treves, L., Harper, E. K., Mladenoff, D. J., Rose, R. A., Sickley, T. A., & Wydeven, A. P. (2004). Predicting human-carnivore conflict: A spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology*, *18*(1), 114–125. https://doi.org/10.1111/j.1523-1739.2004.00189.x

van Eeden, L. M., Eklund, A., Miller, J. R. B., López-Bao, J. V., Chapron, G., Cejtin, M. R., Crowther, M. S., Dickman, C. R., Frank, J., Krofel, M., Macdonald, D. W., McManus, J., Meyer, T. K., Middleton, A. D., Newsome, T. M., Ripple, W. J., Ritchie, E. G., Schmitz, O. J., Stoner, K. J., … Treves, A. (2018). Carnivore conservation needs evidence-based livestock protection. *PLoS Biology*, *16*(9), e2005577. https://doi.org/10.1371/journal.pbio.2005577

Warner, E., Lewis, O. T., Brown, N., Green, R., McDonnell, A., Gilbert, D., & Hector, A. (2022). Does restoring native forest restore ecosystem functioning? Evidence from a large-scale reforestation project in the Scottish Highlands. *Restoration Ecology*, *30*(3), e13530. https://doi.org/10.1111/rec.13530

Watts, S. H., & Jump, A. S. (2022). The benefits of mountain woodland restoration. *Restoration Ecology*, *30*(8), e13701. https://doi.org/10.1111/rec.13701

Williams, J., Sandom, C. J., & Pettorelli, N. (2024). Active management is required to regenerate the Caledonian forest: Alladale as a case study. *Ecological Solutions and Evidence*, *5*(1), e12315. https://doi.org/10.1002/2688-8319.12315

Willoughby, I. H., Jinks, R. L., & Forster, J. (2019). Direct seeding of birch, rowan and alder can be a viable technique for the restoration of upland native woodland in the UK forestry. *An International Journal of Forest Research*, *92*, 324–338. https://doi.org/10.1093/forestry/cpz018

Wilmers, C. C., & Schmitz, O. J. (2016). Effects of grey wolf-induced trophic cascades on ecosystem carbon cycling. *Ecosphere*, *7*(10), e01501. https://doi.org/10.1002/ecs2.1501

Wilson, S., & Campera, M. (2024). The perspectives of key stakeholders on the reintroduction of apex predators to the United Kingdom. *Ecologies*, *5*(1), 52–67. https://doi.org/10.3390/ecologies5010004

Woodland Carbon Code. (2023). UK Carbon Prices. https://woodlandcarboncode.org.uk/uk-land-carbon-registry/uk-carbon-prices

Zahl-Thanem, A., Burton, R. J. F., Blekesaune, A., Haugen, M. S., & Rønningen, K. (2020). The impact of wolves on psychological distress among farmers in Norway. *Journal of Rural Studies*, *78*, 1–11. https://doi.org/10.1016/j.jrurstud.2020.05.010

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