Bird assemblage changes on peatland affected by large-scale non-native afforestation in the Flow Country (Scotland)

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SUMMARY

The Flow Country blanket bogs in the counties of Caithness and Sutherland (northern Scotland, UK) harbour internationally important populations of specialist open-bog breeding bird species. However, commercial afforestation carried out in the 1980s, involving the non-native tree species lodgepole pine (*Pinus contorta*) and sitka spruce (*Picea sitchensis)* covering over 67,000 hectares (ca. 17 %) of the peatland, has significantly affected bird assemblages within and around the plantations. We conducted a literature review to identify the avian winners and losers resulting from this transformation. Our synthesis of existing findings confirms that afforestation has led to changes in the availability of breeding and foraging habitat, alterations in inter- and intra-specific competition dynamics, and the creation of forest edge effects. Crucially, the open-bog bird assemblages have been largely replaced by woodland specialists and generalists. While 33 species (including five Red-listed Birds of Conservation Concern) are observed to benefit from afforestation, these gains are arguably of lower conservation value than the original open-bog assemblages (27 species including 11 Red-listed species). As a mean proportion of the British population range, the Flow Country has a significantly higher proportion of Amber and Green-listed loser species than winners. Understanding the changes in assemblages is crucial for informing future decisions regarding forest planting and re-planting, particularly in the context of the ongoing dual challenges of climate change and biodiversity loss. Further research is necessary to comprehend the effects of afforestation on populations of waterfowl associated with open water features present in the blanket bog landscape. Given the need for woodland creation, bird conservation would benefit from leaving naturally open habitats intact and siting new woodland in areas that were formerly naturally forested.

KEY WORDS: blanket bog, Caithness and Sutherland Peatlands, forestry, loser species, winner species

INTRODUCTION

Landscape fragmentation is one of the main causes of recent biodiversity losses (Tilman *et al.* 2001, Haddad *et al.* 2015) and can pose many threats to species assemblages including: exogenous threats such as habitat loss, degradation and isolation; endogenous threats that change biological behaviours and species interactions; and stochastic threats including demographic, environmental and genetic alterations (Fischer & Lindenmayer 2007). Landscape changes influence most taxonomic groups including birds and mammals (Rivera-Ortíz *et al*. 2015, Presley *et al.* 2019), reptiles (Doherty *et al.* 2020), amphibians (Stuart *et al.* 2004), invertebrates (Larsen & Ormerod 2010) and plants (Hobbs & Yates 2003).

A landscape change that has been particularly prevalent on open peatland in northern Scotland is the planting of non-native conifers for commercial forestry. Open-country birds can lose habitat suitable for breeding and/or foraging following afforestation, and even small numbers of trees in previously open landscapes can facilitate colonisation by woodland bird species which would otherwise be absent (Manning *et al.* 2006). For example, afforestation of semi-natural grasslands in the Portuguese steppes (Reino *et al.* 2010) and Israel's Negev desert (Rotem *et al.* 2014) was followed by increased predation on bird species of high conservation value nesting in adjacent open country. Afforestation can also result in the replacement of open-country bird assemblages with woodland bird assemblages, as observed in

Canadian peatlands (Lachance *et al.* 2005) and an Argentinian delta (Magnano *et al.* 2019).

Biogeographically, forest blocks stand out from open ground, creating a network of island-like areas and fragmenting the landscape. Afforestation of high-quality habitats displaces birds, causing density-dependent reductions in productivity of the remaining populations (Evans & Pienkowski 1984, Thompson *et al.* 1986). It can also affect foraging, especially given that the mosaic of vegetation structures in peatland already makes food availability for many upland breeding bird species spatially patchy (Coulson 1988, Usher & Thompson 1993). In Ireland, the presence of non-native tree plantations was shown to alter the abundance and community composition of bird populations, with effects varying between taxa (McCarthy *et al.* 2021). At many sites, forest planting on peatland requires land drainage that lowers the water table of the area (Anderson *et al.* 2000). In turn, this affects the vegetation assemblage (Hancock *et al.* 2018) and moisture dependent peatland invertebrates such as craneflies (*Tipula* spp.; Carroll *et al.* 2014), which form an important part of the diet of upland breeding bird species (Buchanan *et al.* 2006, Pearce-Higgins 2010).

Between the late 1950s and the 1980s, government tax incentives led to the establishment of non-native commercial plantations of, predominantly, lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*) over > 800,000 ha (~ 20 %) of previously open peatlands in the UK (Artz *et al.* 2014) and > 200,000 ha (~16 %) in Ireland (Farrell 1990, Renou & Farrell 2005). This included 67,000 ha of non-native afforestation within the Flow Country peatlands in the counties of Caithness and Sutherland in northern Scotland, such that 17 % of the previously open peatland habitat was converted to commercial plantation (Stroud *et al.* 1987). Starting in the 1990s, some afforested sites in the Flow Country were restored by removing the plantations and reverting the areas back to bog-like conditions (Anderson & Peace 2017, Hancock *et al.* 2018), a process termed 'forest-to-bog restoration'. Most significantly, The Royal Society for the Protection of Birds (RSPB) have restored approximately 2,593 ha of their afforested land to date (RSPB unpublished data).

The Flow Country is widely regarded as one of the finest examples of blanket bog landscape worldwide (Lindsay *et al.* 1988, Joosten *et al.* 2016), and was recently inscribed as a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Site. The extent (> 4000 km^2) of the naturally unforested contiguous blanket bogs also makes them unique in Europe. Oligotrophic to mesotrophic standing water and natural dystrophic lakes and ponds are dispersed throughout (Lindsay *et al.* 1988). The areas of pooled bog are particularly important habitats for peat forming *Sphagnum* species that are favoured by high water levels (Rydin & Jeglum 2013). The hydrology and vegetation associated with these physical features also support characteristic communities of invertebrates (Downie *et al.* 1998).

Under the name 'Caithness and Sutherland Peatlands', much of the remaining open bog in the Flow Country was designated as Natura 2000 Special Areas of Conservation (SACs) and Special Protection Areas (SPAs) under the European Union (EU) Habitats and Birds Directives (Figure 1). The SPA designation includes nationally important waders such as European golden plover (*Pluvialis apricaria*), dunlin (*Calidris alpina*) and common greenshank (*Tringa nebularia*). In addition, significant numbers of black-throated diver (*Gavia arctica*), golden eagle (*Aquila chrysaetos*), hen harrier (*Circus cyaneus*), merlin (*Falco columbarius*), red-throated diver (*Gavia stellata*), short-eared owl (*Asio flammeus*), wood sandpiper (*Tringa glareola*), common scoter (*Melanitta nigra*) and Eurasian wigeon (*Mareca penelope*) breed in the Flow Country.

Many previous studies have sought to identify the effects of peatland afforestation on individual bird species or species groups (Ratcliffe 1986, Hancock *et al.* 2009, Wilson *et al.* 2014). Here we provide a data-driven synthesis of the changes in Flow Country bird assemblages that have occurred between the more natural pre-afforestation open bog state of the 1960s and the present time. We derive evidence for these changes through a review of ornithological literature.

The afforestation of areas of (> 50 cm) deep peat was enormously controversial (Warren 2000, Avery & Leslie 2010) and is no longer practised (Patterson & Anderson 2000) following recognition of its detrimental effects. However, although afforestation on deep peat is no longer supported (Scottish Forestry 2000), areas with shallower peaty soils - which support many of the same species we mention here - are still being planted. With much of the forestry in the Flow Country currently due to be harvested, this synthesis will indicate likely impacts of such afforestation and thus help to inform future decisions regarding peatland restoration versus commercial restocking on the shallower peat areas. The synthesis is also timely because the Scottish Government has committed to investing over £250 million into peatland restoration through the NatureScot Peatland ACTION Programme during 2021–2032, to help achieve their 'net zero (greenhouse gas) emissions' target by 2045.

