Climate change and migratory species: a review of impacts, conservation actions, indicators and ecosystem services

Part 3 – Migratory species and their role in ecosystems

Department for Environment Food & Rural Affairs

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CMS

The Convention on the Conservation of Migratory Species of Wild Animals (CMS, also known as the Bonn Convention, after the city in which it was signed in 1979) is the global international agreement of the United Nations which addresses the conservation and sustainable use of migratory animals and their habitats. Over the past 40 years, CMS Parties have identified over six hundred species that merit protection under the Convention as they migrate across Range State boundaries and so require co-operative actions between Range States.

The key issue of climate change was first discussed at the fifth meeting of the CMS Conference of the Parties (CoP5) in 1997 and has been addressed at multiple subsequent CoPs.

In support of this work, the Government of the United Kingdom of Great Britain and Northern Ireland (through a contract to the British Trust for Ornithology (BTO) funded by the Department of Environment, Food and Rural Affairs via the Joint Nature Conservation Committee (JNCC)) commissioned a review of the latest evidence on the impacts of climate change on migratory species, with regard also to conservation actions, indicators and ecosystem services.

The results of this review are presented in three parts:

Part 1 – Impacts of climate change on migratory species
Part 2 – Conserving migratory species in the face of climate change
Part 3 – Migratory species and their role in ecosystems.

A Summary for Policy Makers is also available.
Access the full review at jncc.gov.uk/climate-migratory-species-report/

Any enquiries regarding this publication should be sent to communications@jncc.gov.uk

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Climate change and migratory species: a review of impacts, conservation actions, indicators and ecosystem services

Part 3 – Migratory species and their role in ecosystems

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Summary

There is a growing understanding of the way in which certain species support ecosystem functionality, or provide ecosystem services that deliver nature-based solutions to human challenges such as flooding, pollution or food security. In particular, migratory species play a key role within the ecosystems they utilise due to their temporal presence and ability to connect different ecosystems, often thousands of miles apart.

In Part 3 of this review, we carried out a rapid literature review to identify the various ecosystem services migratory species can provide. In particular, we looked at the potential role of these services as nature-based solutions to climate change, as well as the wider benefits they can bring for people and ecosystems, to help decision makers begin to consider these issues in a cross-cutting and holistic way. This builds on the strategies identified in Part 2 for conserving migratory species threatened with climate change, through investigating whether migratory species conservation can provide wider mitigation and adaptation benefits for biodiversity and people.

Our review suggests that migratory species are particularly important for providing services related to the regulation and maintenance of ecosystems. Migratory bird, bat and insect species were found to be particularly key to pollination, seed dispersal and pest control, whilst large terrestrial and marine mammals, as well as sharks, were important for aiding carbon capture and providing other regulation and maintenance services. Other services related to culture (tourism, recreational activities, symbolic value and natural heritage) and provision (predominantly food) were also identified, though to a lesser extent.

The results of the review suggest that conserving migratory species has the potential to improve ecosystem resilience, helping to mitigate the impacts of climate change and promote adaptation to increasingly frequent climatic hazards. Therefore, migratory species should be seen not only as 'victims' of the climate crisis, but also as a key part of a potential 'solution' to tackling the global impacts of climate change.

Contents

1 Introduction

Biodiversity is strongly impacted by climate change drivers in addition to more long-standing threats (Díaz *et al.* 2006; Maxwell *et al.* 2016). As outlined in Part 1 of this review, this is particularly true for species that migrate, as they are subject to changes in a range of, often well separated, locations which need to exist as a coherent network, both spatially to facilitate the migratory journey, and temporally, as they often rely on specifically-timed seasonal resource peaks (Learmonth *et al.* 2006; Robinson *et al.* 2009; Winkler *et al.* 2014). Billions of individuals undertake migratory journeys annually, connecting ecosystems across the globe (Bauer & Hoye 2014). Given their ubiquity, both geographically and taxonomically (e.g. around 20% of birds and 30% of marine mammals are migratory), migratory species not only form significant components of many ecosystems, but also facilitate significant transfers of energy and resources.

Part 2 of this review outlines how a range of mitigation and adaptation practices have previously been employed to help conserve migratory species in the face of climate change, among other threats. Alongside this increasing interest in the potential role humans can play in providing appropriate management to support ecosystem services, there is also a growing understanding of the way in which certain species can make important contributions to the overall functioning of ecosystems, providing the potential mitigation of (some) climate change impacts (e.g. Díaz *et al.* 2006; Schmitz *et al.* 2023). The nature of the roles these species provide has been framed in a variety of ways, including as 'ecosystem engineers' (e.g. Jones *et al.* 1994), or as providing ecosystem services (e.g. Harrison *et al.* 2014; Kleemann *et al.* 2020), nature-based solutions (e.g. Malhi *et al.* 2020) or natural climate solutions (e.g. Schmitz *et al.* 2023).

Part 3 of this review therefore aims to identify the various ecosystem services that migratory species can provide and, in particular, the potential role for these species as nature-based solutions to climate change. The report concentrates on the three overarching ecosystem services outlined by the Common International Classification of Ecosystem Services (CICES): Regulation and Maintenance services, Provisioning services and Cultural services (CICES 2023; e.g. Harrison *et al.* 2014; Figure 1). Some of these services provide important nature-based solutions to human challenges that are not directly relevant, or are only indirectly linked, to the processes of climate change (e.g. tourism, food provisioning, symbolic value, natural heritage) but which are nevertheless vital services to human well-being (e.g. Whelan *et al.* 2015) and ecosystem functioning (e.g. Díaz *et al.* 2006; Civantos *et al.* 2012). Several, though, are directly linked to climate change through carbon capture, or enhancing ecosystem resilience to extreme events such as flooding, sea level rise, droughts, heat waves and wildfire (IUCN 2023; e.g. Schmitz *et al.* 2023). Notably, several directly linked services are specifically related to plants and their growth or abundance. Plants are integral to ecosystem functioning, and retaining plant genetic diversity increases resilience to environmental perturbations, including habitat loss and extreme weather events (Kremen *et al.* 2007).

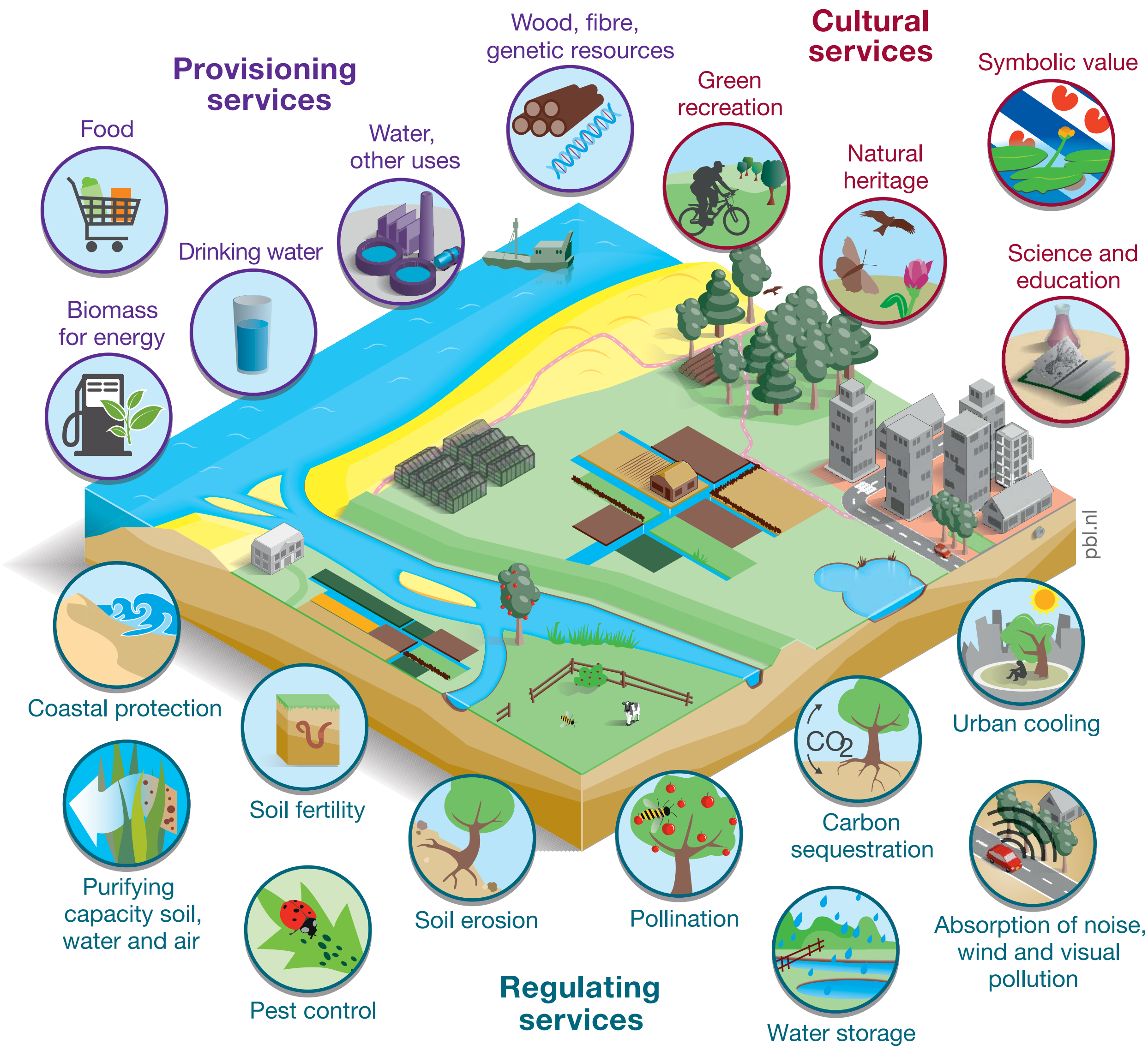


Figure 1. Overview of CICES' three 'sections' of ecosystem services (Regulation and Maintenance services, Provisioning services and Cultural services) and the associated 'divisions' (from Koets, M.J. *et al.* 2017. *Relative price increase for nature and ecosystem services in cost-benefit analysis*. PBL Netherlands Environmental Assessment Agency, The Hague. Open access article distributed under Creative Commons Licence Attribution 3.0 Unported (CC BY); minor modifications made to colour and captions).

In particular, this review aimed to: (1) consider and highlight the roles migratory species play as key components of ecosystems, and specifically through providing ecosystem services; (2) identify the role migratory species have, or could have, in providing nature-based solutions that support adaptation or mitigation to climate change; and (3) provide detailed examples of the ecosystem services that individual migratory species can provide through a selection of case studies. The primary focus is on those species listed on Appendix I and Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), but studies of non-listed migratory species are also drawn upon, where relevant, to highlight key climate change-related, nature-based solutions (see the full list of species from this review in S6 Table 1).

2 Methods

A series of literature searches were conducted in Web of Science using set search terms (full methods are laid out in S1). These searches were filtered to extract the term migratory, using the search term ("migrat*") as an initial filtering step. Results were further filtered per species group using similar search terms to those used for Part 1 of this review (S2 Table 1). For all searches, the first 100 results (or all if fewer than 100) were skimmed for relevance at title and abstract level. Relevance was based on a set of questions (S1) which guided the categorisations into: (1) literature where ecosystem service(s) are provided by migratory species; and (2) literature detailing nature-based solution(s) to climate change provided by migratory species. Additional supplementary searches were conducted *ad hoc* to fill in known gaps (searches were conducted in Web of Science and Google Scholar). Studies from the main or supplementary searches are individually highlighted in the reference list using * = main search and ** = supplementary searches. The results of all the searches were combined and duplicates removed (summarised in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses, PRISMA, flow table – S3 Table 1).

