

TAKING ANIMALS INTO ACCOUNT

The Critical Role of Wild Animals in Shaping Wetland Ecosystems and the Services they Provide.

Case Studies



Rewilding
THE GLOBAL ALLIANCE



TAKING ANIMALS INTO ACCOUNT

A Report to the Ramsar Convention on Wetlands:

The critical role of wild animals in shaping wetland ecosystems and the services they provide.

CASE STUDIES

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Case Study #1: Conservation of Freshwater Pearl Mussel, Atlantic Salmon, and Brown Trout

Henrik Persson, Rewilding Sweden



Figure 1: Freshwater Pearl Mussel (photo credit: Arthur de Bruin)

1. Target Species Overview

- Freshwater Pearl Mussel (*Margaritifera margaritifera*)
 - Status: Endangered (IUCN), Priority Species (EU Habitats Directive)
 - Distribution: Finland, Sweden, Estonia
 - Threats: Habitat degradation, juvenile mortality, silting of river bottoms
- Atlantic Salmon (*Salmo salar*)
 - Status: Declining populations due to habitat loss and migration barriers
 - Role: Host species for Freshwater Pearl Mussel larvae
- Brown Trout (*Salmo trutta*)
 - Status: Declining populations due to habitat loss and migration barriers
 - Role: Host species for Freshwater Pearl Mussel larvae

2. Keystone Species: Freshwater Pearl Mussel

Ecological Importance

The Freshwater Pearl Mussel (FPM) is a keystone species in riverine ecosystems, creating habitats for other species and contributing significantly to ecosystem services. These mussels are filter feeders, purifying up to 50 liters of water per day. This process not only helps in water purification but also produces nutrient-rich mucous lumps that serve as food for

bottom-dwelling animals, which in turn support juvenile fish populations, including salmon and trout.

Habitat Formation and Maintenance

FPMs play a critical role in maintaining riverbed ecosystems. Their shells provide substrates for water mosses and other invertebrates, while their movement helps oxygenate the riverbed gravel, essential for various aquatic organisms. Recent studies indicate that FPMs can filter fish pathogens, enhancing the survival rates of fish carrying FPM larvae.

3. Conservation Challenges

Decline in Populations

FPM populations have been declining across Europe, with significant challenges even in stronghold regions like Finland and Sweden. The primary issues include:

- **Recruitment Failure:** A substantial proportion of populations are not producing new offspring, leading to a slow but inevitable decline.
- **Juvenile Mortality:** High mortality rates among juveniles due to siltation from intensive land use in catchment areas, which blocks water flow and depletes oxygen in the gravel where young mussels develop.

Historical and Modern Threats

While historical pearl fishing contributed to the decline, modern threats are primarily linked to land use changes that increase sediment load in rivers, adversely affecting juvenile mussels.

4. Role of Atlantic Salmon and Brown Trout

Host Relationship

FPM larvae (glochidia) require host fish to develop, with Atlantic salmon and brown trout being the only suitable hosts. The decline in these fish populations due to habitat degradation, channel modifications, eutrophication, siltation, and barriers like hydropower dams has a direct negative impact on FPM recruitment and survival.

5. Rewilding Sweden's Approach to Conservation

Habitat Restoration

Rewilding Sweden works on restoring habitats and processes that create habitats for keystone species in rivers. By expanding their living space and facilitating their functions, they aim to kickstart the ecosystem's self-rewilding processes. Keystone species like the Freshwater Pearl Mussel carry out essential ecosystem functions, such as filtering dirty water. One mussel can filter up to 50 liters of water per day, benefiting numerous aquatic species.

Dependency on Salmonids

FPM larvae depend on young salmonids (e.g., trout and salmon) for survival. The larvae attach to the fish's gills and live there before settling in suitable locations to begin their long lives. Trout can only be "infected" once in their lifetime, making their presence crucial for mussel recruitment. However, trout require natural riverine habitats, which have been degraded due to timber floating and industrial forestry activities.



Figure 2: (photo credit: Arthur de Bruin)

6. Rewilding Initiatives

River and Forest Restoration

Rewilding Sweden's initiatives include:

- Restoring Riverside Forests: Moving blocks, boulders, and tree trunks back to watercourses to recreate natural habitats.
- Reinstalling Hydrogeomorphic Processes: Encouraging natural meandering and braided rivers in areas with fine-grained soil.
- Eliminating Forestry Ditches: Restoring swamp forests and wetlands to improve water retention.
- Promoting Deciduous Trees: Thinning coniferous tree stands to support the comeback of deciduous trees along riparian zones.



Figure 3: *(photo credit: Arthur de Bruin)*

Specific Measures for FPM and Salmonids

- Sand and Gravel Addition: Returning 180 tons of natural sand and gravel to restored river reaches to recreate benthic fauna habitats and facilitate trout spawning as well as river pearl mussel habitats.
- Temporary Relocation of Mussels: Safeguarding mussels during heavy restoration phases by temporarily relocating them. In 2023, over 2000 individuals were collected through snorkeling efforts.
- Trout Reintroduction: Financing programs to reintroduce trout fry in rivers where the local population has been extinct.
- Mussel Reintroduction: Building a mobile field laboratory in a truck in which a river section will be recreated. Here young endemic trout will be manually infected with glochidia larvae from the same river.

7. Conclusion

The conservation of Freshwater Pearl Mussel, Atlantic Salmon, and Brown Trout is vital for maintaining healthy river ecosystems. Given their interdependence, protecting and restoring their habitats requires coordinated efforts across multiple sectors and regions. Rewilding Sweden's integrated approach aims to address both historical and modern threats, ensuring the survival and thriving of these keystone species and the rich biodiversity they support.

Case Study #2: Shorebirds and Deer Shape Coastal Wetlands

Magnus Sylvén, Global Rewilding Alliance

Introduction

This case study explores the roles of shorebirds and Père David's deer in coastal wetlands, focusing on their contributions to ecosystem functions such as nutrient cycling, sediment stabilization, and biodiversity enhancement. Examples from the UK, Canada, and China illustrate how these species interact with and influence their habitats.