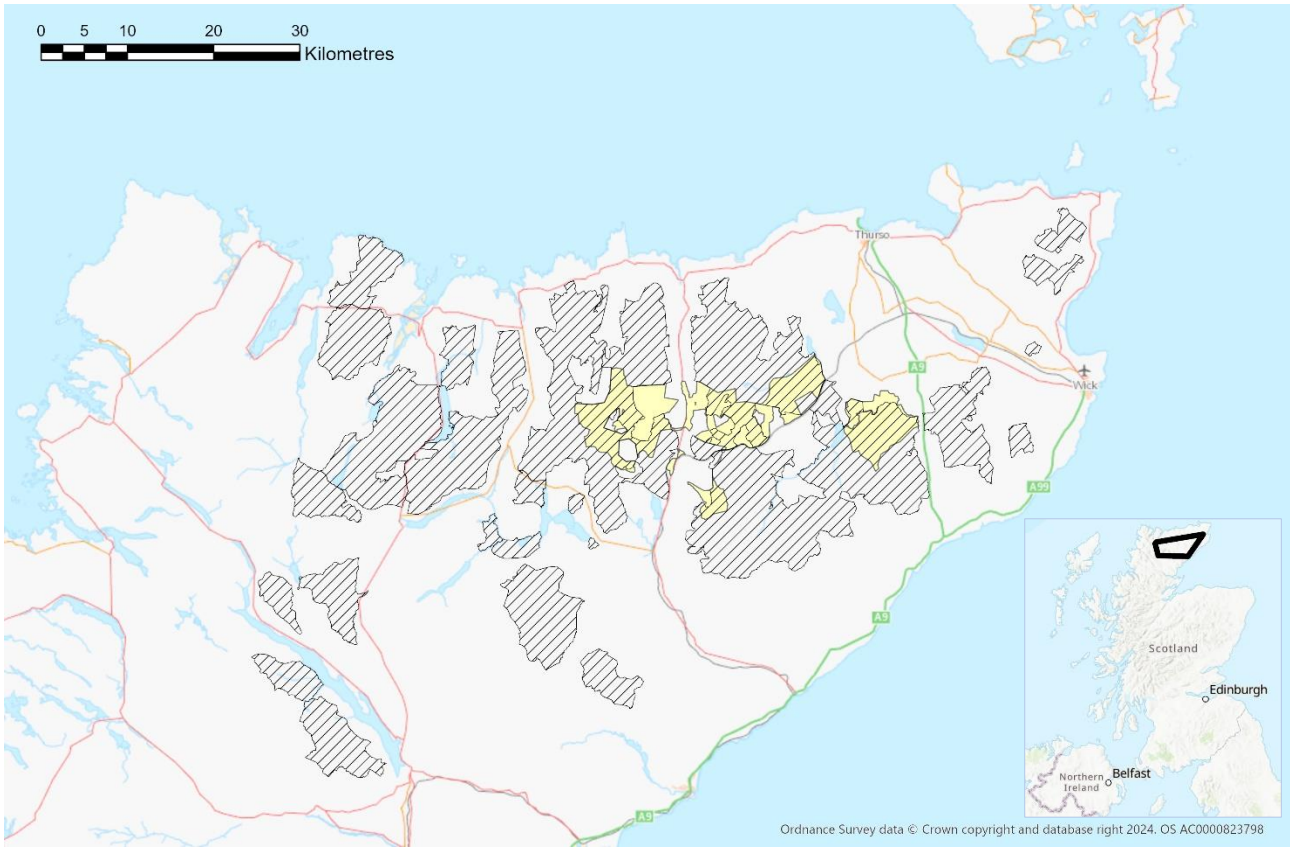

Figure 1. Map of the far north of Great Britain (location indicated by the thick black outline on inset), showing the extent of the designated Caithness and Sutherland Peatlands Special Protection Area (SPA; diagonal shading) and the RSPB Forsinard nature reserve (yellow fill), which lies mostly within the SPA.

Specifically, the objectives of the synthesis are to:

i) identify the avian winners and losers of peatland afforestation in the Flow Country; and

ii) assess possible implications of these changes for the area.

METHODS

We carried out an extensive review of published and grey literature to ensure the comprehensiveness and relevance of the sources included. We primarily utilised the Google Scholar search engine (Google 2024) due to its robust coverage of scientific research in the biological sciences. The search terms were selected after reviewing related literature and consulting local ornithologists. Key words including "bird assemblage changes", "habitat fragmentation", "forest edge effects", "forest birds" and "peatland birds" were used to ensure retrieval of a diverse range of articles. Additionally, we manually searched the reference lists of key articles to identify any potentially relevant studies that might not have surfaced through the electronic search, and searched for citations of the most relevant papers.

We used the most recent Birds of Conservation Concern (BoCC5) status (Stanbury *et al.* 2021) as an index of conservation concern for each species. The number of BoCC Red listed species in Britain has increased from 36 to 70 since the (first) BoCC1 list was published in 1996 (Stanbury *et al.* 2021). The BoCC differs from the International Union for Conservation of Nature (IUCN) Red List process in that the IUCN Red List is concerned solely with extinction risk whilst the BoCC considers conservation more broadly and takes into account changes over a longer period (Stanbury *et al.* 2021).

We classified each species as a 'loser' (i.e., results demonstrating negative effects of afforestation), a 'winner' (i.e., results demonstrating positive effects of afforestation), or 'unknown' (i.e., results presenting conflicting / inconclusive information or data deficiency) based on details extracted from the literature review. Generally, a winner gains breeding and/or foraging habitat that was not present before afforestation, often by immigration; whilst a loser has been forced to emigrate through the loss of breeding

and/or foraging habitat. Unknowns occur where formerly resident species (e.g., mallard (*Anas platyrhynchos*) nesting at a loch edge) do continue to breed and forage when trees have matured around their habitat, but the effect on breeding success of any change in predator pressures associated with forest edges is unknown.

For the analysis, all winner and loser species were grouped according to BoCC status. Eurasian jay (*Garrulus glandarius*), white-tailed eagle (*Haliaeetus albicilla*), red kite (*Milvus milvus*) and red-necked phalarope (*Phalaropus lobatus*) were omitted because their breeding statuses have changed drastically since the last (2007–2011) *Bird Atlas* (Balmer *et al.* 2013) census.

To determine how the extent of a species' natural range within Britain may have been affected by afforestation in the Flow Country we used occupied probable and confirmed breeding 10 km squares from Balmer *et al*. (2013) to calculate the mean proportion of the British breeding range for bird species occurring in the Flow Country that actually lies within the Flow Country.

RESULTS

The main changes in Flow Country bird species indicated by the review are shown in Tables 1–3 and in the Appendix. Afforestation brings both winners and losers. Of the 33 winner species, 88 % (29) were either woodland or forest specialists, and none were open-bog (including wetland) species. Conversely, the 27 loser species included wetland (10), grassland (10), marine (3), coastal (2) and shrubland (2) species but no woodland or forest species. Whilst there were more winners than losers, the losers included more BoCC5 Red and Amber listed species (Figure 2). Thus, although more winners were able to take advantage of the new breeding and foraging opportunities presented by afforestation of the Flow Country, they were generally of lower conservation concern (5 Red, 10 Amber) than the losers (11 Red, 13 Amber).