3 Results

Of the 379 search results (main searches = 336, supplementary searches = 43; S3 Table 1; S4 Figure 1), a total of 73 studies identified migratory species as key components of an ecosystem (S5 Table 1). The roles performed by these species vary, but all contribute towards ecosystem functioning and provide benefits to biomes more broadly. From this review, the ecosystem services identified were predominantly related to Regulation and Maintenance, but also to Provisioning and Cultural services (Figures 2 & 3). Of the different species groups, the greatest number of studies pertained to birds (n = 30, 41%), closely followed by terrestrial mammals (n = 28, 38%), with relatively few on the remaining species groups (Figures 2 & 3). Of the broad categories of ecosystem services, all three (or a combination of the three) were identified for all bird categories, terrestrial mammals, marine mammals and bony fish, whereas only Regulation and Maintenance services were attributed to bats and sharks and rays, and a combination of Cultural and Regulation and Maintenance services were provided by insects (Figures 2 & 3). In addition, a small number of disservices/maladaptations were identified for birds (waterbirds and landbirds) and terrestrial mammals (in 7% and 9% of papers respectively). Geographically, these studies covered species in all regions, from various terrestrial mammals across North America, parts of Africa and China; bats, birds (waterbirds, raptors and landbirds) and insects across Europe, Africa, South America and India; seabirds across the Atlantic, Pacific and Indian Ocean coastal cliffs and islands; marine mammals in the Arctic, Pacific and coastal waters of Oceania; sharks in the Caribbean; and fish in the Arctic, North America and Europe (Figure 4).

Many of the ecosystem services identified through the searches are directly or indirectly linked to climate change regulation. Here, the focus is on species that provide services with direct or indirect links to climate change regulation (IUCN 2023). Whilst Provisioning and Cultural services were also important to consider given the wider cultural and economic well-being impacts of climate change, they were deemed to be outside the scope of this work, however their relevance merits further investigation. Of the 73 identified studies deemed relevant to our review, 71 related to nature-based solutions key to carbon capture and ecosystem resilience to climate change. These were further divided into fire risk, coastal erosion, water quality/flooding, disease control and plant genetic isolation (Figure 4; Table 1; S5 Table 1). This last category was further subdivided into pollination, seed dispersal, nutrient cycling, and pest and disease control.

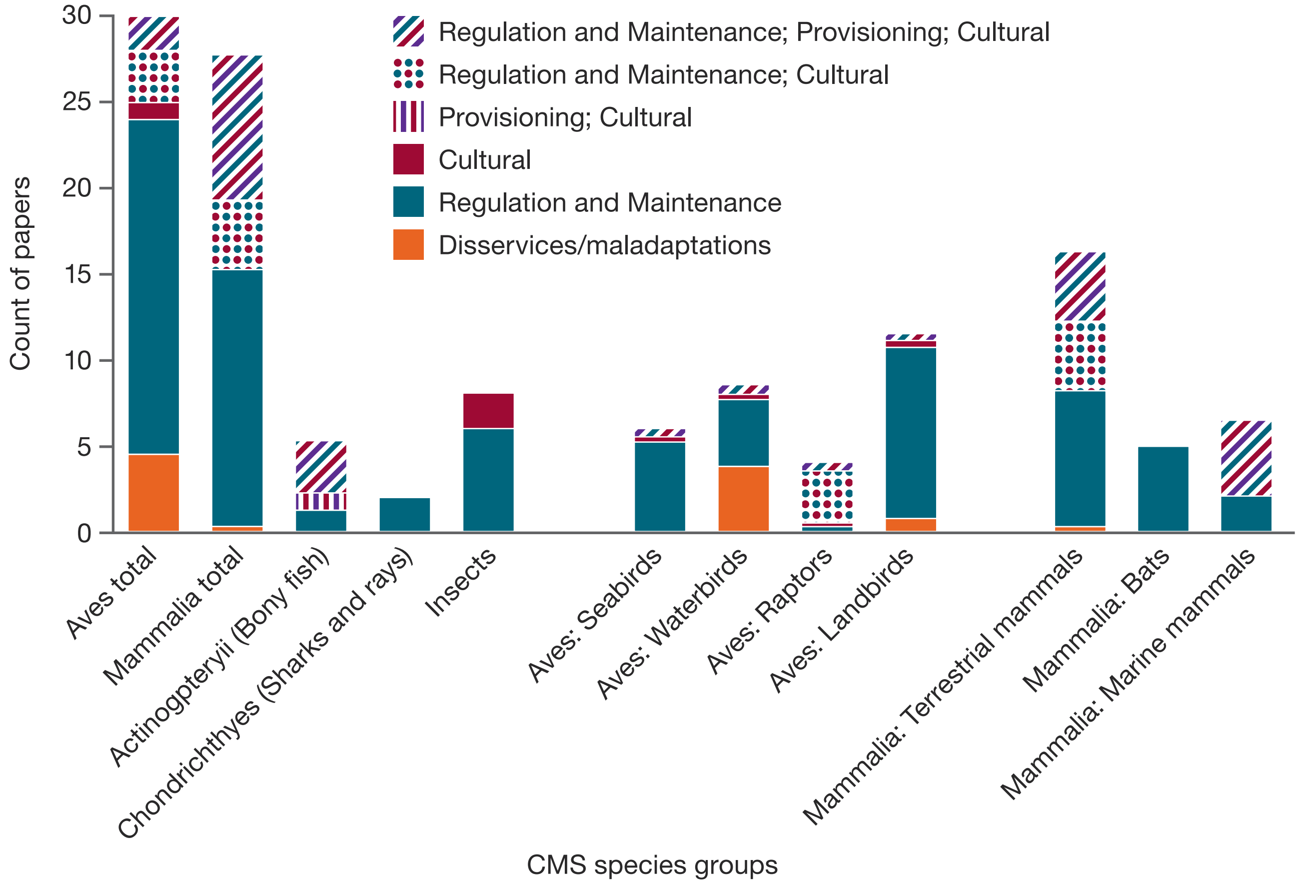


Figure 2. Count of papers from different groups of migratory species (CMS species categories used). Totals for each group are on the left side of the x-axis; the count for subgroups within Aves and Mammalia are shown on the right side of the x-axis. The different services provided by each species group are also compared. Note: this is a count compiled from this study's main and supplementary search results and is not an exhaustive list. Four of the papers found for Aves were general across all species and so are represented equally in the individual Aves groups in the figure (the papers are Sekercioglu 2002; Whelan *et al.* 2008; Whelan *et al.* 2015; Anderson *et al.* 2016).

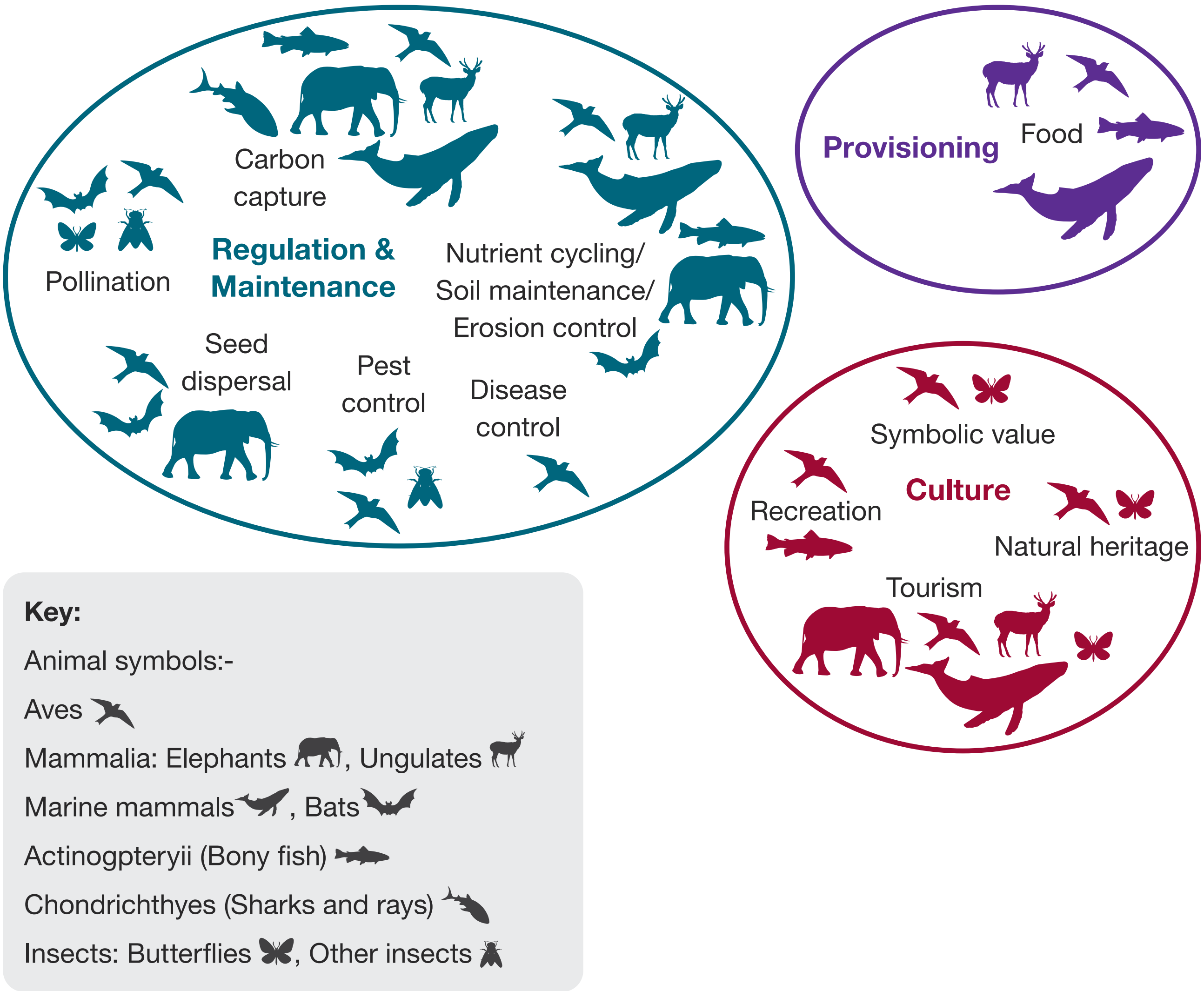


Figure 3. Schematic of the three types of services (Regulation and Maintenance, Provisioning, and Cultural), with specific examples from each of these categories, and symbols around each to show which migratory species group(s) are most often associated with providing these. Note: this diagram is representative of this study's search results and is not an exhaustive list.