*Figure 1: Through ecological cascade, large number of resting Semipalmated sandpipers (*Calidris pusilla*) have been shown to positively impact the sedimentation in mudflats ([image source](#))*

Shorebirds' Ecological Impact

- **Trophic Role & Predation:** Shorebirds are central to mudflat ecosystems, preying on invertebrates, biofilms, and other small organisms. This predation directly influences the abundance and distribution of prey, which, in turn, shapes the structure of the entire ecosystem.
- **Physical and Chemical Alterations:** Through biofilm grazing, defecation, and bioturbation (disturbance of sediment), shorebirds alter the sediment structure and contribute to nutrient cycling. These activities promote primary production, stabilize sediments, and enhance the overall resilience of mudflat ecosystems.
- **Nutrient Cycling:** Shorebirds impact nutrient fluxes, particularly nitrogen and phosphorus, by regulating the exchange between sediments and the water column. They decrease nitrate influx while increasing dissolved organic carbon (DOC) and nitrite efflux, improving nutrient availability, and boosting ecosystem productivity.
- **Sediment Stability and Ecosystem Restoration:** In areas like the Canadian Bay of Fundy, shorebirds, such as semipalmated sandpipers, enhance sediment stability by controlling prey populations (e.g., mud shrimp), improving sedimentation rates and supporting

primary production. A 2023 study in China's Yellow Sea demonstrated that shorebirds could also restore wetland multifunctionality by controlling crab populations, which enabled vegetation recovery and improved sediment accretion. However, the long-term success of these results on a broader scale remains speculative.

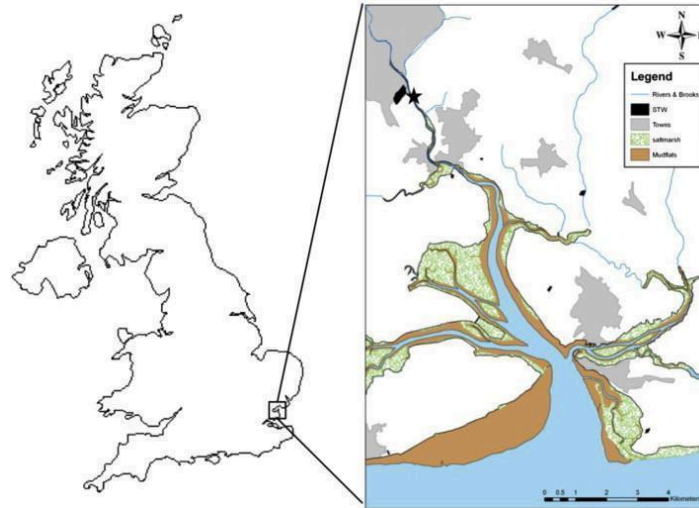


Figure 2: The positive effects of shorebirds in mudflats have been studied in the [Colne Estuary, UK, a Ramsar Site](#).

Père David's Deer's Ecological Role

- **Vegetation Management and Habitat Engineering:** Père David's deer, reintroduced in China's coastal wetlands, graze heavily on invasive Smooth cordgrass (*Spartina alterniflora*). This grazing helps control the spread of *Spartina*, allowing native species to recover and regrow quickly, which supports overall biodiversity. As the deer move through their habitats, they disturb the soil, promoting nutrient cycling and fostering plant diversity, contributing to ecosystem health.
- **Water and Nutrient Cycling:** By grazing near water sources and shallow bogs, Père David's deer influence water flow and nutrient cycling. This helps maintain wetland health by regulating plant growth, ensuring water sources remain accessible, and improving the cycling of organic matter within the ecosystem.
- **Biodiversity Enhancement:** The selective feeding of Père David's deer creates dynamic environments that attract other species, including small mammals and birds. Their presence enhances the overall biodiversity of wetlands, corresponding to the ecological roles played by semi-aquatic deer species in other parts of the world.



Figure 3: The comeback of the unique Père David's Deer along the coastal wetlands in the Yellow Sea, Eastern China, could serve as a powerful tool to combat the invasive alien plant species of Smooth cordgrass (*Spartina alterniflora*) as well as facilitate for migratory shorebirds to enhance many critical functions of the wetlands. [Image source](#)

Combined Effects on Ecosystem Services

- **Ecosystem Functions:** Both shorebirds and Père David's deer play essential roles in maintaining and restoring ecosystem functions. Shorebirds contribute by enhancing sediment stability, nutrient cycling, and primary production, while Père David's deer control invasive species and promote plant diversity. Together, these species support key ecosystem services such as carbon sequestration, sediment stabilization, and nutrient cycling, which are vital for the long-term health of coastal wetlands.
- **Vegetation Restoration:** Field experiments in China show that planting native vegetation alone is ineffective without also managing crab populations (shorebird prey) or invasive plant species like *Spartina alterniflora* (grazed by Père David's deer). The combined actions of these species have proven more effective in restoring vegetation cover and improving ecosystem stability.



Figure 4: A still unspoiled wetland section along the Yellow Sea. About 40% of the tidal flats have been reclaimed in the last 50-100 years. [Image source](#)

Speculative Claims

- **Père David's Deer in Wetland Restoration:** While initial evidence supports Père David's deer as effective managers of *Spartina*, it remains speculative whether expanding their promotion could fully restore wetlands and lead to long-term recovery of shorebirds and other ecosystem functions. Further research is needed to validate this.
- **Shorebirds as Restoration Agents:** The research from China's Yellow Sea suggests that shorebirds, by controlling crab populations, can significantly improve vegetation cover and ecosystem functions. However, the long-term effectiveness of these restoration strategies remains speculative, as their broader impact has yet to be fully tested.