Species that were classified as losers had a significantly higher proportion of their range within the Flow Country than those classified as winners, for Amber-listed (Mann-Whitney test $U = 101$, $p = 0.028$) and Green-listed ($U = 41$, $p = 0.014$) species (Figure 3). There was no significant difference in the proportion of range within the Flow Country for Red-listed winner and loser species ($U = 37$, $p = 0.159$) although they did follow the same pattern, with means 2–5 times higher for losers. Of the species for which > 10 % of occupied breeding 10 km squares across the UK occurred within the Flow Country, the top three were all losers, namely: wood sandpiper (47 %; Amber-listed), common greenshank (19 %; Amber-listed) and dunlin (16 %; Red-listed).

DISCUSSION

It is crucial to exercise caution when interpreting the results. For example, mistle thrush (*Turdus viscivorus*) and hen harrier are both Red-listed species but, while it is possible to establish new tree plantations suitable for mistle thrush anywhere in the UK, it is far more challenging to create suitable habitats for hen harrier. The mistle thrush remains widespread in the UK with an estimated breeding population of 165,000 pairs. Its decline and subsequent Red-listing was believed to be linked primarily to the degradation of farmland (rather than woodland) habitat (BTO 2024a). The hen harrier is much more range-restricted with an estimate of 545 breeding pairs in 2016 (BTO 2024b). Its decline since 2010 has been partly due to the expansion of forests that exclude the harrier and its prey. The specialised habitat requirements of hen harriers make it far less feasible to create suitable new habitat for them than for mistle thrushes.

Bird species likely to be positively affected by forestry in the Flow Country

Without the presence of commercial forestry, some bird species - specifically woodland and forest specialist passerines - would not breed in the Flow Country (see review in the Appendix). For example, crossbills (*Loxia* spp.) are highly dependent on non-native conifer seeds, and their future range and population are likely to be determined by the availability of these seeds, particularly in Caithness where there are very few Scots pine (*Pinus sylvestris*) trees. Ringing recoveries indicate that some species occurring in the Flow Country are non-migratory within the UK; thus, coal tit (*Periparus ater*) and Eurasian bullfinch (*Pyrrhula pyrrhula*) are considered resident (Newton 2000, Gosler 2002). On the other hand, siskin (*Spinus spinus*) and redpoll (*Acanthis* spp.) are typically dispersive, especially when anticipating food shortage (Sellers 1984). It is possible that these species use forests as 'safe stepping-stone islands' to disperse and establish breeding sites farther north than they might have done naturally, along the northern coastline of Caithness and Sutherland. Such 'stepping-stones' are also likely to benefit common chiffchaff (*Phylloscopus collybita*) and willow warbler (*Phylloscopus trochilus*), which are predicted to increase in northern Scotland under climate change (Martay *et al.* 2023). Additionally, the presence of commercial forestry

Table 1. Avian 'winner' species (that have been positively affected by afforestation in the Flow Country), their UK Birds of Conservation Concern (BoCC5) status (Stanbury *et al.* 2021), primary habitat preference (Tobias *et al.* 2022) and trophic niche (Pigot *et al.* 2020).

Species English name	Latin name	BoCC5 status	Habitat preference	Trophic niche	References
Common cuckoo	*Cuculus canorus*	Red	Forest	Invertivore	Moss *et al*. (1979), Fuller (2012)
Common wood pigeon	*Columba palumbus*	Amber	Woodland	Omnivore	Fey *et al*. (2015), Gundelach (2018)
Eurasian woodcock	*Scolopax rusticola*	Red	Forest	Omnivore	Sládeček *et al.* (2023)
Western osprey	*Pandion haliaetus*	Amber	Marine	Aquatic predator	Petty (1996)
Eurasian sparrowhawk	*Accipiter nisus*	Amber	Forest	Vertivore	Moss *et al.* (1979), Newton (1996), Petty (1996), Wilson *et al.* (2006)
Northern goshawk	*Accipiter gentilis*	Green	Forest	Vertivore	Petty (1996), Petty *et al.* (2003)
Red kite	*Milvus milvus*	Green	Shrubland	Omnivore	Newton *et al.* (1996), Petty (1996)
White-tailed eagle	*Haliaeetus albicilla*	Amber	Rock	Aquatic predator	Petty (1996)
Common buzzard	*Buteo buteo*	Green	Grassland	Vertivore	Petty (1996)
Long-eared owl	*Asio otus*	Green	Forest	Vertivore	Petty (1996)
Tawny owl	*Strix aluco*	Amber	Forest	Vertivore	Moss *et al*. (1979), Petty (1996)
Great spotted woodpecker	*Dendrocopos major*	Green	Woodland	Omnivore	Barrientos (2010), Ónodi & Csörgő (2013)
Eurasian jay	*Garrulus glandarius*	Green	Forest	Omnivore	Han & Keeffe (2021)
Dunnock	*Prunella modularis*	Amber	Forest	Invertivore	Moss *et al.* (1979), Graham *et al.* (2017)
Coal tit	*Periparus ater*	Green	Forest	Omnivore	Moss *et al.* (1979), Wilson *et al. (*2006)
Blue tit	*Cyanistes caeruleus*	Green	Woodland	Invertivore	Moss *et al.* (1979), Bibby *et al.* (1989), Hancock & Avery (1998), Graham *et al*. (2017)
Great tit	*Parus major*	Green	Woodland	Invertivore	Moss *et al.* (1979), Bibby *et al*. (1989), Graham *et al.* (2017)
Long-tailed tit	*Aegithalos caudatus*	Green	Forest	Invertivore	Moss *et al.* (1979), Bibby *et al.* (1989)
Willow warbler	*Phylloscopus trochilus*	Amber	Forest	Invertivore	Moss *et al.* (1979)
Common chiffchaff	*Phylloscopus collybita*	Green	Forest	Invertivore	Moss *et al.* (1979), Bibby *et al*. (1989), Graham *et al.* (2017)
Goldcrest	*Regulus regulus*	Green	Forest	Invertivore	Moss *et al.* (1979), Wilson *et al*. (2006), Graham *et al*. (2017)
Eurasian wren	*Troglodytes troglodytes*	Amber	Forest	Invertivore	Moss *et al.* (1979), Hancock & Avery (1998)
Eurasian treecreeper	*Certhia familiaris*	Green	Forest	Invertivore	Moss *et al.* (1979), Bibby *et al.* (1989), Wilson *et al*. (2006)
Song thrush	*Turdus philomelos*	Amber	Forest	Invertivore	Bibby *et al*. (1989), Hancock & Avery (1998)
Mistle thrush	*Turdus viscivorus*	Red	Forest	Omnivore	Bibby *et al.* (1989)
Common blackbird	*Turdus merula*	Green	Forest	Omnivore	Moss *et al.* (1979), Bibby *et al*. (1989), Graham *et al.* (2017)
Spotted flycatcher	*Muscicapa striata*	Red	Forest	Invertivore	Bibby *et al*. (1989), Graham *et al.* (2013)
European robin	*Erithacus rubecula*	Green	Forest	Omnivore	Moss *et al.* (1979), Hancock & Avery (1998)
Common chaffinch	*Fringilla coelebs*	Green	Forest	Invertivore	Moss *et al.* (1979), Hancock & Avery (1998)
Eurasian bullfinch	*Pyrrhula pyrrhula*	Amber	Forest	Omnivore	Moss *et al.* (1979), Bibby *et al.* (1989), Graham *et al.* (2017)
Redpoll	*Acanthis* spp.	Red	Forest	Granivore	Moss *et al.* (1979), Hancock & Avery (1998), Graham *et al.* (2013, 2017)
Crossbill	*Loxia* spp.	Green	Forest	Granivore	Moss *et al.* (1979), Petty & Avery (1990)
Eurasian siskin	*Spinus spinus*	Green	Forest	Granivore	Moss *et al.* (1979), Bibby *et al.* (1989), Petty & Avery (1990)

Table 2. Avian 'loser' species (that have been negatively affected by afforestation in the Flow Country), their UK Birds of Conservation Concern (BoCC5) status (Stanbury *et al.* 2021), primary habitat preference (Tobias *et al.* 2022) and trophic niche (Pigot *et al.* 2020).