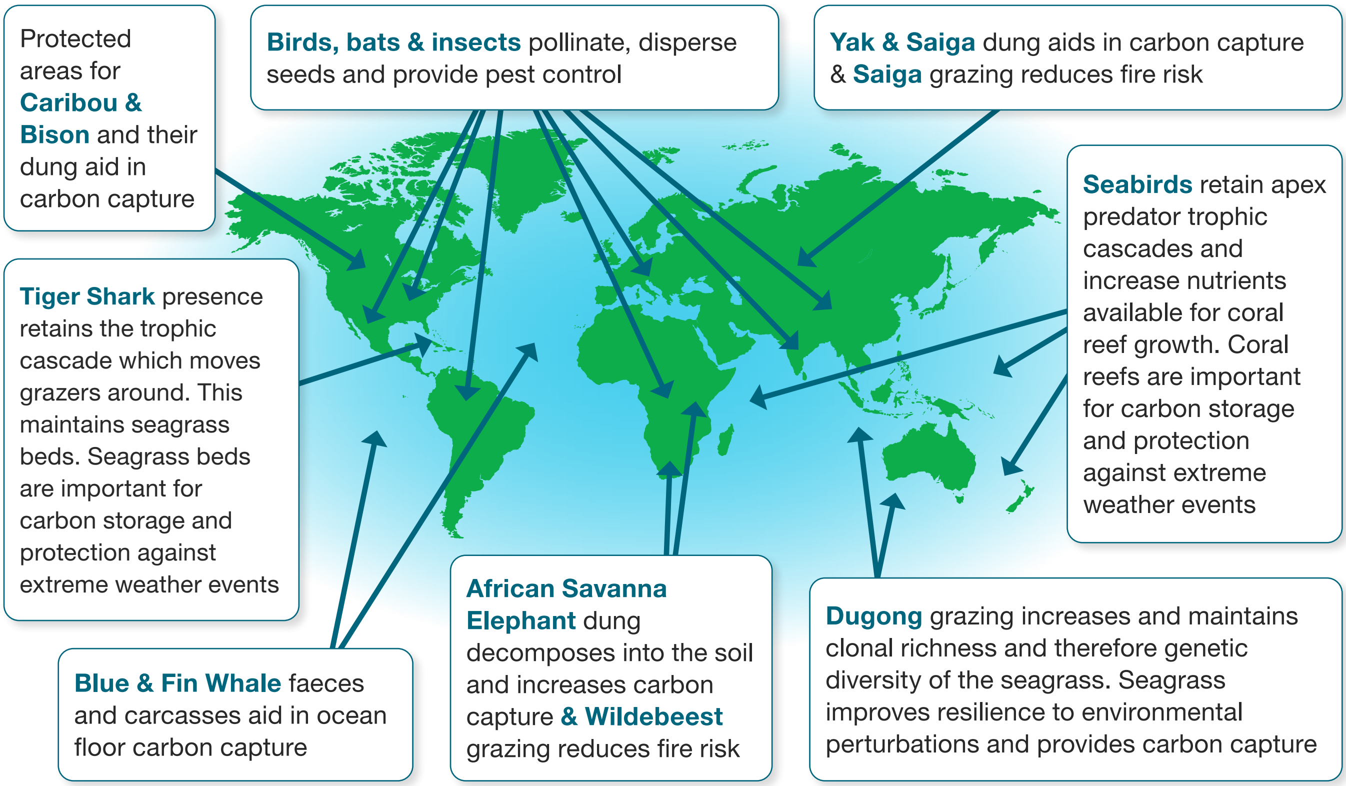


Figure 4. World map showing example migratory species and the climate change-related services they provide, with approximate geographical locations of where they can be found. References and more details of the studies can be found in Table 1 and S5 Table 1. Note: this is an example list compiled from this study's search results and is not an exhaustive list.

Table 1. Directly linked climate change-related ecosystem services and nature-based solutions compiled from this study.

CMS species group	Habitat	Species/ Species group	Service(s)	References
Ecosystem services related to climate change mitigation:				
Mammalia: Terrestrial mammals	Boreal woodland	Caribou	Safeguarding soil carbon through protecting woodland and grassland	Johnson *et al.* 2022
	Grassland	Bison	Keeping snow compact retains carbon in the grassland. Dung left on grassland increases carbon storage	Gilgert & Zack 2010; Schmitz *et al.* 2023
	Alpine grassland	Yak	Dung left on the grassland increases carbon storage	Zhang *et al.* 2016
	Steppes and semi-desert habitats of Central Asia	Saiga Antelope	Dung left on the grassland increases carbon storage	Brinkert *et al.* 2016
	African Savanna	African Savanna Elephants	Elephant dung decomposes into the soil and increases carbon storage	Sandhage-Hofmann *et al.* 2021
Mammalia: Marine mammals	Ocean	Whales	Whale excretion and sinking carcasses increases carbon storage	Malinauskaite *et al.* 2022a, 2022b; Pearson *et al.* 2023; Schmitz *et al.* 2023
	Seagrass beds	Dugongs	Moderate Dugong grazing aids in retaining genetic diversity in seagrass beds (a globally important carbon store) making them more resilient after environmental perturbation	Preen 1995; McMahon *et al.* 2017

CMS species group	Habitat	Species/ Species group	Service(s)	References
Actinogpteryii (Bony fish)	Rivers/ocean	Anadromous fish	Fish excretion in the ocean and carcasses in riparian habitat increase carbon storage (a globally important carbon store)	Wilcove 2008; Almeida *et al.* 2023
Chondrichthyes (Sharks and rays)	Seagrass beds	Tiger Sharks	Tiger Shark presence retains the trophic cascade which moves seagrass grazers around. This maintains seagrass beds	Atwood *et al.* 2015; Gallagher *et al.* 2022
Aves: Seabirds	Coastal areas	Breeding seabirds (e.g. Red-footed Booby)	Seabird predation retains the trophic cascade, and their guano goes into the water. This increases the nutrients available for coral to grow which buffers the coastline from extreme weather events and reduces coastal erosion	Savage 2019; Berr *et al.* 2023
Ecosystem services related to climate change resilience:				
Species important for retaining genetic diversity of plants				
Aves: Waterbirds	Agriculture	Waterbirds: Asian Openbill Stork, Black-headed Ibis	Pest control	Menon 2021

CMS species group	Habitat	Species/ Species group	Service(s)	References
Aves: Landbirds	Forest	Corvidae (Crows) Northern Nutcracker	Increases in air temperature enable tree lines to advance; this often relies on dispersal of seeds by birds	Holtmeier 2012 Pesendorfer *et al.* 2016
	Forest	Frugivorous thrushes	Seed dispersal	Rodríguez-Pérez *et al.* 2017
	Oak savanna	Insectivores (Parulidae - Neotropical migrants)	Pest control	Wood & Pidgeon 2015
	Agriculture	Insectivores Afro-Palearctic Nearctic-Neotropical migrants	Pest control	Kleemann *et al.* 2020 Jedlicka *et al.* 2021
	Grassland	Insectivores (Icteridae)	Pest control. Pollination	Bedford *et al.* 2013
	Grassland-Forests	Hummingbirds (Trochilidae)	Pollination	Leimberger *et al.* 2022
	Agriculture (Lowquat, *Eriobotrya japonica*) Shrubs (*Salvia*)	White-eyes (e.g. Mountain White-eye, Orange River White-eye)	Pollination	Wester & Claßen-Bockhoff 2006 Fang *et al.* 2012
	Shrubs (*Salvia*)	Sunbirds (e.g. Southern Double-collared Sunbird)	Pollination	Wester & Claßen-Bockhoff 2006

CMS species group	Habitat	Species/ Species group	Service(s)	References
Mammalia: Bats	Forest and volcanic plateau	Mexican Long-tongued, Mexican Long-nosed and Mexican Lesser Long-nosed Bats	Nectivorous bats pollinate and disperse seeds as well as provide pest control	Burke *et al.* 2021
	Forest	Megabats/ Flying Foxes/ Old World Fruit Bats (Pteropodidae)	Important pollinators and seed dispersers as well as pest regulators	Frafjord 2007
	Forest	Neotropical Leaf-nosed Bats (Phyllostomidae)	As frugivores, they distribute tree seeds enabling forest range-shifts and -expansions, needed to track rising temperatures and changing rainfall patterns. Pest control	Ramírez-Fráncel *et al.* 2022
	Agriculture	Brazilian/ Mexican Free-tailed Bats	Pest control of moths	Krauel *et al.* 2015; Lopez-Hoffman *et al.* 2017
	Agriculture	Bats	Pest control (reduced benefit due to white-nose syndrome)	Manning & Ando 2022
Actinogpteryii (Bony fish)	From oceans to rivers	Migratory bony fish	Nutrient transfer	Wilcove 2008; Kovach *et al.* 2013; Beard *et al.* 2019; Steiner *et al.* 2019; Hare *et al.* 2021; Almeida *et al.* 2023

CMS species group	Habitat	Species/ Species group	Service(s)	References
Insects	Generally in Europe	Insects	Aid in long-distance pollination	Tzilivakis *et al.* 2015; Satterfield *et al.* 2020; Hawkes *et al.* 2022
	Globally	Hoverflies (Syrphidae, e.g. Marmalade Hoverfly)	Aid in long-distance pollination and pest control	Doyle *et al.* 2020; Jia *et al.* 2022
	Europe-Africa	Painted Lady Butterfly	Aid in pollination	Hawkes *et al.* 2022
Rainfall				
Mammalia: Terrestrial mammals	Wetlands	Bison	Wallowing in wetlands modifies the habitat, aiding in flood management	Gilgert & Zack 2010; Johnson *et al.* 2012
Temperature				
Aves: Landbirds	Forest	Corvidae (crows) Northern Nutcracker	Increases in air temperature enable tree lines to advance; this often relies on dispersal of seeds by birds	Holtmeier 2012; Pesendorfer *et al.* 2016
Aves: Waterbirds	Grassland, UK-Iceland	Pink-footed Goose	Long-distance dispersal of plant seeds, enabling plants to disperse to cooler latitudes	Lovas-Kiss *et al.* 2023
Mammalia: Terrestrial mammals	African Savanna Steppes and semi-desert habitats of Central Asia	African savanna ungulates (including Wildebeest) Saiga Antelope	Grazing regimes reduce fire risk	Dobson 2009; Holdo *et al.* 2009; Schmitz *et al.* 2023 Brinkert *et al.* 2016

CMS species group	Habitat	Species/ Species group	Service(s)	References
Wind/storms/extreme weather events				
Mammalia: Marine mammals	Seagrass beds	Dugong	Moderate Dugong grazing aids in retaining genetic diversity in seagrass beds (a globally important carbon store which helps reduce coastal erosion), making them more resilient after environmental perturbations	Preen 1995; McMahon *et al.* 2017
Chondrichthyes (Sharks and rays)	Seagrass beds	Tiger Sharks	Tiger Shark presence retains the trophic cascade which moves seagrass grazers around. This maintains seagrass which helps reduce coastal erosion	Atwood *et al.* 2015; Gallagher *et al.* 2022
Aves: Seabirds	Coastal habitats	Breeding Seabirds	Seabird predation retains the trophic cascade, and their guano goes into the water, increasing the nutrients available for coral to grow which reduces coastal erosion	Savage 2019; Berr *et al.* 2023
Disease control				
Aves: Raptors	Agriculture	Vultures	Pest control, especially of rodents in agriculture and through consuming livestock carcasses, reduces the availability of food for stray dogs (which can also carry diseases)	Markandya *et al.* 2008; Donázar *et al.* 2016; van den Heever *et al.* 2021

4 Analysis of the ecosystem services provided by each species group

4.1 Aves: Seabirds

Maintaining functioning migratory populations of seabirds is important for transporting nutrients from across the globe to coastal and near-coastal habitats. This nutrient transfer aids carbon capture by the coastal habitats, which in turn improves ecosystem resilience. (See the case study on page 29 for a focus on how seabirds can contribute to coastal resilience.)

Many coastal nesting seabirds are important migratory species influencing both terrestrial and marine habitats. During the breeding season, seabirds return to colonies bringing nutrients (in the form of guano, feathers and remnants of prey items) from across the globe back to cliff edges and, often isolated, islands. Burrow-nesting seabirds are also considered ecosystem engineers, facilitating soil aeration and nutrient cycling, which is important for the regulation and maintenance of soils (McKechnie 2006).

Seabirds not only aid in nutrient cycling through nest building and burrow nesting, but their guano also increases nutrients in the surrounding coastal area, both on land and in the sea (Berr *et al.* 2023). This nutrient seepage aids carbon capture of the surrounding habitats (e.g. coral reefs), which creates denser habitat, providing greater coastal defence against storms and reducing coastal erosion (Lorrain *et al.* 2017; Savage 2019; Berr *et al.* 2023). This can be exemplified by a study that compared the nutrients left by seabirds on rat-infested and rat-free islands, finding that invasive rats disrupted the nutrient cycle flow from seabirds and therefore substantially decreased the available nutrients on and around the islands (Graham *et al.* 2018). However, further research is needed to establish the vulnerability that nitrogen-enriched corals may have to coral bleaching (Lorrain *et al.* 2017).

A key habitat found around seabird nesting grounds is kelp forest, which is an important habitat for carbon storage. For example, primary production of kelp forests in the Atlantic Ocean can exceed 1 kg carbon.m^{-2}.yr^{-1}, which for an area of 8,000 km^2 (the size of Scotland) would equate to 8 million tons of carbon stored per year (Smale *et al.* 2013). In addition, kelp forests also protect the coast and help to reduce coastal erosion, especially from climate change-induced extreme weather events (Schmitz *et al.* 2023).

4.2 Aves: Waterbirds

Maintaining functioning migratory populations of waterbirds is important for plants, both for pest control and seed dispersal, the latter of which facilitates the poleward migration of plants in response to increasing temperatures. Through these maintenance roles, migratory waterbirds improve the ecosystem resilience of global wetlands.