Conclusion

Shorebirds and Père David's deer play critical roles in maintaining and restoring coastal wetlands. Shorebirds contribute to nutrient cycling, sediment stabilization, and ecosystem resilience through their predation and bioturbation. Père David's deer help control invasive plant species and enhance biodiversity through their grazing and habitat modification. While their combined roles show promise for restoring wetlands, some aspects of their long-term effectiveness, particularly in broader applications, remain speculative and require further research.



*Figure 5: Like the semi-aquatic Marsh deer (*Blastocerus dichotomus*) in Latin America and the Southern lechwe (*Kobus leche*) in Africa, the Père David's deer play an important role in the functioning of wetlands. [Image source](#)*

Case Study #3: The Effect of Larger Terrestrial Herbivores on Wetland Habitats

Leo Linnartz, ARK Rewilding the Netherlands

Introduction

Over 35 years of rewilding practice, ARK has observed the significant impact of large terrestrial herbivores on wetland habitats. In our approach, grazing animals receive no supplemental food, and populations are managed to minimize food shortages during harsh winters or dry summers. Although animals may lose weight during these periods, they do not starve. These low-density populations support lush summer vegetation, habitat heterogeneity, and increased biodiversity.

Wood grassland cycle

Large herbivores maintain grazing lawns and slow woodland encroachment, keeping these open areas intact for longer periods (Vera, 1997). Elephants, in particular, can destroy woodlands, converting them into grazing lands. The balance between plant growth and herbivore consumption dictates whether woodlands dominate, or open landscapes prevail (Erhart et al., 2024).

Hippos, horses, and bovines help create high-quality grazing lawns by consuming rough grasses and herbs. The fresh regrowth attracts deer and antelope, which feed on tree and bush seedlings, further slowing woodland expansion.

Wood encroachment is also influenced by inundation periods. On high, dry ground, thorny shrubs can survive both flooding and grazing, allowing trees to germinate within the protection of these shrubs. However, in river ecosystems, floodwaters and erosion can remove woodlands. Once the waters recede, herbivores return to feed on regrowth.

River valleys and estuaries, enriched by nutrient deposits from rain and floodwaters, are highly productive. Migratory fish also contribute nutrients after spawning, creating palatable vegetation that attracts large numbers of herbivores, helping reduce woodland encroachment (Doughty et al., 2015).

Willow and poplar trees are especially palatable and vulnerable to deer grazing, preventing their regeneration. In Yellowstone, predators like wolves and bears reduced deer pressure, but bison, being less susceptible to predation, replaced deer and continued grazing, hindering woodland recovery (Painter & Ripple, 2012).

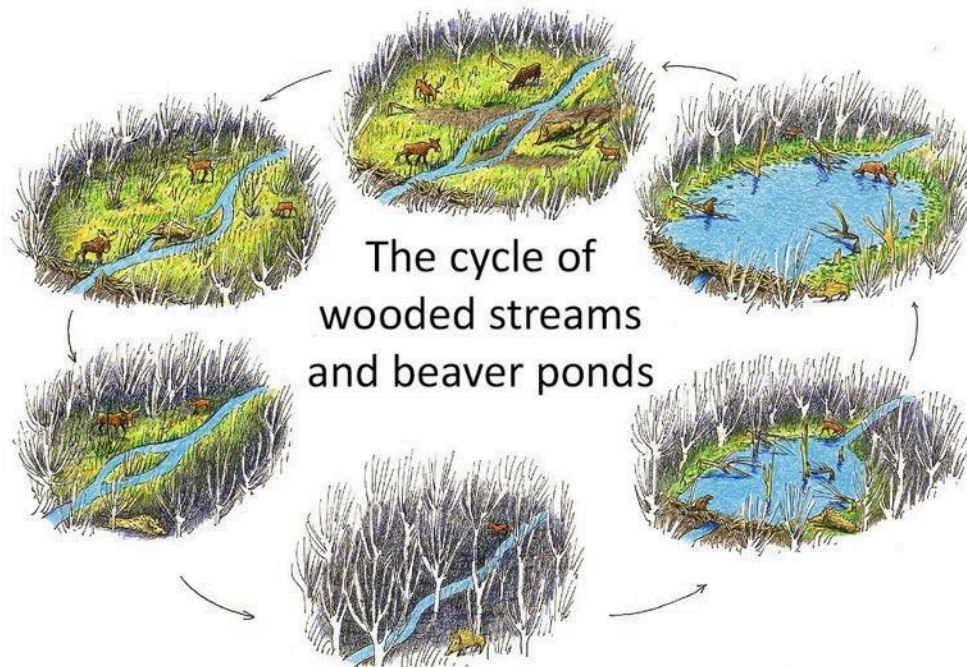


Figure 1: The cycle of wooded streams and beaver ponds over time. Along the stretch of a stream different segments will be in different states, each state being present along multiple segments of the stream. ([Image source](#))

Beavers play a significant role in shaping wetland ecosystems, particularly along small, shallow wooded streams. They build dams to create ponds, where they make their homes—hollow piles of wood and mud with underwater entrances. These dams cause streams to fill the ponds, with water slowly percolating through the dam, leaving behind silt. Over time, the ponds become shallower, and the trees near the water, which beavers feed on, become depleted.

Beavers rarely venture more than 20 meters from the water's edge because they are vulnerable to predators like wolves, lynx, and bears. As food becomes scarce, they abandon the pond and create a new one farther upstream or downstream.

Without the beavers' constant repairs, the dam eventually breaks, or water finds a way around it, creating a new streambed. The old pond then drains and dries up, leaving behind mineral-rich muddy areas that are quickly colonized by wet hay meadow vegetation. This lush and nutrient-rich environment attracts many herbivores. Initially, these animals keep woodland encroachment at bay, maintaining flower-rich grasslands at the valley bottom. However, over time, thorny bushes and trees gradually take over, and a wooded stream reappears, allowing the beavers to return.