Species English name	Latin name	BoCC5 status	Habitat preference	Trophic niche	References
Red grouse	*Lagopus scotica*	Green	Grassland	Herbivore terrestrial	Thompson *et al.* (1988), Hancock & Avery (1998)
Black grouse	*Tetrao tetrix*	Red	Grassland	Herbivore terrestrial	Pearce-Higgins *et al.* (2006), White *et al*. (2013)
Eurasian oystercatcher	*Haematopus ostralegus*	Amber	Coastal	Aquatic predator	Thompson *et al.* (1988)
Northern lapwing	*Vanellus vanellus*	Red	Wetland	Omnivore	Thompson *et al.* (1988), Stroud *et al*. (1987)
European golden plover	*Pluvialis apricaria*	Green	Grassland	Invertivore	Thompson *et al.* (1988), Wilson *et al*. (2014)
Common ringed plover	*Charadrius hiaticula*	Red	Coastal	Aquatic predator	Thompson *et al.* (1988)
Eurasian curlew	*Numenius arquata*	Red	Grassland	Aquatic predator	Thompson *et al.* (1988), Stroud *et al*. (1987)
Dunlin	*Calidris alpina*	Red	Wetland	Aquatic predator	Thompson *et al.* (1988), Wilson *et al*. (2014)
Common snipe	*Gallinago gallinago*	Amber	Wetland	Aquatic predator	Thompson *et al.* (1988), Hancock & Avery (1998)
Red-necked phalarope	*Phalaropus lobatus*	Red	Wetland	Aquatic predator	Walpole *et al.* (2008)
Common sandpiper	*Actitis hypoleucos*	Amber	Wetland	Aquatic predator	Stroud *et al.* (1987), Yalden (1992)
Common redshank	*Tringa totanus*	Amber	Wetland	Aquatic predator	Thompson *et al.* (1988), Stroud *et al*. (1987)
Wood sandpiper	*Tringa glareola*	Amber	Wetland	Aquatic predator	Thompson *et al.* (1988)
Common greenshank	*Tringa nebularia*	Amber	Wetland	Aquatic predator	Thompson *et al.* (1988)
Black-headed gull	*Chroicocephalus ridibundus*	Amber	Wetland	Aquatic predator	Hancock & Avery (1998)
Great black-backed gull	*Larus marinus*	Amber	Marine	Aquatic predator	Hancock *et al.* (2009)
Great skua	*Stercorarius skua*	Amber	Marine	Aquatic predator	Thompson *et al.* (1988)
Parasitic jaeger	*Stercorarius parasiticus*	Red	Marine	Aquatic predator	Thompson *et al.* (1988)
Hen harrier	*Circus cyaneus*	Red	Grassland	Vertivore	Thompson *et al.* (1988), Sheridan *et al.* (2020)
Short-eared owl	*Asio flammeus*	Amber	Grassland	Vertivore	Thompson *et al.* (1988)
Eurasian skylark	*Alauda arvensis*	Red	Grassland	Omnivore	Thompson *et al.* (1988), Hancock & Avery (1998), Graham *et al.* (2013)
European stonechat	*Saxicola rubicola*	Green	Shrubland	Invertivore	Moss *et al.* (1979), Thompson *et al.* (1988)
Northern wheatear	*Oenanthe oenanthe*	Amber	Grassland	Invertivore	Thompson *et al.* (1988)
Meadow pipit	*Anthus pratensis*	Amber	Grassland	Invertivore	Moss *et al*. (1979), Thompson *et al*. (1988), Hancock & Avery (1998)
Twite	*Linaria flavirostris*	Red	Grassland	Granivore	Thompson *et al.* (1988)
Common linnet	*Linaria cannabina*	Red	Shrubland	Granivore	Moss *et al.* (1979)
Common reed bunting	*Emberiza schoeniclus*	Amber	Wetland	Omnivore	Wilson *et al. (*2006)

Table 3. Avian species for which the effect of afforestation in the Flow Country is 'unknown', their UK Birds of Conservation Concern (BoCC5) status (Stanbury *et al.* 2021), primary habitat preference (Tobias *et al.* 2022) and trophic niche (Pigot *et al.* 2020). Note that, for several of these species, we were unable to find any references in published literature.

Species English name	Latin name	BoCC5 status	Habitat preference	Trophic niche	References
Greylag goose	*Anser anser*	Amber	Wetland	Herbivore terrestrial	Guðjónsson *et al.* (2015)
Eurasian wigeon	*Mareca penelope*	Amber	Wetland	Omnivore	
Mallard	*Anas platyrhynchos*	Amber	Wetland	Herbivore aquatic	
Eurasian teal	*Anas crecca*	Amber	Wetland	Herbivore aquatic	
Tufted duck	*Aythya fuligula*	Green	Wetland	Herbivore aquatic	
Common scoter	*Melanitta nigra*	Red	Wetland	Aquatic predator	
Common goldeneye	*Bucephala clangula*	Red	Wetland	Aquatic predator	Sénéchal *et al.* (2008)
Common merganser	*Mergus merganser*	Green	Riverine	Aquatic predator	Lemelin *et al.* (2010)
Red-breasted merganser	*Mergus serrator*	Amber	Wetland	Aquatic predator	
Rock ptarmigan	*Lagopus muta*	Red	Grassland	Herbivore terrestrial	
Little grebe	*Tachybaptus ruficollis*	Green	Wetland	Aquatic predator	
Common gull	*Larus canus*	Amber	Coastal	Omnivore	Hancock & Avery (1998)
Red-throated loon	*Gavia stellata*	Green	Wetland	Aquatic predator	Eriksson & Sundberg (1991), Dewar & Lawrence (2023)
Black-throated loon	*Gavia arctica*	Amber	Wetland	Aquatic predator	Dewar & Lawrence (2023)
Golden eagle	*Aquila chrysaetos*	Green	Grassland	Vertivore	Marquiss *et al.* (1985), Watson *et al.* (1987), Watson (1992)
Western barn owl	*Tyto alba*	Green	Human modified	Vertivore	
Common kestrel	*Falco tinnunculus*	Amber	Shrubland	Vertivore	
Merlin	*Falco columbarius*	Red	Woodland	Vertivore	Bibby & Nattrass (1986), Rebecca *et al.* (2022)
Peregrine falcon	*Falco peregrinus*	Green	Grassland	Vertivore	
Western jackdaw	*Coloeus monedula*	Green	Human modified	Omnivore	Moss *et al*. (1979), Graham *et al.* (2013)
Carrion crow	*Corvus corone*	Green	Human modified	Omnivore	Moss *et al.* (1979), Hancock & Avery (1998)
Hooded crow	*Corvus cornix*	Green	Human modified	Omnivore	Moss *et al.* (1979), Graham *et al*. (2013, 2017)
Northern raven	*Corvus corax*	Green	Forest	Omnivore	Moss *et al.* (1979)