Waterbirds, including geese, storks, ibis and cranes, provide a variety of services related to the Regulation and Maintenance of ecosystems, including pest control, seed dispersal, carbon capture and maintenance of soil health; they also provide Cultural services (Buij *et al.* 2017; Beard *et al.* 2019; Menon 2021; Valkó *et al.* 2022; Lovas-Kiss *et al.* 2023), and Provisioning services, as food (Lopez-Hoffman *et al.* 2017).

One example is the Pink-footed Goose (CMS Appendix II; Least Concern), which migrates between the UK and Iceland. It is a long-distance disperser of plant seeds, which enables plants to disperse to cooler latitudes, shifting their range in response to climate change (Lovas-Kiss *et al.* 2023). However, other studies have highlighted an ecosystem disservice where a disproportionate increase in geese density meant there were higher levels of grazing and so the carbon captured by the tundra decreased (Buij *et al.* 2017). This was similarly modelled by Beard *et al.* (2019), who concluded that if Brant Geese arrived earlier to their breeding grounds (which would be beneficial for their breeding success), their grazing of a species of sedge, *Carex subspathacea*, would reduce its growth and genetic diversity, and cause the tundra to turn from a carbon sink to a carbon source. Furthermore, three other papers have shown that with increased densities of migratory birds in wetland patches, increased concentrations of guano can lead to eutrophication, thus negatively impacting plants and other communities (Kerbes *et al.* 1990; Manny *et al.* 1994; Post *et al.* 1998). Careful management is therefore required to balance potentially high densities of geese with the maintenance of healthy, functioning ecosystems, ensuring enough suitable habitat is available to support entire populations (Morecroft *et al.* 2019).

4.3 Aves: Raptors

Maintaining functioning migratory populations of raptors is important for disease and pest control, which is important for human health and associated habitats in the changing climate. (See the case study on page 30 for how vultures help to reduce disease transmission.)

Raptors provide Regulation and Maintenance services through pest control, especially of rodents in agriculture and through consuming livestock carcasses, and also through Cultural services as food and for natural heritage and symbolic value (Markandya *et al.* 2008; Whelan *et al.* 2008; Donázar *et al.* 2016). The scavenging behaviours of vultures help to regulate and prevent the spread of disease to humans. For example, studies have shown that when vulture populations decrease (e.g. due to poisoning from the veterinary drug diclofenac), stray dog populations increase due to the food provided by leftover animal carcasses; this consequently increases the source of rabies, with knock-on effects to humans (Markandya *et al.* 2008; van den Heever *et al.* 2021).

4.4 Aves: Landbirds

Maintaining functioning migratory populations of landbirds is important to support seed dispersal and pest control, which improves the survival and resilience of native plant species and ecosystems, and also provides important services for cropping systems.

There are various migratory landbird species/groups that provide Regulation and Maintenance and/or Cultural ecosystem services within different habitats globally (Sekercioglu 2002; Whelan *et al.* 2008). These habitats include grassland, forest and agriculture (e.g. coffee plantations), and relate to providing pest control (both insects and weeds), seed dispersal and pollination (Table 1). This is important because plants, especially isolated plants, rely on animals for pollination and seed dispersal (Kremen *et al.* 2007). Seed dispersal facilitates the ability of plant species to shift their ranges in response to climate change, typically poleward (Hansson *et al.* 2021), and various bird species aid in this, such as the Northern Nutcracker (Holtmeier 2012). However, the ability of these and other animals (including bats and insects) to perform such services has been impacted by factors such as biodiversity loss, habitat loss / increased habitat patchiness (Fricke *et al.* 2022), and climate change-induced shifts in their own ranges to higher elevations and latitudes (Hansson *et al.* 2021). For isolated plants, there is an increasing risk of maladaptation due to climate change-induced phenological mismatches of migration timings by pollinators and seed dispersers (Bedford *et al.* 2013).

4.5 Mammalia: Terrestrial mammals

Maintaining functioning migratory populations of ungulates is important to aid in reducing wildfires and to improve ecosystem resilience. (See the case study on page 31 for how Saiga Antelopes support grassland resilience to wildfires.)

Terrestrial mammals predominantly support Regulation and Maintenance ecosystem services through carbon storage. This is mostly through the process of dropping dung, which contributes to the carbon stored in the soil as it decomposes. Examples of this include Wild Yak and Saiga Antelope dung in alpine grasslands (Brinkert *et al.* 2016; Zhang *et al.* 2016), and Reindeer/Caribou dung in boreal grasslands (Beard *et al.* 2019). Other terrestrial mammals aid in carbon storage indirectly. This can be through compacting snow, which reduces the carbon released from permafrost; for example, American Bison in the Arctic, where ~500 Gt of carbon is stored in permafrost (Schmitz *et al.* 2023). It can also be through species-driven protected area designations; for example protected woodland, such as for Boreal Woodland Caribou, is also important for carbon storage (Johnson *et al.* 2022).

Wildebeest and other African migratory ungulates are important for nutrient cycling and carbon storage as they graze along their migration routes (Dobson 2009). When ungulate populations have previously declined due to disease, this has increased the amount of standing grass available to burn in wildfires, which releases carbon dioxide into the atmosphere and causes the savanna to act as a carbon source rather than a carbon sink (Holdo *et al.* 2009; Rouet-Leduc *et al.* 2021; Schmitz *et al.* 2023).

Additional services terrestrial mammals provide include:

- soil maintenance, regulating vegetation dynamics, nutrient cycling, seed dispersal and erosion control (e.g. African Savanna Elephants as ecosystem engineers, Fritz 2017).
- fire management of grassland savanna (grazing by: Common Wildebeest, Dobson 2009; Holdo *et al.* 2009; Rouet-Leduc *et al.* 2021; Saiga Antelope, Brinkert *et al.* 2016; Akçakaya *et al.* 2018).
- maintaining grassland biodiversity via grazing (Bison: Gilgert & Zack 2010; Johnson *et al.* 2012; Saiga Antelope: Brinkert *et al.* 2016).
- habitat modification via wallowing in wetlands, which are beneficial for many migratory birds and other resident species e.g. Prairie Dogs (American Bison; Gilgert & Zack 2010; Johnson *et al.* 2012).
- food, as a Provisioning service (van Moorter *et al.* 2020).
- Cultural ecosystem services through tourism opportunities (Fritz 2017), as the terrestrial species that provide ecosystem services are largely charismatic, large megafauna.

Potential climate change-related trophic mismatches are also important to consider. For example, the delayed migration of Caribou can allow more time for vegetation to grow in Greenland, which provides a greater net carbon sink (Beard *et al.* 2019). Conversely, the earlier emergence of elderberries (*Sambucus racemosa*) reduces Salmon predation from Grizzly Bears, which in turn reduces the amount of nutrients from Salmon carcasses (discarded by the bears) entering the surrounding riparian habitat (Beard *et al.* 2019). Furthermore, a population decline in some long-distance seed dispersers can have a knock-on effect on associated plant distributions, limiting their ability to adapt to climate change (Fricke *et al.* 2022).

4.6 Mammalia: Bats

Maintaining functioning migratory populations of bats is important for supporting plant pollination, seed dispersal, pest control and nutrient uptake, all of which aid plants to retain genetic diversity amidst patchy habitats, thereby improving ecosystem resilience.

Bats contribute to Regulation and Maintenance ecosystem services through pollination and seed dispersal (which aids in reducing genetic isolation of plants) and pest control (Frafjord 2007; Krauel *et al.* 2015; Lopez-Hoffman *et al.* 2017; Burke *et al.* 2021; Ramírez-Fráncel *et al.* 2022; Manning & Ando 2022). For example, Megabats (or Flying Foxes, including one CMS Appendix II species: Straw-coloured Fruit Bat, Near Threatened), which are predominantly frugivores, are important for the regeneration of rainforest habitat, on both the mainland and islands, which is important given the reduction in rainforest habitat (Frafjord 2007). Other nectivorous bats which migrate between the US and Mexico are important pollinators and seed dispersers of columnar cacti and *Agave*. These plants are found in tropical dry forests; however, the distribution of this habitat is becoming increasingly patchy and so continued pollination and seed dispersal by the bats will be imperative for these plant species in order to retain genetic diversity whilst also maintaining food availability for the bats to survive. An increase in land protection (through habitat conservation and responsible plant population management) will be important for the survival of both the plants and bats (Burke *et al.* 2021). Many plants also need to shift their range poleward in response to climate change (Hansson *et al.* 2021), and various different species groups aid in this, including frugivorous bats (e.g. the Neotropical leaf-nosed bats, *Phyllostomidae*), by distributing tree seeds along their migration routes and thus enabling forest expansion (Ramírez-Fráncel *et al.* 2022).

Similar to landbirds and insects, the seed dispersal and pollination services provided by migratory bats, which are important for retaining plant genetic diversity (Kremen *et al.* 2007), are being affected by biodiversity loss, anthropogenic impacts of habitat loss / increased habitat patchiness (Fricke *et al.* 2022) and climate change-induced range shift changes (Hansson *et al.* 2021), causing concern for the longevity of isolated plants (Bedford *et al.* 2013).

4.7 Mammalia: Marine mammals

Maintaining functioning migratory populations of marine mammals is important for supporting and increasing carbon storage in the world's oceans. (See the case study on page 32 for the role of whales in carbon sequestration.)

Whales (and likely smaller cetaceans too) contribute predominantly to Regulation and Maintenance ecosystem services through carbon capture by carcass fall. All bodies retain carbon, but the longer lived, and larger, the animal, the more carbon that is stored. As whales are both large and long-lived, their carcasses lock a substantial amount of carbon into the ocean floor substrate when they decompose (Pearson *et al.* 2023; Schmitz *et al.* 2023), thus directly contributing to climate change mitigation. Whales also aid in marine nutrient cycling, acting as 'pumps' circulating nutrients vertically between ocean floors and surface waters (Schmitz *et al.* 2023), as well as globally due to their long migratory journeys (Pearson *et al.* 2023). Whales are also important Culturally as a traditional food source (Butman *et al.* 1995; Malinauskaite *et al.* 2022a, 2022b; Pearson *et al.* 2023; Schmitz *et al.* 2023).

Other marine mammals also provide important ecosystem services. Dugong grazing helps seagrass to retain genetic diversity, creating furrows which allow space for seed recruitment. As seagrass is important for carbon capture, Dugongs therefore indirectly aid climate change mitigation (Preen 1995; McMahon *et al.* 2017).

4.8 Actinogpteryii (Bony fish)

Maintaining functioning migratory populations of bony fish is important for retaining nutrient transfers from the ocean back to land, which improves the resilience of both ecosystems.

Within both freshwater river systems and in the ocean, bony fish provide all three types of ecosystem services. This is exemplified across various continents (including the Arctic, North America and Europe), indicating the potential global importance of this group of migratory species. Salmonids (*Oncorhynchus* and *Salvelinus*) and river herring (Alewife and Blueback Herring) are example groups of bony fish which are integral to providing nutrients to riverine systems (Regulation and Maintenance services). This is due to their extensive migrations, where they migrate from the open ocean back to the riverine systems when they breed (Wilcove 2008; Kovach *et al.* 2013; Hare *et al.* 2021). Furthermore, bony fish provide an important food source and support recreational activities for many communities, and so they provide not only Provisioning services in the form of food but also a Cultural service through sport fishing as a recreational activity (Steiner *et al.* 2019).

Climate change-related trophic mismatches are also a concern for some bony fish species. For example, changes in fish migration dates due to increases in water temperature (Salmonids: Kovach *et al.* 2013), and population declines and range shifts in species such as Arctic Cod (*Boreogadus saida*) due to warming waters (Steiner *et al.* 2019), may cause cascading impacts for the human and wildlife populations that rely on them.

4.9 Chondrichthyes (Sharks and rays)

Maintaining functioning migratory populations of sharks and rays is important for increasing carbon capture in coastal habitats.