Beavers mark long stretches of the stream as their territory, allowing them to continuously move within their area. Other beaver territories exist further upstream or downstream. This results in a dynamic landscape with various stages of habitat development along the stream, supporting a diverse range of species.

For example, grass snakes, green sandpipers, wood sandpipers, greenshanks, snipes, black storks, trout, wild boar, moose, and deer all benefit from the different habitats created by the beaver-woodland cycle.



Figure 2: Beavers are important ecosystem engineers. ([Image source](#))

Grazing the edges of swamps

Water buffalo and lowland tapirs, in addition to cervids, feed on submerged aquatic plants. Horses also graze on the bulbs and rhizomes of reeds, sedges, and rushes, particularly in areas that dry up seasonally. By eating the roots of dominant species, they create more space for less dominant plants to flourish.

Horses also graze on the above-ground parts of reeds and sedges. Along with bovines, they push reed beds back into deeper water, leaving the shallow shoreline with shorter and less dense vegetation. This transformation benefits young fish, frogs, dragonflies, and other species that thrive in warm, shallow waters, which are protected from larger fish by the dense reed beds. Wading birds such as herons, spoonbills, and ibises frequently forage in these zones created by large herbivores.

In tidal mudflats and salt marshes, water buffalo are better adapted to penetrate the muddy areas than horses, bovines, or bison. Being the largest of these animals, they feed more indiscriminately. Water buffalo move on when all the vegetation is grazed down to about 1 decimeter in length, leaving the area increasingly muddy. The time it takes for the mud to settle

allows plants ample time to regenerate and flower. Since both palatable and less palatable plants are grazed, this process reverses plant succession, resulting in a species-rich vegetation.

Bovines, on the other hand, tend to stay in drier areas and selectively graze only the most palatable plants. This reduces vegetation biodiversity in those areas, as only two species of plants typically survive in regions grazed by bovines.



Figure 4: Konik horses feeding on aquatic plants in the Netherlands. ([Image source](#))



Figure 4: Grazed wetland vegetation in shallow water is a highly productive habitat, full of frogs and young fish, giving birds such as this spoonbill good feeding opportunities. ([Image source](#))

Example 1: Kaziranga National Park, India

In Kaziranga National Park, the Brahmaputra River carries monsoon rainwater and sediments from the Himalayan mountains into the Indian lowland floodplains. Each flood deposits large amounts of sediment, raising the height of the riverbanks and filling ponds and old river tracks.

Simultaneously, the monsoon waters erode the riverbanks and redistribute these sediments elsewhere. Trees and other vegetation at the water's edge are often washed downstream in this process (Figure 4). The river acts as the dominant natural force that interrupts the natural succession from bare ground to grassland and eventually to mature subtropical forests.

Higher areas dry out faster once the floodwaters recede. Once dry, vegetation begins to grow. Sandbars become covered with pioneer grasslands, which eventually turn into tall grasslands and reed beds, trapping even more sediment ([Figure 5](#)). As sediment builds up, these areas become higher, allowing trees and bushes to take root. Over time, forests will cover these areas ([Figure 6](#)).



[Figure 5](#): The river Brahmaputra erodes the water edge and new sandbars elsewhere. Trees and other vegetation growing at the water's edge get flushed downstream in the process, countering the process of natural succession from sandbar to mature subtropical forest. ([Image source](#))



Figure 6: A large, low lying former river track gets slowly filled in with sediment. Tall grasses grow unto the water's edge, leaving only a small area for silt and short pioneer grassland. ([Image source](#))

However, this natural succession is interrupted by the large herbivores that inhabit the region. Elephants consume vast amounts of woody species and tall grasses, while Indian rhinos and wild water buffalo graze on tall grasses and reeds ([Figure 7](#)). Together, they transform overgrown areas into short-grazed grasslands ([Figure 8](#)).



Figure 7: Old river tracks will become smaller over time and as the banks grow, mature forest will cover the entire bank. ([Image source](#))

Once the grass is short, species such as barasingha, muntjak, and Indian hog deer move in to feed. Indian and greylag geese, along with various ducks, also graze the grasslands, keeping them very short ([Figure 9](#)). Water buffalo and rhinos feed not only on short grass but also on rough, tall grasses, creating a grazing mosaic that benefits species like the swamp francolin. At the edges of these areas, the tall grasslands are converted into shorter grasslands, expanding grazing opportunities for other animals.



[Figure 8](#): Both Indian rhino and wild water buffalo feed on the tall grasses and reeds. ([Image source](#))



[Figure 9](#): Without grazing animals, this area would have been completely overgrown by tall grasses or even trees. ([Image source](#))

Tigers and other predators hunt in the tall grasses and bushes ([Figure 10](#)), making these areas dangerous for many herbivores, except for elephants and adult rhinos. The short, open

grasslands provide ample food for species like the Barasingha deer, geese, and ducks, and offer a safer environment with clear visibility to spot predators from a distance.

Open, shallow water attracts waterfowl and waders of various species. Large herbivores help maintain these open shallow waters and keep the surrounding grasslands short. As the shoreline becomes trampled and muddy, dung is deposited, increasing the number of worms and invertebrates in the soil. This boosts the food supply for waders like snipes, lapwings, and sandpipers ([Figure 11](#)).



[Figure 10](#): Tiger and other predators hunt in the area, making tall grasslands and bushes for many herbivores a dangerous place to stay. ([Image source](#))



[Figure 11](#): The Barasingha deer and Indian geese depend on short grasslands for food. ([Image source](#))



Figure 12: Barasingha deer and gees keep the grass very short. Water buffalos and rhinos also feed on the short grass, but their big bodies need the rough tall grasses as well. ([Image source](#))

In the woodland areas, elephants, sambar deer, and gaur are the main herbivores. While they slow down bush encroachment, their numbers are not sufficient to completely prevent it. Thus, the river remains the primary force converting mature floodplain forests into grasslands or new river tracks.