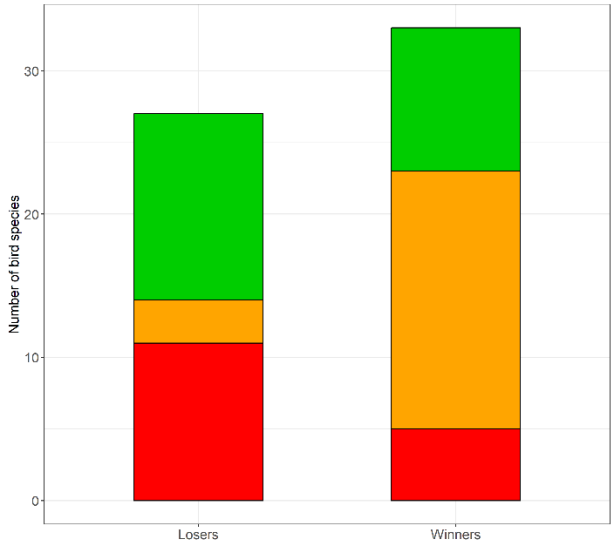

Figure 2. Numbers of bird species expected to be negatively (losers) or positively (winners) affected by afforestation in the Flow Country, with species separated on the basis of their BoCC5 status (Red, Amber or Green) according to Stanbury *et al.* (2021); see Methods.

may benefit species such as redwing (*Turdus iliacus*) and fieldfare (*Turdus pilaris*) that currently breed very scarcely and irregularly (Davey *et al.* 2016) but whose breeding presence could potentially increase in the future. This has already occurred in the case of Eurasian jay (*Garrulus glandarius*), which is expanding its range in Scotland including into Caithness and Sutherland (Hughes in press). The first confirmed wild record for Caithness was in May 2008 (Davey *et al.* 2016) and sightings, mainly in forest plantations, have become more regular since then.

Generalist omnivores such as ravens and crows (*Corvid* spp.) have taken advantage of commercial plantations in the Flow Country (Davey *et al.* 2016), with crow species occurring in higher densities in the UK than in other European countries (Roos *et al.* 2018). As well as being known to predate wader nests (Ausden *et al.* 2009, Amar *et al.* 2010), crows compete with raptor species for resources.

Following recolonisation and reintroduction schemes (Love 2003), the white-tailed eagle (*Haliaeetus albicilla*) is expanding its range back into its former territory and now breeds in commercial plantations in the Flow Country (Manson 2024). This brings new conservation challenges in forest-to-bog restoration as tree-nesting and -roosting white-tailed eagles are protected under the Wildlife and Countryside Act 1981 even though the trees are not necessary for them to breed or roost.

Bird species likely to be negatively affected by forestry in the Flow Country

While a wider variety of species gained from the afforestation, species that did not benefit were generally of higher conservation value (Figure 2). Our results demonstrate not only that more Red-listed species were affected negatively by afforestation, but also that a greater proportion of the British range of BoCC Green- and Amber-listed loser species was affected. Therefore, it cannot be concluded that creating non-native plantations was advantageous for bird conservation. The importance of the UK's peatlands should not be under-estimated, since lodgepole pine and Sitka spruce can be established elsewhere whereas new peatland habitat cannot.

Waders were particularly negatively affected by the planting of commercial forestry, which has resulted in an estimated loss of 17–19 % of the Flow Country populations of common greenshank, dunlin and golden plover (*Pluvialis apricaria*) (Stroud *et al.* 1987, Lindsay *et al.* 1988). High breeding site fidelity has been documented in long-lived birds such as waders (Méndez *et al.* 2018) and has been specifically observed in these three species (see Thompson *et al.* (1988) for common greenshank, Jackson (1994) for dunlin and Johnson *et al.* (1993) for golden plover). It is unclear where displaced birds might relocate. Upland waders that lose their breeding habitat to afforestation are thought to breed less successfully in subsequent years on new ground, possibly due to the loss of a reliable breeding partner during displacement (Thompson *et al.* 1988).

Two raptors that breed quite commonly in the open bogs of the Flow Country are the hen harrier (*Circus cyaneus*) and the short-eared owl. These species have broadly similar diets, preying on birds such as meadow pipit (*Anthus pratensis*) and Eurasian skylark (*Alauda arvensis*) as well as small rodents (*Muroidea* spp.) and shrews (*Soricidae* spp.) (Littlewood *et al.* 2021). They also have similar breeding habitat requirements, nesting on the ground, and are likely to be affected by the same conservation challenges (Orta *et al.* 2014, Olsen *et al.* 2019), and habitat loss through afforestation has been identified as a significant threat to both species (Fernandez-Bellon *et al.* 2021). Although hen harriers and short-eared owls commonly nest and forage in newly afforested areas, they tend to abandon these areas once the forest canopy closes (Shaw 1995, Wilson *et al.* 2010). While young forestry may be attractive to them for the higher availability of rodents resulting from continuous forest management (felling/ stocking), it simultaneously reduces the available open-ground breeding habitat. Furthermore, forestry has created new breeding habitat for several tree-

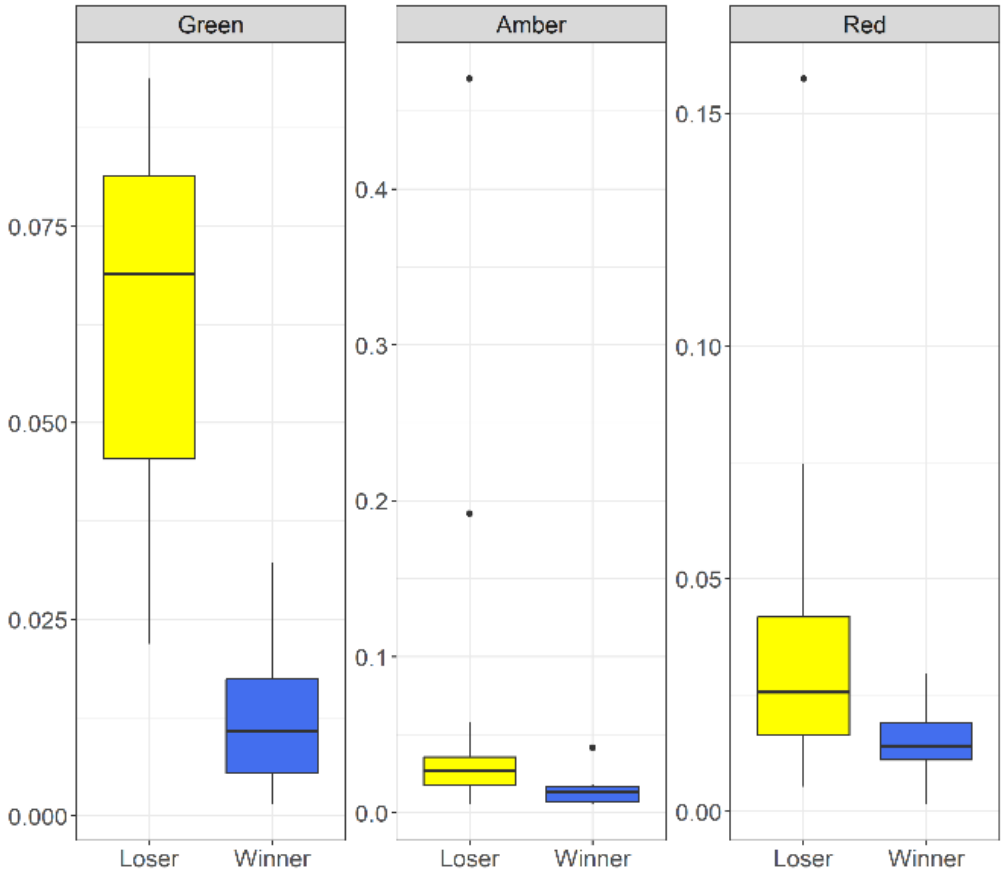

Figure 3. Comparisons of afforestation 'loser' and 'winner' species, categorised according to their BoCC5 status (Green, Amber or Red), in terms of the number of 10 km squares occupied within the Flow Country as a proportion of the total number of squares occupied in Britain. The boxplots show median (horizontal line), inter-quartile ranges (box), and minimum and maximum values (whiskers). Data from Stanbury *et al.* (2021).

nesting raptors such as the Eurasian sparrowhawk (*Accipiter nisus*), common buzzard (*Buteo buteo*), long-eared owl (*Asio otus*), tawny owl (*Strix aluco*) and common kestrel (*Falco tinnunculus*), increasing the competition for prey.