Sharks provide important Regulation and Maintenance ecosystem services, including carbon capture and reducing coastal erosion through maintaining top-down trophic cascades (Gallagher *et al.* 2022). For example, the presence of migratory Tiger Sharks (*Galeocerdo cuvier*) in seagrass beds (*Thalassia testidinum* and *Syringodium filiforme*) promotes the movement of grazers through predator avoidance, which prevents over-grazing and thus maintains the natural balance of the seagrass bed ecosystem as a carbon store (Atwood *et al.* 2015). Continued conservation of marine predators, such as Tiger Sharks, and their habitat (e.g. through Marine Protected Areas) is likely to aid the carbon storage potential of seagrass and therefore the ecosystem resilience of coastal communities (Gallagher *et al.* 2022; Schmitz *et al.* 2023). This demonstrates that migratory marine predators can be important for protecting carbon stored in marine vegetation, and further research on the potential ecosystem services provided by other marine, as well as terrestrial, apex predators will improve our understanding of the wider ecosystem benefits associated with migratory predator conservation (Atwood *et al.* 2015).

4.10 Insects

Maintaining functioning migratory populations of insects is important for plant pollination and pest control, which will help plants to retain genetic diversity amidst patchy habitats and therefore aid in improving ecosystem resilience.

Only one insect species is currently listed on the CMS Appendices - the Monarch Butterfly. It is important as a Cultural service for tourism and it also provides inspiration, symbolic value and natural heritage (Lopez-Hoffman *et al.* 2017; Lemelin & Jaramillo-López 2020). Other migratory butterfly and insect species also provide Regulation and Maintenance, and Cultural, services along their migration routes (Hawkes *et al.* 2022). For example, the Painted Lady Butterfly and the Marmalade Hoverfly (and other migratory hoverflies) aid in pollination, and several hoverfly species aid in pest control (Hoverflies: Tzilivakis *et al.* 2015; Doyle *et al.* 2020; Satterfield *et al.* 2020; Jia *et al.* 2022; Painted Lady Butterfly: Hawkes *et al.* 2022). As with migratory landbirds and bats, migratory insects are important in aiding long-distance pollination to reduce isolation of plants and aid in pest control (Kremen *et al.* 2007). However, the effectiveness of insects doing this is being impacted by biodiversity loss, anthropogenic impacts of habitat loss / increased habitat patchiness (Fricke *et al.* 2022), intensive agricultural practices, and climate change-induced range shift changes (Hansson *et al.* 2021), raising long-term concerns for isolated plants. Therefore, insects and their associated services will be important to consider in light of their population declines due to the use of neonicotinoids and other insecticides (Siviter & Muth 2020).

5 Conclusions and recommendations

This review has demonstrated that many migratory species are integral to various aspects of ecosystem function, and that their conservation can support nature-based solutions to climate change. Migratory species not only form significant components of many ecosystems, but also facilitate significant transfers of energy and resources between ecosystems along their migration routes. In some cases, resulting conservation actions will not only protect and enhance the species of interest, but also associated species and surrounding habitats. This highlights the importance of understanding and, as necessary, restoring the functional role of migratory species within ecosystems.

In particular, migratory species support important ecosystem Regulation and Maintenance services, including carbon capture, seed dispersal and improving coastal resilience, which are essential for climate change mitigation and adaptation. Migratory species are also important for a range of other services related to Culture (e.g. tourism, recreational activities, symbolic value and natural heritage) and Provisioning (predominantly food), and provide other valuable roles, such as that of ecosystem engineers (e.g. elephants: Fritz 2017; burrow nesting seabirds: McKechnie 2006).

There is strong evidence that the conservation of migratory species, particularly large megafauna, can support climate change mitigation. For example, ecosystem services related to carbon sequestration are provided by large terrestrial grazers, such as Caribou and African Elephants; large marine mammals, such as whales and Dugongs; large marine predators, such as Tiger Sharks; bony fish; and cliff- or island-nesting seabirds (Table 1). Conserving these migratory species will not only help to increase carbon capture, both directly and indirectly, but measures to protect and restore these species, such as designating protected areas (terrestrial and marine) and enacting habitat restoration (e.g. invasive predator removal at seabird breeding grounds), can also increase biodiversity and ecosystem resilience, and promote other mechanisms of carbon capture (e.g. from the carbon locked in mature trees in protected areas).

As well as aiding climate change mitigation, migratory species can contribute towards climate change adaptation and ecosystem resilience. In particular, we identified examples of species which aid in retaining the genetic diversity of plants through pest control, pollination and seed dispersal (e.g. frugivorous and insectivorous bats and birds, and pollinating insects), as well as species that enhance coastal resilience (e.g. seabirds), reduce fire risk (e.g. Saiga Antelope) and limit disease transmission (e.g. vultures). Actions to conserve such migratory species can retain and boost the resilience of habitats to climate change hazards, whilst also safeguarding important habitat for a range of other species. For example, as apex predators, Tiger Sharks maintain trophic cascades and thus promote healthy seagrass beds, whilst seabird guano promotes the growth and resilience of coral reef systems. Designating and maintaining protected areas will be important to maintain such systems (e.g. protected areas designated for Tiger Sharks protect seagrass beds and other species that are reliant on them: Gallagher *et al.* 2022). These principles are also likely to apply to other habitats and climate change-related hazards, such as flood management, wildfires and snow melt, but were less represented in the literature and require further investigation.

Despite the growing understanding of how certain species can aid climate change mitigation or adaptation (e.g. Díaz *et al.* 2006; Schmitz *et al.* 2023), studies pertaining specifically to the importance of migratory species as nature-based solutions to climate change are uncommon. Further work is required to better understand the climate change mitigation and adaptation services these species provide, and thus their full potential as nature-based solutions to climate change. This will be particularly key for the smaller and less charismatic fauna (e.g. insects, bats, birds) for which there are fewer studies linking the ecological function(s) of species groups to ecosystem services. Furthermore, most studies identified focussed on species in the Global North, and therefore given the large-scale climate impacts projected in the Global South, as well as the lack of resources and capacity to mitigate or adapt to climate change in many parts of this region, there is a pressing need for more research on the potential for migratory species in the Global South to provide nature-based solutions to climate change.

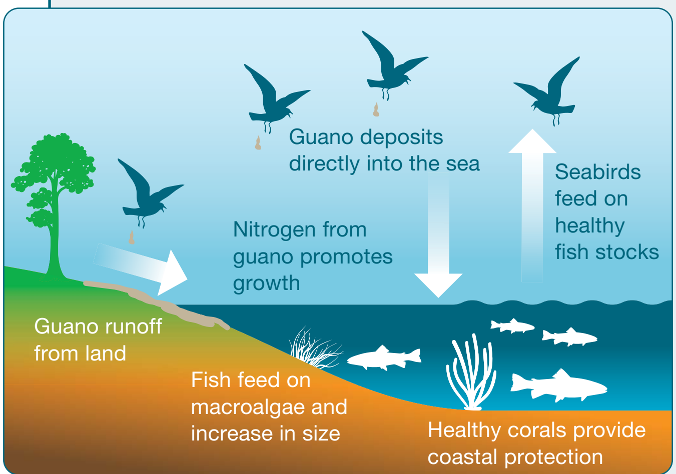
As outlined in Part 2 of this review, some conservation management tools already exist to identify the potential role(s) humans can play in providing appropriate ecosystem management to support the ecosystem services and functions provided by migratory species (e.g. Díaz *et al.* 2006; Schmitz *et al.* 2023). For example, Schmitz *et al.* (2023) argue that restoring specific wild animals to their natural functional roles through conservation (e.g. restoration and protection) can aid climate change mitigation (e.g. through carbon storage - see the case study on whales on page 32). For many of the studies in this review (though notably not whales), the transfer of energy and resources directly, or indirectly, relates to a change in vegetation biomass. It will therefore be important to understand how human land and coastal use overlaps with the ranges of migratory species (Morecroft *et al.* 2019) and to consider potential management options in light of the ecosystem services they provide (Mitchell *et al.* 2013). This also applies to the marine environment, where interdisciplinary, local and stakeholder discussions will be important to unify ways forward for species management and conservation again in the light of the ecosystem services they provide (e.g. Malinauskaite *et al.* 2022a, 2022b; Ramírez-Fráncel *et al.* 2022).

As biodiversity is strongly impacted by climate change, adaptation will become an increasingly important consideration for species conservation in a changing climate. At the same time, there is a pressing need to consider how best to manage natural systems to support climate change mitigation and limit greenhouse gas concentrations in the atmosphere (Morecroft *et al.* 2019). These measures have the potential to synergise or conflict with migratory species adaptation, hence the need for careful consideration of how best to respond to climate change. This review highlights examples where the conservation of migratory species can provide wider benefits for people and ecosystems, and it is suggested that decision makers, engaging with regional experts from around the world where relevant, begin to consider these issues in a cross-cutting and holistic way to maximise the effectiveness of management interventions. Given the high uncertainty associated with the effectiveness of adaptation (e.g. Pearce-Higgins *et al.* 2022), it is also recommended that management interventions are properly monitored and evaluated, and the results made available, to inform wider decision making.

6 Seabirds promote coastal resilience to storm surges

Ecosystem – coral reefs: Coral reefs are found globally in tropical coastal waters. They are threatened by multiple drivers, including overfishing, pollution, invasive non-native species and climate change (Riegl *et al.* 2009; Hughes *et al.* 2017). Coral depends on a symbiotic relationship with 'zooxanthellae' algae, which provides both organisms with essential nutrients. However, high water temperatures driven by climate change damage the zooxanthellae, which can cause the coral to expel them and die, termed 'coral bleaching' (Riegl *et al.* 2009).

Species group – seabirds: Most migratory seabirds spend the non-breeding season at sea, and only return to their breeding grounds (often cliffs and islands) to breed (Dias *et al.* 2019). Many seabirds are listed on CMS Appendix I and/or II, and a third are classified as Vulnerable or higher on the IUCN Red List (Berr *et al.* 2023). This is due to the threats they face globally, including from fisheries bycatch, invasive non-native species and climate change (Dias *et al.* 2019).



The role of seabird guano in aiding nutrient transfer

Ecosystem services – nutrient transfer and coastal protection: Coral reefs contribute to ecosystem services such as coastal protection, maintaining water quality, supporting fish stocks and tourism (Woodhead *et al.* 2019). Seabirds support these services by maintaining the trophic cascade through predation and also by aiding nutrient transfer (see graphic). Many seabirds nest along coastal and island edges and leave ornithogenic nutrients (guano and other detritus) on land and in the nearby sea (Dias *et al.* 2019). These nutrients are taken up by zooxanthellae and support the growth and maintenance of healthy coral reefs (Lorrain *et al.* 2017; Graham *et al.* 2018; Savage 2019). Because of their hard structure, coral reefs provide important coastal protection, reducing wave energy by 97% and protecting coastlines from erosion and flooding (Ferrario *et al.* 2014). However, invasive non-native species, such as rats, can decimate seabird populations through egg predation. This severely limits the nutrients seabirds provide to corals, thereby reducing coral reef growth and coastal protection (Graham *et al.* 2018).

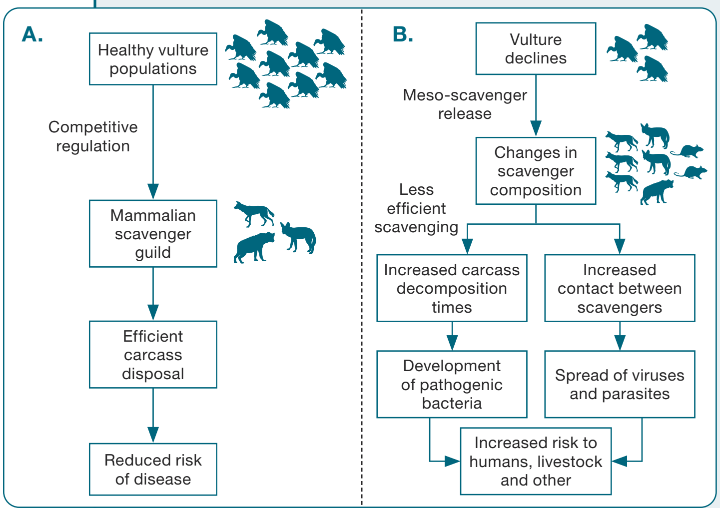
Conservation actions: Marine protected areas provide important protection to coastal ecosystems, whilst catchment-to-reef management is necessary to account for terrestrial anthropogenic threats (Savage 2019). Eradication programmes for invasive non-native species will improve the breeding success of seabirds and enable them to retain their ecological functions and associated ecosystem services (Graham *et al.* 2018). AEWA and ACAP are key multilateral agreements under CMS that co-ordinate international activities to conserve seabirds.