Water buffalo also play a role in shaping the floodplains. They enjoy wallowing in muddy ponds and rubbing their muddy skin against tree trunks. Over time, they repeatedly select the same trees, wearing down the bark and eventually causing the trees to die. Additionally, water buffalo feed on young trees, sometimes debarking them or breaking them to access the leaves at the top. These behaviors help to keep the floodplains open, free from trees and bushes.



Figure 13: Shorelines and shallow water are short-grazed and get trampled and muddy. Deposited dung increases insect life, creating excellent feeding habitat for wading birds like the grey-headed lapwing. ([Image source](#))



Figure 14: Sambar deer browse and help counteract bush encroachment. ([Image source](#))



Figure 15: Elephants eat a lot of trees and bushes and are big enough to push over tall trees. But many elephants are needed to destroy a complete woodland. ([Image source](#))

Example 2: Saeftinghe, the Netherlands

From 2021 onward, a herd of water buffalo grazed during the summer months in the Baalhoek salt marsh. This salt marsh had previously been ungrazed and was developing toward climax vegetation that no longer qualified as Natura2000 habitats.

Water buffalo consume rough, fiber-rich plants more effectively than cattle and are better suited to exploring muddy areas. It was expected that, unlike cattle, water buffalo would venture deeper into the salt marshes and feed on the fiber-rich plants that dominate climax vegetation ([Figure 16](#)). By grazing on these plants, the dominance of climax vegetation could be reduced, opening opportunities for earlier succession stage vegetation to thrive.

Before the pilot project began, it was anticipated that species such as reed, sea couch grass, and sea clubrush would gradually give way to more species-rich salty vegetation that would qualify for Natura2000 habitats. After evaluating the first three years of the project, the results appeared promising (Calle et al., 2023⁵). Through their grazing, trampling, trail-making, and the creation of self-made pools, water buffalo introduced more structure to the salt marsh compared to when it was ungrazed. In areas where they frequently crossed small tidal creeks, blockages formed, creating new small wet environments. Species richness began to increase, with plants like seaside arrowgrass, common saltmarsh-grass, sea aster, common sea-lavender, common scurvy-grass, and seaside plantain benefiting from the additional light and space created by the buffalo's grazing.



Figure 16: Water buffalo feed more on rough, fiber-rich food than cattle. ([Image source](#))

Compared to cattle, water buffalo graze more evenly across the vegetation, leaving about 10 cm of standing plants. As they graze, the salt marsh becomes increasingly trampled, muddy, and less accessible. At this point, the buffalo shift to another area of the salt marsh that has longer grasses and herbs. The grazed, muddy areas are then left to recover, benefiting all the plant species. As a result, the climax vegetation is gradually restored into a species-rich mosaic of salt marsh habitats, better aligning with Natura2000 targets.



Figure 17: Water buffalo in the saltmarsh of Baalhoek in southern-western delta in the Netherlands. Photo: Het Zeeuwse Landschap.

In contrast, cattle grazing in the nearby Saeftinghe salt marsh is much more selective. Cattle tend to stay closer to freshwater ponds, avoiding deeper gullies, and therefore graze less

extensively in the salt marsh than water buffalo. This selective grazing allows for more rugged climax vegetation to persist in the deeper areas of the marsh. Ideally, a more accurate comparison would require both species to graze the same area.



Figure 18: The higher areas are grazed very short. In time, this will allow for a transition towards another vegetation type. ([Image source](#))

Almost all the trees and shrubs in the Baalhoek salt marsh were either eaten or trampled by the water buffalo, and they are now dead. In other areas grazed by water buffalo, they have also proven highly effective at preventing bush encroachment. Looking ahead, it is expected that water buffalo grazing will continue to positively contribute to the Natura2000 conservation objectives of the Westerschelde Estuary and remain an attraction for residents and visitors alike.

Conclusion

Large herbivores like elephants, water buffalo, and beavers are crucial for maintaining biodiversity and preventing the overgrowth of wetland habitats. Through grazing and habitat alteration, they keep landscapes open, supporting a wide range of plant and animal species.

In Kaziranga National Park, herbivores help maintain grasslands and shallow water habitats, preventing forest succession and creating feeding grounds for various species. In Baalhoek and Saeftinghe, the introduction of water buffalo has transformed the salt marshes by reducing dominant vegetation, promoting plant diversity, and supporting Natura2000 conservation targets. Water buffalo, particularly in Saeftinghe, are more effective than cattle in grazing deeper, muddier areas, preventing bush encroachment, and maintaining open habitats.

Overall, large herbivores are vital to the health of wetland ecosystems. Their presence ensures diverse, open landscapes that benefit both plant and animal life, as seen in the successful rewilding efforts in Kaziranga and Saeftinghe. Sustainable management of these herbivores is key to continuing these ecological benefits.



Figure 19: An exclosure full of sea couch grass surrounded by a grazed flower rich saline vegetation. ([Image source](#))



Figure 20: Grazing and trampling of the high and dry sand bars changes the vegetation from dominant tall grasses to a mixed grassland with forbs and less dominant grasses. ([Image source](#))



Figure 21: The botanical value of the area increases year by year. ([Image source](#))



Figure 22: From rough tall grasses to saline grassland due to water buffalo grazing with patches of saltmarsh rush appearing as dark spots in the grassland. ([Image source](#))



Figure 23: Water buffalo grazing on taller vegetation. ([Image source](#))



Figure 24: Dead trees due to water buffalo grazing, debarking, and breaking. ([Image source](#))



Figure 25: Open salt marsh pioneer vegetation created by water buffalo grazing and trampling the area. Snipes this landscape full of holes and bumps. ([Image source](#))



Figure 26: To the left shows the effect of water buffalo grazing. Tall reeds are transformed into open pioneer salt marsh vegetation. ([Image source](#))



Figure 27: In the shallow water there is lots of food for wading birds. ([Image source](#))

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Case Study #4: Eurasian Beaver as Ecosystem Engineer