Point counts in peatland plots (Hancock *et al.* 2009) have shown that great black-backed gulls (*Larus marinus*) breed in the Flow Country but declined significantly (by 81 %) between 1988 and 2000, whilst black-headed gulls (*Chroicocephalus ridibundus*) declined significantly (by 88 %) in forest plots. The latest (2015–2021) national seabird census ("Seabirds Count") demonstrated that both species are still heavily declining, particularly at inland breeding locations (Dunn & Francis 2023, Lewis 2023). It is known that the nests of gull species are predated by foxes (Weseloh *et al.* 2022).

Forest edge effects

Ecologically, edge effects are changes that occur in population or community structures at the edges of habitats. Lower densities of some open-nesting bird species close to forest edges have been demonstrated in the Flow Country and elsewhere (Stroud *et al.* 1990, Hancock *et al.* 2009, Wilson *et al.* 2014, Holmes *et al.* 2020, Pálsdóttir *et al.* 2022). The Flow Country plantations have become suitable habitat for generalist predators such as red fox (*Vulpes vulpes*) (Stroud *et al.* 1987, Lindsay *et al.* 1988), pine marten (*Martes martes*) (Croose *et al.* 2013) and hooded crow (*Corvus cornix*) (Stroud *et al.* 1987, Lindsay *et al.* 1988) - red fox and crow species being amongst the most important predators of wader eggs (Pienkowski 1984, Parr 1993, Macdonald & Bolton 2008). Dunlin densities were found to be lower and red grouse decline was more likely near forest edges in the Flow Country, suggesting they would benefit from forest removal (Hancock *et al.* 2009). Dunlin and golden plover have also been shown to avoid areas close to forest edges (Wilson *et al.* 2014) and evidence from scat density measurements suggests that mammalian predators are responsible for lower wader densities near forest edges (Hancock *et al.* 2020). Lower curlew breeding productivity linked to

fox predation has also been found in close proximity to forest edges outside of the Flow Country (Valkama *et al.* 1999). On the other hand, Wilson *et al.* (2014) found no evidence of edge effect on common greenshank densities, perhaps due to their predator mobbing behaviour and their occupation of bog areas within native woodland elsewhere in their range (Nethersole-Thompson & Nethersole-Thompson 1979). This suggests that edge effects do not influence all bog breeding bird species to the same extent.

Access tracks and deer fencing came with the forestry. Whilst common buzzards and kestrels, for example, benefit from fencing posts as prominent viewpoints that aid hunting (Village 2010, Cieśluk *et al*. 2023), they also introduce a collision risk for birds, particularly grouse species (Baines & Summers 1997). Research that is currently underway aims to understand how predators use access tracks in the Flow County and will assist in understanding predator access to birds breeding on forest edges.

Species adaptable to addition of forestry to the area

Species that can switch prey or are generalists are more likely to withstand landscape changes (Fischer & Lindenmayer 2007). The merlin (*Falco columbarius*), primarily an open-bog breeding species, has adapted to the plantations in the Flow Country in terms of breeding habitat by nesting in trees (Bibby & Nattrass 1986) and using afforested areas for foraging. Although the selection of nest sites was influenced by the proximity of open-ground foraging habitat, no long-term effects on breeding performance could be linked to increased afforestation in Ireland (Lusby *et al.* 2017). However, the opposite was found in north-east Scotland, where breeding productivity was lower in forest-nesting compared to moorland-nesting pairs (Rebecca *et al.* 2022). In addition to foraging 'traditionally' on bog passerine species, merlin will also forage on passerines breeding in forest plantations including thrushes, tits, and finches (Newton *et al.* 1984, Petty *et al.* 1995). In some areas of Scotland outside of the Flow Country, hen harriers also continue to breed in forestry plantations.

Whilst afforestation causes direct losses of breeding and foraging habitat for greenshank as described above, this species appears to have adapted better than dunlin and golden plover to the presence of nearby forests, in that it is less affected by forestry edge effects (Wilson *et al.* 2014).

Knowledge gaps

Even in recent times we have lost species that were likely candidates for Red-listing, and we may never fully understand the reasons behind their disappearance. For instance, Temminck's stint (*Calidris temminckii*) once bred in small numbers in the Flow Country (Stroud *et al.* 1987) but was last recorded breeding in the UK in 1993 and is now considered to have ceased breeding here (Eaton *et al.* 2015). Similarly, whimbrel (*Numenius phaeopus*) also bred in small numbers historically but is no longer known to breed in the Flow Country (*Whimbrel Survey 2021* data, RSPB, unpublished). The loss of these species serves as a stark reminder of the fragility of our ecosystems and the gaps in our understanding of what drives species declines.

The Flow Country hosts nationally important numbers of common scoter, Eurasian wigeon, black-throated diver and red-throated diver. Approximately half of the UK's common scoter population breeds in the Flow Country and is Red-listed because of this localised breeding (Stanbury *et al.* 2021). It was unknown how these waterbirds, which naturally breed in forested areas elsewhere in their range, are affected by the forestry not only through the edge effects described above but also via changes, such as enrichment, in their wetland habitat (Robson *et al*. 2019, 2023). Although waterfowl may not have lost their foraging and loch-edge breeding habitats, chemical changes in some lochs have occurred through increased phosphate levels from fertilisation of the forest (Robson *et al.* 2019, Gaffney *et al*. 2021) and this may affect vegetation as well as invertebrate and fish assemblages.

There are unknowns about how woodland passerines such as goldcrest and coal tit will disperse when their breeding woodland is permanently removed; and how summer migrants such as willow warbler, arriving in mass, will respond to the loss of their breeding habitat.

The majority of the UK's breeding wood sandpiper population is concentrated in the north and west of Scotland (Chisholm 2007), where they appear to be increasing with survey of apparently suitable areas often revealing new breeding sites (McQueen 2017). This species resembles common greenshank in that, whilst they lose breeding habitat through afforestation, they may be more tolerant than other waders of forest edge effects.

Wider issues

When assessing bird assemblage changes linked to forest removal, other factors may also need consideration. Some of these are discussed below. Any or all of these confounding factors may mean that species abundances in the Flow Country are unlikely to return to the levels seen pre-1980s forestry.