Key to abbreviations: CMS = Convention on Conservation of Migratory Species of Wild Animals; IUCN = International Union for the Conservation of Animals; AEWA = Agreement on the Conservation of African-Eurasian Migratory Waterbirds; ACAP = The Agreement on the Conservation of Albatrosses and Petrels.

7 Vultures help to reduce disease transmission

Zoonotic disease transmission: Global changes are altering human-wildlife interactions, and the conditions zoonotic diseases need to spread (Rupasinghe *et al.* 2022). Opportunist species, such as rats and stray dogs, have adapted to urban and agricultural environments, taking advantage of available food, whilst increasing the likelihood of human-wildlife disease transmission (Donázar *et al.* 2016).

Species group – vultures: Vultures are divided into 'Old World' species, found across Africa, Europe and Asia, and 'New World' species, found across North and South America. All vulture species are listed on the Appendices of the CMS, and most 'Old World' species are globally Threatened or Near Threatened (Botha *et al.* 2017). Key threats to vulture populations are intentional or accidental persecution from humans, collisions with energy infrastructure and climate change impacts such as droughts (Santangeli *et al.* 2019; BirdLife International 2021). In particular, intentional and retaliatory poisoning, which aim to hide the location of illegally killed wildlife and prevent livestock predation respectively, are having catastrophic impacts on vulture populations, which scavenge on poisoned carcasses.



The impact of healthy vulture populations (A) and vulture declines (B) on the regulation of mammalian scavengers and disease transmission. (From van den Heever, L. *et al*. 2021. Reviewing the role of vultures at the human-wildlife-livestock disease interface: An African perspective. *Journal of Raptor Research*, 55, 311-327. Reproduced with permission from the Journal of Raptor Research)

Ecosystem service – disease and pest control: As scavengers, vultures are important for disposing of animal carcasses. This reduces the amount of food available to opportunist mammalian scavengers, such as stray dogs, keeping their populations under control, and reducing the risk of zoonotic disease spillover to humans (see graphic). For example, when vulture populations in India crashed due to diclofenac poisoning, stray dog populations grew, which led to more people being bitten by stray dogs and a subsequent increase in rabies-related deaths; similarly, the rat population increased due to reduced predation pressure, with likely impacts on crop consumption and disease transmission (Markandya *et al.* 2008).

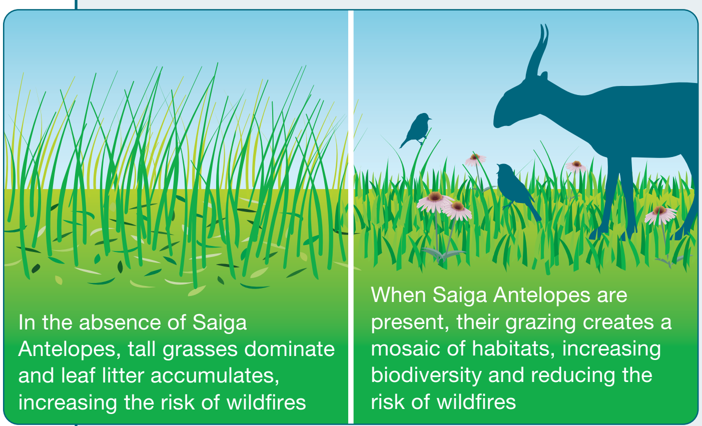
Conservation actions: Actions to reduce vulture poisoning and raise awareness of both their persecution and benefits to ecosystem and human health will be key to their conservation. The CMS Raptors MoU provides a mechanism to co-ordinate international actions to conserve vultures.

Key to abbreviations: CMS = Convention of the Conservation of Migratory Species of Wild Animals; Raptors MoU = Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia

8 Saiga Antelopes support grassland resilience to wildfires

Ecosystem – steppes and semi-desert of Central Asia: The steppes and semi-deserts of Central Asia are characterised by sparse vegetation and extreme climatic conditions, where temperatures can vary between -40°C in the winter and 50°C in the summer. Intensive farming, poaching and infrastructure expansion threaten these habitats and the species adapted to survive here. In particular, the management of livestock grazing areas has polarised in recent years; grasslands are now either intensely grazed or not grazed at all, leading to competition between livestock and wildlife, as well as wider ecosystem impacts (Kamp *et al.* 2016).

Species – Saiga Antelope: Saiga Antelope (Critically Endangered; CMS Appendix I) are herbivorous grazers found across the steppe grasslands and semi-arid deserts of Central and Eastern Asia. They are threatened by various human-induced factors, including hunting, competition with livestock, and climate change-induced droughts and grassland fires (Singh *et al.* 2010; Kamp *et al.* 2016; Khanyari *et al.* 2022).



Role of the Saiga Antelope in supporting the ecosystem of the Central Asian Steppe

Disease transmission has posed a key threat to the species; in 2015, more than 200,000 Saiga Antelope died from a bacterium, representing 62% of the global population (Kock *et al.* 2018).

Ecosystem services – biodiversity enhancement and fire resilience: Steppe and semi-desert grasslands provide a variety of ecosystem services. Established grasslands store vast amounts of carbon in both their vegetation and soil, reduce soil erosion and increase water retention (Zhao *et al.* 2020). Long-distance, migratory herbivores like the Saiga Antelope (Akçakaya *et al.* 2018) are important ecosystem engineers in grassland systems due to their grazing patterns, which create a mosaic of habitats that support various other animals and plants (Kamp *et al.* 2016). In the absence of herbivore grazing, tall growing grasses dominate and leaf litter accumulates, increasing the risk of wildfires (Brinkert *et al.* 2016). Grazing from long-distance migratory herbivores prevents this accumulation of leaf litter, creating moving mosaics of biodiverse grasslands that support vital ecosystem services, such as resilience to wildfires (Brinkert *et al.* 2016). (See graphic.)

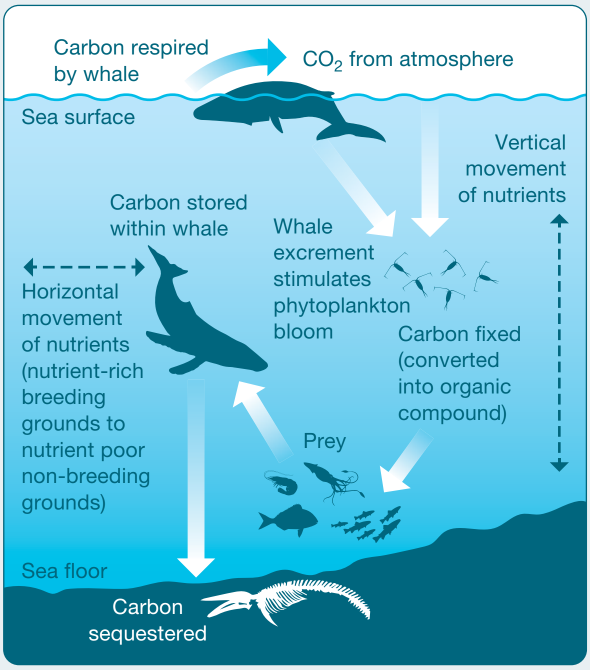
Conservation actions: The implementation of dynamic, 'moving' protected areas can protect Saiga Antelopes as they move along their migratory routes, enabling them to retain their ecological function as a dominant grazer on the Central Asian steppes (Singh *et al.* 2010; Bull *et al.* 2013). The CMS Saiga MoU is the only international instrument for the conservation of Saiga Antelopes, providing a mechanism to guide co-ordinated conservation action.

Key to abbreviations: CMS = Convention for the Conservation of Migratory Species of Wild Animals; Saiga MoU = Memorandum of Understanding concerning Conservation, Restoration and Sustainable Use of the Saiga Antelope

9 Whales aid carbon capture and ocean nutrient cycling

Ecosystem – the deep sea: The deep sea starts at around 200 m below the ocean surface and incorporates around 90% of the world's ocean. It comprises a wide range of habitats and associated species, many of which are slow growing, have long lifespans and are highly adapted to the deep sea ecosystem, making them particularly vulnerable to environmental change (Roberts *et al.* 2002).

Species group – whales: Whales are found across the world's oceans, from icy regions at the poles, to tropical waters on the equator. Baleen whales, such as the Blue Whale (Endangered; CMS Appendix I) and Fin Whale (Vulnerable; CMS Appendix I and II), are among the largest and longest-lived inhabitants of the deep sea, weighing in excess of 200 and 45 tonnes respectively, and with a lifespan of 80 to 90 years. Baleen whales often undertake long seasonal migrations between tropical calving grounds and high latitude feeding grounds (Learmonth *et al.* 2006). Whales face a wide range of threats, including overfishing, bycatch, pollution, global warming and disturbance from human activities.



The importance of whales for carbon capture

Ecosystem services – carbon capture and nutrient cycling: As whales are large and long-lived, they store vast amounts of carbon in their bodies. When they die, their carcasses fall to the ocean floor and the carbon is locked into the substrate. This has the potential to sequester an estimated 0.062 megatonnes of carbon per year (Pearson *et al.* 2023; Schmitz *et al.* 2023). Whales also move nutrients vertically from their foraging zone in the water column to the surface when they breathe, and release nutrients via excrement which stimulates phytoplankton growth and captures atmospheric carbon dioxide. This nutrient provisioning is estimated to sequester 0.4 to 22.0 megatonnes of carbon per year (Pearson *et al.* 2023). Whales also transfer nutrients across the oceans via migration from their nutrient-rich breeding grounds to their nutrient-poor non-breeding grounds (Pearson *et al.* 2023). (See graphic.)

Conservation actions: Efforts to reduce anthropogenic impacts, such as bycatch and pollution, will not only support their recovery and carbon sequestration potential, but will also benefit entire marine ecosystems that rely on whales for nutrient cycling. ACCOBAMS, ASCOBANS and the Pacific Islands Cetaceans MoU are key international frameworks for the co-ordinated conservation of whales and cetaceans.

Key to abbreviations: CMS = Convention on the Conservation of Migratory Species of Wild Animals; ACCOBAMS = Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic area; ASCOBANS = Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas; Pacific Islands Cetaceans MoU = Memorandum of Understanding for the Conservation of Cetaceans and their Habitats in the Pacific Islands Region.

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Note: * = paper identified in the main review process. ** = paper identified in Supplementary search.

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10.2 Case studies

Seabirds promote coastal resilience to storm surges

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Vultures help to reduce disease transmission

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Saiga Antelopes support grassland resilience to wildfires

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Whales aid carbon capture and ocean nutrient cycling

Learmonth, J.A., MacLeod, C.D., Santos, M.B., Pierce, G.J., Crick, H.Q.P. & Robinson, R.A. 2006. Potential effects of climate change on marine mammals. *Oceanography and Marine Biology: An Annual Review*, **44**, 431

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11 Supplementary materials

11.1 S1: Methods – full methods in detail

A preliminary literature search was conducted on 14/04/2023 in Web of Science (databases searched included: the Web of Science Core Collection, BIOSIS Citation Index, MEDLINE(r), Zoological Record, KCI_Korean Journal Database and SciELO citation Index databases; 1991-2023 inclusive), using the search terms below (searching in the basic search bar searching under 'topic'), and produced 10,149 results.