Sophie Ramsay, Nonie Coulthard, Bamff Wildland



Figure 1: Like the North American beaver, Eurasian beaver is a very important ecosystem engineer. [Image source](#)

Introduction

Bamff is a family-run estate on the edge of the Scottish Highlands in Perthshire. In 2002, Eurasian Beavers (*Castor fiber*) were introduced onto a straightened farm drainage ditch, initially in enclosures, making Bamff the oldest, most established beaver site in Scotland. The estate and the Ramsay family formed a relationship with academic institutions, in particular Stirling University, who have used Bamff as a research base for over 20 years. Encouraged by the experience of helping a degraded ecosystem tangibly improve, and seeing robust scientific data affirming lived experience, a decision was taken to go further. In 2020, a pioneering rewilding project began, with the removal of around 300 sheep from 12 fields and the establishment of an expert Steering Committee. A perimeter fence was built in early 2021, around approximately a third of the estate, to create ‘Bamff Wildland’, a 170ha area, including the 12 fields, 6 woods (a mixture of semi-natural and former tree plantations) and extensive beaver wetlands. In 2022, hardy, native breeds of cattle and pigs were introduced in low numbers, with access to the whole area, as proxies for the auroch and wild boar, as part of a natural grazing regime. January 2024 saw the introduction of a breeding herd of Exmoor ponies as additional large herbivore proxies.

Bamff Wildland (WL) is an experiment in how to repair a degraded ecosystem and restore function and resilience. In recognition of the relatively low ecological starting point, Bamff WL takes a ‘catalysed rewilding’ approach, occasionally intervening on a small scale. For example, planting small, protected copses of good progeny native trees and thorny shrubs that are missing or scarce, or sowing certain small areas with Yellow Rattle (*Rhinanthus minor*) and other native wildflower seeds. Bamff WL is also committed to removing invasive non-native species (INNS), including *Rhododendron ponticum* and New Zealand Pigmyweed (*Crassula helmsii*). Numbers of Roe deer (*Capreolus capreolus*) are managed by shooting. Some other species reintroductions may be considered (e.g. small mammals, amphibia) if native species which would naturally be part of Bamff wetland ecosystems do not return, despite the creation of suitable habitats by beavers. This approach seeks to enable the re-establishment of natural processes that should result in a dynamic ‘self-willed’ landscape, rather than attempting to conserve a more static ecosystem state that requires ongoing, highly prescriptive management to maintain. The approach is also adaptive, and Bamff Wildland is committed to adjusting management where there is evidence from monitoring and research to support the need for this (e.g. adjusting proxy herbivore numbers or excluding them from areas or habitats which appear to be ‘over-grazed’). The purpose of this is not only to significantly enhance and maintain biodiversity at Bamff, but also to contribute to evidence on best practice restoration through rewilding locally, nationally (in Scotland) and further afield.

The Bamff Wildland Monitoring Plan has been systematically implemented since 2020, with baseline surveys and annual repeat monitoring. There is a wealth of additional records prior to this, from formal studies, anecdotal evidence, photographic records and citizen science, collected since the introduction of beavers in 2002. Ongoing monitoring and research cover

various ecological aspects across Bamff Wildland, including vegetation and habitat surveys; various animal surveys including amphibians, reptiles, bats, breeding birds, invertebrates (pollinators and other insects, freshwater invertebrates), mammals, fish; soils and sediments, carbon and nutrient cycling and water levels and flows. Much of the monitoring and restoration is carried out and supported by volunteers, PhD students and *pro bono* experts. Bamff welcomes community involvement in all activities, which enhances learning, public engagement and understanding. In 2022-23, a project led by Bamff WL and collaborating with neighbouring land managers received a government grant to explore scaling up riparian restoration activities, connectivity, ecosystem monitoring and research across a wider landscape “Braes of Alyth”. This took a ‘cores and corridors’ approach in 2 sub-catchments, with Bamff WL as the principal core: both as a source of practical experience and best practice expertise to support other sites and land managers and as a source of evidence (potentially as a benchmark reference site).

[<https://bamff.land/rewilding/>; <https://bamff.land/braes/>]



Figure 2.: Eurasian Beaver in Bamff Wildland (photo credit @Dave Maric)

Here we provide a very brief synthesis of more than 20 years of monitoring, key research findings and practical experience of rewilding a site, with beavers as the engineers of wetland creation within a highly modified landscape (previously drained and intensively managed agricultural land, livestock pasture and woodland). In terms of larger wild herbivore impacts, beavers have acted as the principal animal agent of change and restoration at Bamff since 2002, in particular through the creation of dams and beaver pools and modifications to watercourses and adjacent grassland and woodland. With the introduction of proxy grazing herbivores in low

numbers, including a breeding herd of free-living Exmoor ponies, there is exciting potential to use monitoring and research to explore many more questions and contribute to the body of knowledge and best practice on restoring and rewilding wetland ecosystems with the help of beavers, other native wild animals and proxy herbivores. Several other case studies here focus on ‘megafauna’ and large herbivores and predators. In relation to Bamff WL we also note the importance (especially in a highly modified ecosystem) of understanding the interactions between other animal species (including proxy herbivores and smaller fauna: e.g. invertebrates in soils, grassland and woodland as well as in freshwater habitats) - and their combined impacts on plants, soils, water and (particularly) ecosystem functions of wetlands. These are some of the least understood and most exciting areas of current and future research, rewilding experimentation and adaptive management at Bamff WL (see examples in ‘Key Findings’, in References and ‘Ongoing Research’, below).

Past and current investigations and Key Findings from Bamff WL work relating to species and ecosystems are grouped under the ‘*Ecological functions of animals relating to wetlands*’ headings supplied, (those for which Bamff WL has particularly relevant data and experience), i.e.: *Ecosystem Engineering*, *Nutrient Cycling*, *Mediating cross-ecosystem linkages (water-terrestrial)*, *Herbivory and vegetation management*, *Habitat modification for other organisms*. A sixth side-heading is added to cover ‘*Human influences, attitudes and perceptions*’. The focus is on the question posed, as to “**How wild animals help to shape wetlands**” and the **ecological importance of wild animals for the functions of wetlands**; coupled with the requirement to provide best-practice recommendations (based on practical rewilding experience) for how wild animal species can add value to meeting the overall objectives of the Ramsar Convention. (i.e. “**the conservation and wise use of all wetlands through local and national actions and international cooperation, as a contribution towards achieving sustainable development throughout the world**”).