Extreme weather events

Globally, bird assemblage changes are expected due to climate change (Bender *et al.* 2019, Gahbauer *et al.* 2022, Wayman *et al* 2022). Globally, extreme weather events such as droughts are predicted to increase over the next century (Arnell *et al.* 2019, 2021), as are the frequency and intensity of wildfires (Doerr & Santín 2016). Both drought and wildfire have occurred in the Flow Country in recent years; there were widespread droughts in 2018 and 2021 and an extensive (> 6,500 ha) wildfire in 2019 (Andersen *et al.* 2024). Peatland fires have important ecological effects on biodiversity (Kirkland *et al.* 2023). The effects on birds are complex (Davies *et al.* 2016) and can be caused by natural or human-made scenarios. Fires have been shown to boost invertebrate prey (Usher & Thompson 1993) as well as bird diversity (Tharme *et al.* 2001). While adult birds can escape wildfires during the breeding season, their eggs and/or chicks are likely to be destroyed, and the time taken for bird populations to return to pre-fire levels varies between species (Baker *et al.* 1997, Walesiak *et al.* 2022). A study in Canada concluded that peatland birds in particular, including *Tringa* wader species, avoided burnt areas following severe fires and were likely to be more susceptible than other birds to fire-driven habitat changes (Knaggs *et al.* 2020). In the longer term, however, breeding densities of golden plover, lapwing, red grouse and curlew were elevated on managed red grouse moors with prescribed burning while the densities of passerines including meadow pipit, skylark and whinchat were lowered (Tharme *et al.* 2001). Knaggs *et al.* (2020) recommended that the need to understand the long-term risks to these species from climate change requires additional efforts that link fire to bird populations.

Renewable energy development

Land use can also put pressure on bird populations. For example, there has been a sharp increase in the number of onshore wind turbines on the periphery of the Caithness and Sutherland SPA/SAC, with 256 already constructed, another 126 approved since 1989, and more planned (Highland Council 2023). The bird taxa most affected by turbine displacement include the orders Gaviiformes (divers and loons), Anseriformes (ducks, geese and swans), Accipitriformes (hawks, eagles, kites, etc.) and Falconiformes (falcons) (Marques *et al.* 2021), all of which are represented amongst the bird species breeding in the Flow Country. Golden plover has been shown to avoid wind turbines by a distance of at least 200 m (Pearce-Higgins *et al.* 2008). Birds are also killed by collisions with wind turbines as well as other human-made structures including vehicles, power lines and communication towers (Erickson *et al.* 2001).

Disease

Wild deer use forestry plantations for shelter unless effective excluding fences are in place. Deer host populations of ticks, such as *Ixodes ricinus*, which are primary vectors of zoonotic pathogens in Europe (Gray & Kahl 2001). It has been demonstrated that tick densities are lower where fenced enclosures are in place, compared to unfenced forests (Gilbert *et al.* 2012). Birds are known to carry ticks and tick-borne pathogens (summarised by Loss *et al.* 2016), which particularly affect ground foraging birds (Wright *et al.* 2006, Newman *et al.* 2015). How ticks affect birds in the Flow Country is yet to be studied.

Natural regeneration of non-native conifers

Forest regeneration is another edge-effect problem associated with forestry in the Flow Country, where seeds from standing non-native conifer plantations are dispersed onto adjacent open bog including areas undergoing forest-to-bog restoration. Self-seeding of non-native trees (most commonly Sitka spruce) has also been documented in the Scottish Highlands, where it compromises natural regeneration of native trees (Summers 2023). This comes as an additive cost to restoration efforts and could also affect bird assemblages by propagating the negative effects of forestry beyond the edges of the original plantations. Generally, the ecotone of this habitat is a sharp change from open bog to even-aged forestry, often planted as a block enclosed within a deer fence. However, in time, forest regeneration tends to extend and initially 'soften' the spatial transition. Thus, new questions are emerging as to whether the ecological edge effect of standing mature forestry is extended by forest regeneration onto open bog.

Broader environmental pressures and the uncertain future of loser species

A number of bird species from the 'losers' and 'unknown' categories use other habitats beyond the Flow Country during parts of their life cycles, including the coastal and/or marine environment where additional pressures including infrastructure (Benjamins *et al.* 2020) and climate-linked changes in prey availability (Kendall *et al.* 2004) may operate. Long distance Afro–Palaearctic migrants are facing drought and habitat changes on their non-breeding grounds (summarised by Vickery *et al.* 2014) as well as hunting on both their non-breeding grounds and

their migration routes (McCulloch *et al.* 1992, Richardson & Porter 2020, Vickery *et al.* 2014). Within the UK, shorter-distance migrants escaping parts of the frozen winter of their upland breeding habitats face similar challenges, such as the persecution of hen harriers linked to gamebird management (Ewing *et al.* 2023).

Policy implications and conservation management

The recent adoption of the Convention on Biological Diversity (CBD) Global Biodiversity Framework has set ambitious global targets for protected area establishment and habitat restoration, emphasising the need for enhanced conservation efforts (CBD 2022). Internationally, there is growing recognition of the critical role that peatlands play in carbon sequestration, leading to several Ramsar Convention resolutions advocating for their restoration (see https://www.ramsar.org). Initiatives like the Global Peatlands Initiative and the EU's Green Deal (EC 2019) and draft Nature Law (EC 2022) further underscore the priority afforded to restoring these vital ecosystems. The significance of wetlands for carbon sequestration is also acknowledged within the Paris Agreement, where they are recognised as vital components of Nationally Determined Contributions (NDCs) (UN 2015). Additionally, the Inter-governmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Land Degradation and Restoration Assessment highlights the urgent need for habitat restoration to combat environmental degradation (IPBES 2018).

In this context, the Flow Country presents a unique opportunity to achieve multiple international targets and deliver significant environmental benefits, given its substantial potential for restoration. However, the scale of afforestation in the Flow Country has had a profound effect on bird populations in this internationally important area, illustrating the broader challenge of balancing conservation priorities. The RSPB has focused on restoring afforested areas back to bog-like conditions to improve the fortunes of species with high conservation value. Yet, while restoration efforts within the Caithness and Sutherland Peatlands designated sites aim to maintain and enhance former bird assemblages, and other land managers like Forestry and Land Scotland are undertaking large-scale peatland restoration in the north Highlands (e.g., at Dalchork Forest and Benmore Forest), the broader region still requires further assessment, especially regarding the 'effects unknown' species.

Beyond bird species, afforestation has altered the assemblages of other wildlife groups including mammals (Hancock *et al.* 2020, Littlewood *et al.* 2021), invertebrates (Pravia 2019, Pravia *et al.* 2020) and vegetation (Hancock *et al.* 2018). The cumulative effects of these changes on the resilience of the entire ecosystem, particularly in the face of climate change, demand additional attention.

As the UK faces pressures to increase woodland expansion, determining the best approach to achieving this within the Flow Country is critical. Non-native woodland blocks have been planted into naturally open habitats, requiring significant habitat modifications such as drainage and fertiliser applications, which has resulted in fragmented woodland and open habitats. An alternative approach would be to extend or restore native woodland within its natural range, as exemplified by the Cairngorms Connect Project in Central Scotland (Gullett *et al.* 2023, Cairngorms Connect 2024). This method preserves open habitats while creating woodlands in historically wooded zones, benefiting both open-habitat and woodland species. Therefore, continued forest-to-bog restoration and sensitively located new forestry plantations are imperative to conserving the afforestation 'loser' bird species in the Flow Country, which are of high conservation value and range-restricted.

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AUTHOR CONTRIBUTIONS

RH originated, conceptualised and planned the study, led the writing of the first draft, and is the lead author responsible for overall coordination of the manuscript. MH contributed significantly to development of the analytical framework and provided key input to the analysis section of the manuscript. RoA, RuA, AP, PG and NL provided expertise on ecological processes, particularly in relation to the changes in bird populations and their implications. All authors contributed equally to the sections on species diet, behaviour and ecology, and were involved in reviewing and editing the manuscript for intellectual content.