The search terms were:

> ((“Climate*” OR “Global warming” OR “Sea-level rise” OR “Global environmental change”)
>
> AND
>
> (“keystone service*” OR “nature based solution*” OR “natural climate solution*” OR “climate change adaptation” OR “climate change mitigation” OR “ecological service*” OR “trophic rewilding”)
>
> AND
>
> (“specie*” OR “ecolog*” OR “bio* diversity” OR “ecosystem”))

From these results, the Web of Science refine filter was used to extract the term migratory, using the search term: (“migrat*”) as an initial filtering step (324 results). The first 100 results were skimmed for relevance at title and abstract level. Relevance was based on the following questions which guided the categorisations:

- Is a species a key component of ecosystem(s) discussed? (Y/N)
- If yes, which ecosystem service does it fit into? (Broad categories: Regulation and Maintenance, Provisioning and/or Culture. Specific services were then identified and noted under each category.)
- Is the solution/service aided by migratory species? (Y/N)
- If yes, is it a nature-based solution / ecosystem service? (Y/N)
- If yes, does it help mitigate climate change? (Y/N)
- If yes, is the nature-based solution aiding: reducing greenhouse gas emissions, carbon capture and/or ecosystem resilience?
- If ecosystem resilience, which broad category of climate threat is it aiding: rainfall, temperature, snow, wind/storms (all of these include category-specific extreme events)?

Of the initial 100 results, just five were deemed to detail a species as a key component of an ecosystem(s) and of these, all five were deemed relevant to migratory species aiding climate change as nature-based solutions. Based on this preliminary search, additional search terms were added to ensure additional key terms were included for a broader search. Note that "ecosystem functioning" was not included in the final set of search terms due to this adding many irrelevant papers to the research results. The main search was conducted on 18/04/2023 and 19/04/2023 in Web of Science (databases searched included: the Web of Science Core Collection, BIOSIS Citation Index, MEDLINE(r), Zoological Record, KCI_Korean Journal Database and SciELO citation Index; 1962-2023 inclusive), using the search terms below (searching in the basic search bar searching under 'topic'), and produced 30,366 results.

The search terms were:

> (("Climate*" OR "Global warming" OR "Sea-level rise" OR "Global environmental change")
>
> AND
>
> ("keystone service*" OR "nature based solution*" OR "natural climate solution*" OR "climate change adaptation" OR "climate change mitigation" OR "ecosystem service*" OR "trophic rewilding" OR "ecosystem approach" OR "ecosystem based adaptation" OR "ecological restoration")
>
> AND
>
> ("specie*" OR "ecolog*" OR "bio* diversity" OR "ecosystem"))

From this search, the results were similarly filtered down to extract the term migratory, using the search term: ("migrat*") which left 902 results. Again, the first 100 papers were skimmed (26/04/2023 - 27/04/2023).

Finally, further search terms were used to individually filter the ("migrat*") search per species group using similar search terms to the Part 1 report (S2 Table 1; dates the searches were conducted: 18/04/2023 - 19/04/2023).

Additional supplementary *ad hoc* searches were conducted to fill in known gaps (searches were conducted in Web of Science and Google Scholar). Studies from the main or supplementary searches are individually highlighted in the reference list using * = main search and ** = supplementary searches.

The results of all the searches were combined and duplicates removed (summarised in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses, PRISMA, flow table – S3 Table 1).

11.2 S2: Methods – detailed species search terms

S2 Table 1. Detailing the searches used to filter the "migrat*" search, to identify any remaining papers specific to the CMS list. List of search terms was based on the search terms used for in Part 1 of this review.

Date(s) searched	Additional search terms to extract additional papers, by species
18/04/2023	(duck OR goose OR swan)
18/04/2023	(albatross OR petrel OR shearwater OR procellariiformes)
18/04/2023	(accipiter OR eagle OR aviceda OR buzzard OR falco OR kite OR circus OR osprey)
18/04/2023	(owl)
18/04/2023	("microcarbo pygmaeus" OR "phalacrocorax nigrogularis" OR "fregata andrewsi")
18/04/2023	(diver OR loon)
18/04/2023	(flamingo)
18/04/2023	("podiceps auritus" OR"podiceps grisegena")
18/04/2023	(gull OR tern)
18/04/2023	(egret OR heron OR bittern OR ibis OR pelican)
18/04/2023	(sporophila OR seedeater OR tyrant OR bobolink)
18/04/2023	(warbler)
18/04/2023	("Afro-palearctic migrant")
18/04/2023	(muscicapidae OR sylviidae OR turdidae OR motacillidae)
18/04/2023	(bustard)
18/04/2023	("spheniscus demersus" OR "spheniscus humboldti")
18/04/2023	(corncrake OR crake OR crane OR flufftail)
18/04/2023	(stork)
18/04/2023	(vulture OR condor)
18/04/2023	(wader OR shorebird OR Charadriidae OR Scolopacidae OR Laridae OR Haematopodidae OR Burhinidae OR Ibidorhynchidae OR Recurvirostridae OR Pluvianellidae OR Dromadidae OR Glareolidae OR Laridae OR Alcidae)
19/04/2023	(mammal OR cetacea* OR carnivor* OR seal OR lion OR manatee OR dugong)
19/04/2023	(turtle)
19/04/2023	(sturgeon OR actinopterygii OR shovelnose)
19/04/2023	(shark OR ray OR chondrichthyes OR sawfish)
19/04/2023	(bat*)
19/04/2023	(ungulate OR gazelle OR antelope)
19/04/2023	(gorilla OR chimpanzee)
19/04/2023	("Ursus maritimus" OR "Ursus arctos isabellinus")

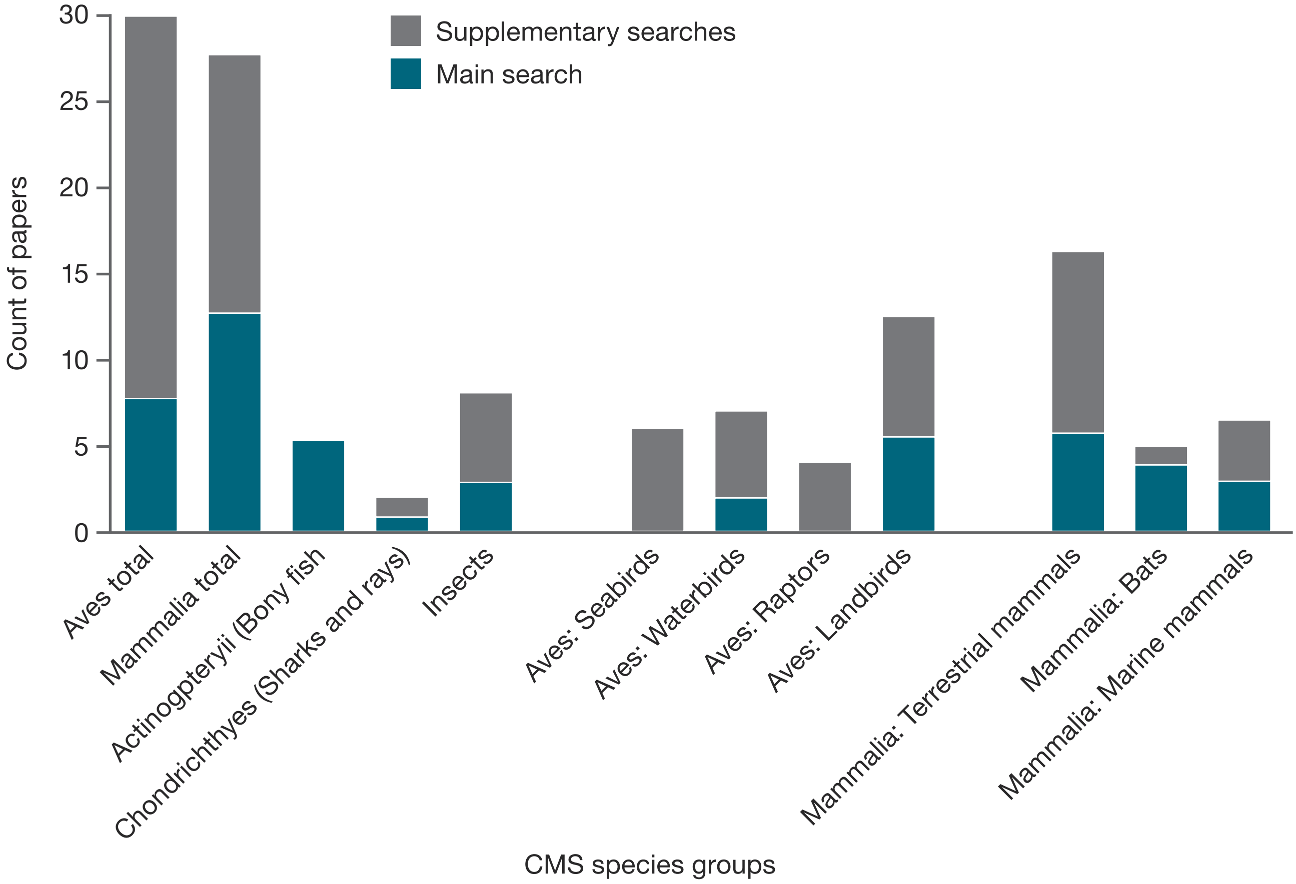
Date(s) searched	Additional search terms to extract additional papers, by species
19/04/2023	(Elephant) NOT (Seal)
19/04/2023	(Lontra)
19/04/2023	("Lycaon pictus" OR "Acinonyx jubatus" OR "Panthera onca" OR "Panthera pardus" OR "Panthera leo" OR "Uncia uncia")
19/04/2023	("Danaus plexippus" OR Moth OR (Butterfly NOT fish))

11.3 S3: Methods – PRISMA flow diagram table

S3 Table 1. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flow table of sifting of research studies identified by Web of Science search and the total supplementary studies added.

Sifting criteria	Web of Science search	Total
Literature search total	336	336
Filtered for ecosystem service provided by migratory species	48	48
Number of duplicates removed	18	18
Total number remaining after duplicates removed	30	30
Filtered for climate change solutions from migratory species (duplicates removed)	28	28
Supplementary searches	-	43
Total number of papers filtered for ecosystem service(s) provided by migratory species		73
Total number of papers detailing nature-based solution(s) to climate change provided by migratory species		71

11.4 S4: Results – number of papers from main and supplementary searches



S4 Figure 1. Count of papers from different CMS species groups (totals for each group on left; results for subgroups within Aves and Mammalia on right), comparing the main search to the supplementary searches. Note 1: this is a count compiled from this study's main and supplementary search results and is not an exhaustive list. Note 2: four of the papers found for Aves were general across all species and so are represented equally in the individual Aves groups in the figure (these papers are: Sekercioglu 2002; Whelan *et al.* 2008; Whelan *et al.* 2015; Anderson *et al.* 2016).

11.5 S5: Results – ecosystem services provided by group

S5 Table 1. Supplementary table summarising the broad ecosystem service(s) categories and specific services from the 73 studies identified in the Results section (section 3).