Key Findings – how wild animals (beavers and other species) help shape wetlands

1. Ecosystem Engineering

Beavers as Ecosystem Engineers

Beavers are known globally as ecosystem engineers, helping to shape and create wetland ecosystems, restoring biological and structural diversity, function and resilience and with the ability to produce positive landscape-scale impacts which help to tackle the linked crises of biodiversity loss and climate change (Fairfax & Westbrook 2024). They are increasingly appreciated and used as agents of habitat restoration, creation and rewilding. Bamff WL has the longest-term studies and evidence of the success of these approaches in the UK, showing positive beaver impacts (ecological restoration, wetland creation and modification), within formerly degraded agricultural landscapes (e.g. Wilson et al, 2020).

A small number of Eurasian Beavers, reintroduced to Bamff in 2002, have significantly reshaped former straightened farm drainage ditches, increasing wetland area, complexity, and biodiversity. They have impacted water flows, hydrology and sedimentation across the Wildland and adjacent farmland and, through dam building, grazing and other behaviours, also had significant impacts on wider terrestrial and aquatic habitats, woody and non-woody plants and other animal species.

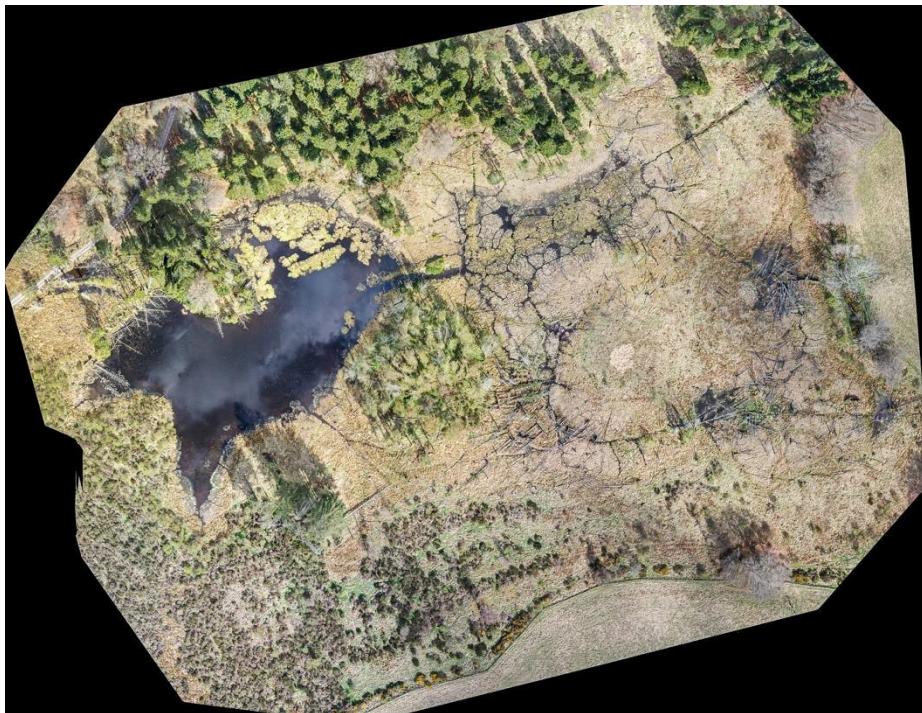


Figure 3. Aerial views and video of Eurasian Beaver impacts in Bamff Wildland: the creation and modification of structural and vegetation diversity in a wetland ecosystem (all credits: @Dave Maric)

See also video link (showing diversity of beaver-created wetlands at Bamff and small 'catalysed rewilding' interventions: 'ponds and scrapes'): 'Autumnal Wetlands at Bamff Wildland' (@Dave Maric) <https://www.facebook.com/watch/?v=1186847692379201&ref=sharing>

Wetland Plant Diversity: Long-term studies at Bamff following release of beavers into previously drained fenland showed that after 12 years of beaver presence there was a threefold increase in species richness of wetland macrophytes, attributed to beaver activities, including tree felling and grazing – see Figs. 4 and 5 below (Law et al, 2014; Law et al, 2017). See also 4, Herbivory and Vegetation Management.