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Appendix: Information on the forestry 'winner' species.

Species	BoCC5 status	Effects of afforestation
Eurasian sparrowhawk *Accipiter nisus*	Amber	A description from 1933 indicates that there were few breeding pairs of Eurasian sparrowhawk in Caithness, and the habitat was deemed unsuitable. Therefore, the recent success of this species in the county is associated with the increase in plantations (Davey *et al*. 2016).
Red kite *Milvus milvus*	Green	Due to reintroduction schemes, the UK range of red kite has expanded dramatically since their earlier near-extinction through persecution, with a 1935 % increase in numbers between 1995 and 2020 (Harris *et al*. 2021). In recent years, red kites have started breeding in in commercial forestry plantations in the Flow Country (R. Hughes personal observation), adding to interspecific competition for habitat with other raptors.
White-tailed eagle *Haliaeetus albicilla*	Amber	Following recolonisation and reintroduction schemes (Love 2003), the range of white-tailed eagle is now expanding back towards this species' former territory. Although it traditionally bred on coastal cliffs, islands in lochs and inland crags in the Flow Country (Evans *et al.* 2012, Davey *et al.* 2016), it now breeds in the commercial forestry plantations.
Common buzzard *Buteo buteo*	Green	The UK and Flow Country breeding distributions of common buzzard have increased since the 1970s, although underlying mechanisms are not well understood. The reduction in illegal killing (Prytherch 2013), the ban on organochlorine pesticides, the recovery of European rabbits following their infection with the myxomatosis virus, and upland afforestation are all thought to have contributed (Taylor *et al.* 1988, Davey *et al.* 2016, Balmer *et al.* 2013).
Tawny owl *Strix aluco*	Amber	Tawny owl was once restricted to the southern parts of Caithness; however, the forestry plantations have this species to access formerly open countryside (Davey *et al.* 2016).
Eurasian jay *Garrulus glandarius*	Green	Recent coloniser of the Flow Country (Hughes in press).
Dunnock *Prunella modularis*	Amber	Considered a widespread breeder, the dunnock is thought to take advantage of the felling and re-planting of forests and is likely to continue to flourish in line with Scottish trends due to increased forestry management (Davey *et al.* 2016).
Coal tit *Periparus ater*	Green	Coal tits were first suspected to breed in Caithness in 1907 and were confirmed breeding in the north of Caithness in the 1960s (Davey *et al.* 2016). Being a primarily insectivorous species, the coal tit was a widespread breeder as the commercial plantations expanded in the 1970s and 1980s (Davey *et al.* 2016). The coal tit has also benefited from afforestation in other parts of Scotland including Sutherland (Vittery 1997).
Willow warbler *Phylloscopus trochilus*	Amber	Willow warblers commonly breed in the Flow Country plantations (Davey *et al.* 2016). Some increases of this species in Scotland more generally (in contrast to the UK) have been linked to woodland expansion (Martay *et al.* 2023), and it is likely that this has been assisted by the establishment of forestry plantations (Forrester *et al*. 2007).
Common chiffchaff *Phylloscopus collybita*	Green	The common chiffchaff was first recorded as a breeder in North Sutherland and Caithness in 1971–1972, has increased in abundance since (Forrester *et al.* 2007), and continued to increase between 1995 and 2020. Although this species is less numerous than the willow warbler (an Afro-Palaearctic migrant) in Scotland, common chiffchaff numbers are likely to increase with climate change, which also forces willow warbler further north (Martay *et al*. 2023).
Goldcrest *Regulus regulus*	Green	The range of goldcrest expanded in line with commercial plantations. It is now a widespread resident (Forrester *et al.* 2007, Davey *et al.* 2016) and one of the commonest forest birds in the Flow Country.

Species	BoCC5 status	Effects of afforestation
Eurasian wren *Troglodytes troglodytes*	Amber	Eurasian wren has been described as common and widespread in commercial forestry plantations (Davey *et al.* 2016).
Eurasian treecreeper *Certhia familiaris*	Green	Eurasian treecreeper breed in commercial plantations but little detailed information is available (Davey *et al.* 2016).
Song thrush *Turdus philomelos*	Amber	Song thrush has been described as prospering in commercial forestry habitat, where it is a regualar breeder (Davey *et al.* 2016).
Mistle thrush *Turdus viscivorus*	Red	Mistle thrushes are regular breeders in commercial forestry, which is a preferred habitat for the species in Caithness (Davey *et al.* 2016).
Common blackbird *Turdus merula*	Green	Common blackbirds are regular breeders in commercial forestry (Davey *et al.* 2016).
European robin *Erithacus rubecula*	Green	European robin is also described as common and widespread in commercial forestry (Davey *et al.* 2016).
Common chaffinch *Fringilla coelebs*	Green	The common chaffinch has recently declined in the UK and this has been linked partly to outbreaks of trichomonosis (Robinson *et al.* 2010) and habitat change (Macleod *et al.* 2004, Hanmer *et al.* 2022). Finches in the Flow Country have been affected by trichomonosis but appear to be recovering (Manson 2020).
Eurasian bullfinch *Pyrrhula pyrrhula*	Amber	One of the larger seed-eating finches, Eurasian bullfinch was restricted as a localised breeder in southern Caithness until the early 1970s, when it reached the commercial plantations in the north of the county. Bullfinches are now much more widespread, and their population size is thought to be at the highest level ever (Davey *et al*. 2016).
Redpoll *Acanthis* spp.	Red	Redpoll species are common forestry seed eaters in the Flow Country. Lesser redpoll (*Acanthis cabaret*) increased in abundance over a similar timescale to Eurasian siskin (see below) and it is likely that its recent status as a regular breeder is due to the increase of forestry and scrub between the 1988-1991 and 2007-2012 atlas surveys (Davey *et al.* 2016). Common redpoll (*Acanthis flammea*) has also bred successfully in Caithness in small numbers, presumably due to the new forests, and was probably under-recorded in the Flow Country previously (Davey *et al*. 2016). For data analysis, we grouped common and lesser redpolls as *Acanthis* spp.
Crossbill *Loxia* spp.	Green	Crossbills feed almost exclusively on conifer seeds (Newton 1972, McNab *et al.* 2019) and were casual visitors to Caithness in the 1860s. Common crossbill (*Loxia curvirostra*) was able to colonise all of the major commercial forestry plantations once they had matured (Davey *et al.* 2016). The Scottish crossbill has also been recorded in small numbers (Summers *et al.* 2004, Summers & Buckland 2011). The future status and range of both species are likely to be determined by trajectory of commercial forestry, as crossbills are unlikely to breed in the Flow Country without this. Owing to complexities surrounding the identification / separation of common and Scottish crossbill in the field (Lewis & McInerny 2022), we grouped them as crossbill spp. in the analysis.
Eurasian siskin *Spinus spinus*	Green	Eurasian siskins are nowadays common forestry seed eaters in the Flow Country. Historically, however, this species was a rare breeder in Caithness, described as only an occasional migrant visitor by Harvie-Brown & Buckley (1887). By 1907 there had been little change in this status (Horne 1907). The British breeding range of European siskin increased dramatically following forestry planting throughout large areas of the uplands (Holloway 2002, Balmer *et al.* 2013), and the increase in conifer plantations in Caithness allowed the breeding population here to dramatically increase and subsequently over-winter (Davey *et al*. 2016). In the 2000s, the estimated number of breeding pairs in Scotland was 3.5 million, almost exclusively in conifer plantations (Forrester *et al*. 2007).