Species group	Habitat	Species/ Species group	Service(s)	Specifics	References
Aves	-	Birds	Cultural	Tourism. Sense of place. Inspiration	Sekercioglu 2002
	-	Birds	Regulation and Maintenance	Pollination	Anderson *et al*. 2016
	-	Birds	Regulation and Maintenance. Cultural. Provisioning	Everything!	Whelan *et al.*, 2008; Whelan *et al.* 2015
Aves: Seabirds	Coastal	Seabirds	Regulation and Maintenance	Soil nutrients. Carbon capture.	McKechnie 2006; Lorrain *et al.* 2017; Graham *et al.* 2018; Savage 2019; Berr *et al.* 2023
Aves: Waterbirds	-	Birds	Disservices/ maladaptations	-	Kerbes *et al.* 1990; Manny *et al.* 1994; Post *et al.* 1998; Buij *et al.* 2017; Beard *et al.* 2019
	Grassland	Waterbirds	Regulation and Maintenance	Pest control. Carbon capture. Healthy soils. Seed dispersal	Buij *et al.* 2017; Beard *et al.* 2019; Menon 2021; Valkó *et al.* 2022; Lovas-Kiss *et al.* 2023

Species group	Habitat	Species/ Species group	Service(s)	Specifics	References
Aves: Raptors	Agriculture	Vultures	Regulation and Maintenance. Cultural	Disease control. Pest control. Cultural	Markandya *et al.* 2008; Donázar *et al.* 2016; van den Heever *et al.* 2021
Aves: Landbirds	-	Birds	Disservices/ maladaptations	-	Bedford *et al.* 2013; Fricke *et al.* 2022
	Grassland	Frugivores	Regulation and Maintenance	Pest control. Pollination	Bedford *et al.* 2013
	-	Birds	Regulation and Maintenance	Seed dispersal	Fricke *et al.* 2022
	Woodland	Nutcrackers	Regulation and Maintenance	Seed dispersal	Holtmeier 2012
	Agriculture	Insectivores	Regulation and Maintenance	Pest control	Kleemann *et al.* 2020; Jedlicka *et al.* 2021
	Grassland-Forest	Hummingbirds	Regulation and Maintenance	Pollination	Leimberger *et al.* 2022
	Woodland	Corvids	Regulation and Maintenance	Seed dispersal	Pesendorfer *et al.* 2016
	Woodland	Frugivores	Regulation and Maintenance	Seed dispersal	Rodríguez-Pérez *et al.* 2017
	Agriculture	White-eyes and sunbirds	Regulation and Maintenance	Pollination	Wester & Claßen-Bockhoff 2006; Fang *et al.*2012
	Oak Savanna	Insectivores	Regulation and Maintenance	Pest control	Wood & Pidgeon 2015

Species group	Habitat	Species/ Species group	Service(s)	Specifics	References
Mammalia: Terrestrial mammals	-	Mammals	Disservices/ maladaptations		Fricke *et al.* 2022
	Grassland	American Bison	Regulation and Maintenance	Carbon capture. Habitat modification (grazing - biodiversity. wallowing - flooding)	Gilgert & Zack 2010; Johnson *et al.* 2012; Schmitz *et al.* 2023
	-	Mammals	Regulation and Maintenance	Seed dispersal	Fricke *et al.* 2022
	Grassland	Mammals	Regulation and Maintenance	Fire management	Rouet-Leduc *et al.* 2021
	Grassland	Reindeer/ Caribou	Regulation and Maintenance	Carbon capture	Beard *et al.* 2019; Johnson *et al.* 2022
	Grassland	Saiga Antelopes	Regulation and Maintenance	Carbon capture. Fire management. Habitat modification (grazing - biodiversity)	Brinkert *et al.* 2016; Akçakaya *et al.* 2018
	Grassland	Wild Yaks	Regulation and Maintenance	Carbon capture	Zhang *et al.* 2016
	Grassland	African Savanna Elephants	Regulation and Maintenance. Cultural	Soil maintenance. Nutrient cycling. Seed dispersal. Erosion control	Wittemyer *et al.* 2014; Smit & Prins 2015; Fritz 2017; Sandhage-Hofmann *et al.* 2021
	Grassland	Common Wildebeest	Regulation and Maintenance. Cultural. Provisioning	Fire management. Nutrient cycling	Dobson 2009; Holdo *et al.* 2009; Conradi *et al.* 2020; van Moorter *et al.* 2020

Species group	Habitat	Species/ Species group	Service(s)	Specifics	References
Mammalia: Bats	Mountains	Bats	Regulation and Maintenance	Pollination. Seed dispersal	Burke *et al.* 2021
	Forest	Bats	Regulation and Maintenance	Pollination. Seed dispersal	Frafjord 2007
	Agriculture	Bats	Regulation and Maintenance	Pest control	Krauel *et al.*, 2015; Manning & Ando 2022
	Globally	Bats	Regulation and Maintenance	Pollination. Seed dispersal. Pest control. Fertiliser via guano	Ramírez-Fráncel *et al.* 2022
Mammalia: Marine mammals	Coastal	Dugongs	Regulation and Maintenance	Carbon capture. Coastal resilience to storms	Preen 1995; McMahon *et al.* 2017
	Ocean	Whales	Regulation and Maintenance. Cultural. Provisioning	Carbon capture. Food. Tourism	Butman *et al.* 1995; Malinauskaite *et al.* 2022a, 2022b; Pearson *et al.* 2023; Schmitz *et al.* 2023
Actinogpteryii (Bony fish)	Ocean	Fish	Provisioning. Cultural	Food. Fishing as recreation	Steiner *et al.* 2019
	Rivers	Fish	Regulation and Maintenance	Nutrients	Wilcove 2008; Beard *et al.* 2019
	Rivers	Fish	Regulation and Maintenance. Cultural. Provisioning	Nutrients. Food. Fishing as recreation	Kovach *et al.* 2013; Hare *et al.* 2021; Almeida *et al.* 2023

Species group	Habitat	Species/ Species group	Service(s)	Specifics	References
Chondrichthyes (Sharks and rays)	Coastal	Sharks	Regulation and Maintenance	Carbon capture	Atwood *et al.* 2015; Gallagher *et al.* 2022
Insects	Forest	Butterflies	Cultural	Tourism. Symbolic value. Natural heritage	Lemelin & Jaramillo-López 2020
	Forest	Butterflies	Cultural	Symbolic value	Lopez-Hoffman *et al.* 2017
	Forest	Butterflies	Regulation and Maintenance	Pollination	Hawkes *et al.* 2022
	Flowers; Agriculture	Hoverflies	Regulation and Maintenance	Pollination. Pest control.	Tzilivakis *et al.* 2015; Doyle *et al.* 2020; Jia *et al.* 2022
	Agriculture	Insects	Regulation and Maintenance	Pest control	Siviter & Muth 2020
	-	Insects	Regulation and Maintenance	Pollination. Pest control.	Satterfield *et al.* 2020

11.6 S6: Species list

S6 Table 1. List of species considered in articles within the literature review. Species marked with * are migratory, but not CMS-listed. Where species are included in CMS Appendix I or II (or both), the CMS instruments for conservation are also provided. Note that where studies considered more than 25 species, or grouped species into assemblages, individual species are not listed (Frafjord 2007; Pesendorfer *et al.* 2016; Doyle *et al.* 2020; Kleemann *et al.* 2020; Jedlicka *et al.* 2021; Al-Asif *et al.* 2022; Hawkes *et al.* 2022; Leimberger *et al.* 2022; Ramírez-Fráncel *et al.* 2022; Almeida *et al.* 2023; Berr *et al.* 2023; Pearson *et al.* 2023). Note: key to abbreviations at end of the table.

Common name	Scientific name	CMS Appendix	Conservation instruments
Aves: Landbirds			
Baltimore Oriole*	*Icterus galbula*		
Blackbird*	*Turdus merula*		
Bobolink	*Dolichonyx oryzivorus*	II	CMS, Southern South American Grassland Birds
Brown-headed Cowbird*	*Molothrus ater*		
Common Grackle*	*Quiscalus quiscula*		
Fieldfare*	*Turdus pilaris*		
Mistle Thrush*	*Turdus viscivorus*		
Mountain White-eye*	*Zosterops japonicus*		
Northern Nutcracker*	*Nucifraga caryocatactes*		
Orange River White-eye*	*Zosterops pallidus*		
Orchard Oriole*	*Icterus spurius*		
Palm Warbler*	*Setophaga palmarum*		
Redwing*	*Turdus iliacus*		
Red-winged Blackbird*	*Agelaius phoeniceus*		
Ring-ouzel*	*Turdus torquatus*		
Song Thrush*	*Turdus philomelos*		
Southern Double-collared Sunbird*	*Nectarinia chalybea*		
Tennessee Warbler*	*Oreothlypis peregrina*		
Western Meadowlark*	*Sturnella neglecta*		
Yellow-headed Blackbird*	*Xanthocephalus xanthocephalus*		
Yellow-rumped Warbler*	*Setophaga coronata*		

Common name	Scientific name	CMS Appendix	Conservation instruments
Aves: Seabirds			
Brown Booby	*Sula leucogaster plotus*		
Great Frigatebird	*Fregata minor*		
Red-footed Booby	*Sula sula*		
Roseate Tern	*Sterna dougallii*	II	CMS, AEWA
Aves: Waterbirds			
Asian Openbill Stork*	*Anastomus oscitans*		
Black-headed Ibis*	*Threskiornis melanocephalus*		
Brant Geese*	*Branta bernicla nigricans*		
Pink-footed Goose	*Anser brachyrhynchus*	II	CMS, AEWA
Aves: Raptors			
Long-billed Vulture	*Gyps indicus*	I&II	CMS, Raptors
Oriental White-backed Vulture	*Gyps bengalensis*	I&II	CMS, Raptors
Slender-billed Vulture	*Gyps tenuirostris*	I&II	CMS, Raptors
Mammalia: Terrestrial mammals			
African Savanna Elephant	*Loxodonta africana*	II	CMS, West African Elephants
African savanna ungulates (including Wildebeest*)	*Connochaetes taurinus*		
Bison*	*Bison bison*		
Caribou*	*Rangifer tarandus*		
Prairie Dog*	*Cynomys ludovicianus*		
Saiga Antelope	*Saiga borealis mongolica*	II	CMS, Saiga Antelopes
Saiga Antelope	*Saiga tatarica*	II	Central Asian Mammals Initiative, Saiga Antelopes
Grizzly Bear	*Ursus arctos middendorffi*		
Yak	*Bos grunniens/Bos mutus*	I	CMS, Central Asian Mammals Initiative
Mammalia: Bats			
Brazilian or Mexican Free-tailed Bat	*Tadarida brasiliensis*	I	CMS
Mexican Lesser Long-nosed Bat*	*Leptonycteris yerbabuenae*		
Mexican Long-nosed Bat*	*Leptonycteris nivalis*		

Common name	Scientific name	CMS Appendix	Conservation instruments
Mexican Long-tongued Bat*	*Choeronycteris mexicana*		
Straw-coloured Fruit Bat	*Eidolon helvum*	II	CMS
Mammalia: Marine mammals			
Antarctic Minke Whale	*Balaenoptera bonaerensis*	II	CMS, Pacific Islands Cetaceans
Blue Whale	*Balaenoptera musculus*	I	CMS, ACCOBAMS, Pacific Islands Cetaceans
Dugongs	*Dugong dugon*	II	CMS, Dugongs
Fin Whale	*Balaenoptera physalus*	I&II	CMS, ACCOBAMS, Pacific Islands Cetaceans
Humpback Whale	*Megaptera novaeangliae*	I	CMS, ACCOBAMS, Pacific Islands Cetaceans
Southern Right Whale	*Eubalaena australis*	I	CMS, Pacific Islands Cetaceans
Actinogpteryii (Bony fish)			
Alewife*	*Alosa aestivalis*		
Blueback Herring*	*Alosa pseudoharengus*		
European Sturgeon*	*Acipenser sturio*		
Salmon	*Oncorhynchus nerka*		
Salmonids*	*Oncorhynchus and Salvelinus*		
Chondrichthyes (Sharks and rays)			
Tiger Shark*	*Galeocerdo cuvier*		
Insects			
Marmalade Hoverfly*	*Episyrphus balteatus*		
Monarch Butterfly	*Danaus plexippus*	II	CMS
Painted Lady Butterfly*	*Vanessa cardui*		

Key to abbreviations: **Southern South American Grassland Birds** = Memorandum of Understanding on the Conservation of Southern South American Migratory Grassland Bird Species and their Habitats; **AEWA** = Agreement on the Conservation of African-Eurasian Migratory Waterbirds; **Raptors** = Memorandum of Understanding on the Conservation of Migratory Birds of Prey in Africa and Eurasia; **West African Elephants** = Memorandum of Understanding concerning Conservation Measures for the West African Populations of the African Elephant (*Loxodonta africana*); **Saiga Antelopes** = Memorandum of Understanding concerning Conservation, Restoration and Sustainable Use of the Saiga Antelope; **Pacific Islands Cetaceans** = Memorandum of Understanding for the Conservation of Cetaceans and their Habitats in the Pacific Islands Region; **ACCOBAMS** = Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area; **Dugongs** = Memorandum of Understanding on the Conservation and Management of Dugongs (*Dugong dugon*) and their Habitats throughout their Range.

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