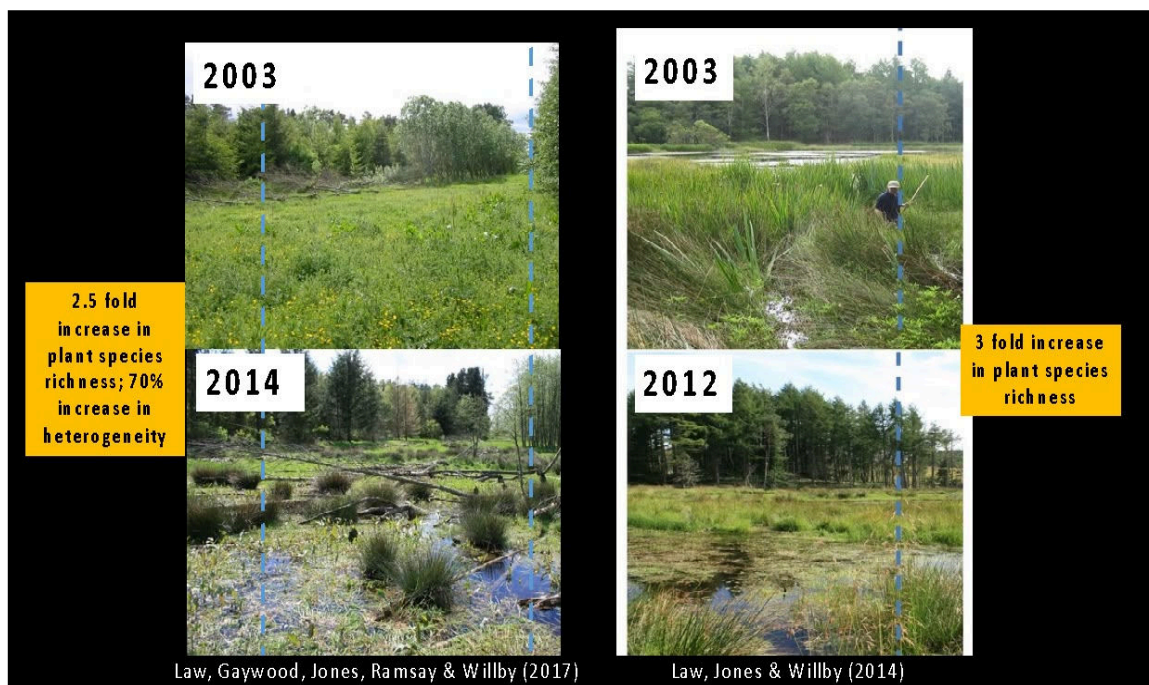


Figure 4: Impacts of beavers on plant species richness and heterogeneity in wetlands on Bamff Wildland over 12 years (references in Figures).

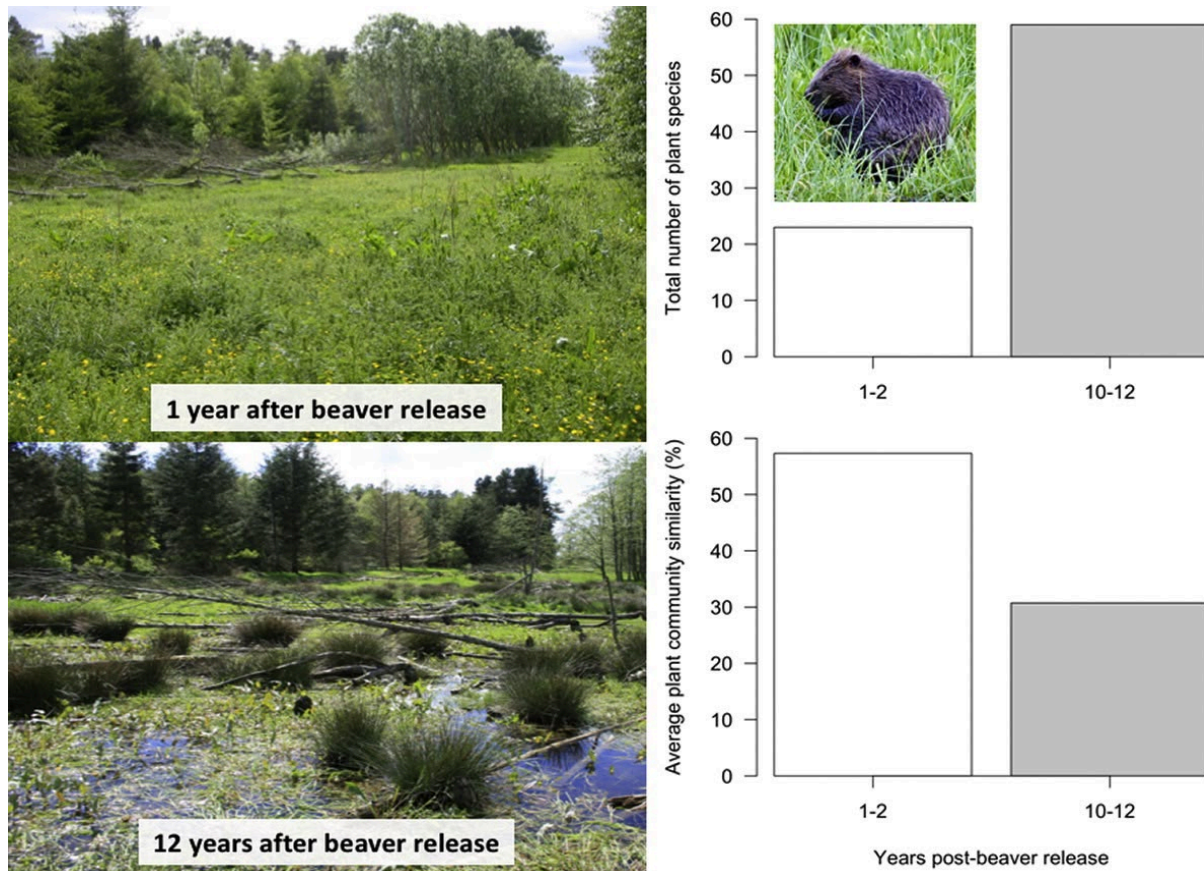


Figure 4: An overview of the study site on Bamff WL 1 year post release (spring 2003) (a) and 12 years post release (early summer 2014) (b). [Law et al 2017]

Water levels/ fluxes and storage

A major ecosystem engineering impact of dam building by Eurasian Beavers is on the physical components of wetland ecosystems. Beaver dams impound water and cause a cascade of interacting changes to water fluxes and storage. These effects of beaver dams are poorly understood and there are few quantified studies of site-scale effects on the water balance or average flows around a site. A PhD study monitored and compared catchments with beaver dams (Bamff WL) and a nearby reference site without beaver dams to investigate the hydrological effects of beaver dams and to construct the first conceptual model of the hydrological impacts of a series of small beaver dams across a site (van Biervliet, 2024). Key findings included the strong modulating effect of soil permeability and the fact that the flood attenuation effects of beaver dams appear to be largely a result of water stored not in beaver ponds themselves but in the water table in adjacent floodplain fields (especially where soils are permeable). Beaver dams can therefore help to restore floodplain wetland hydrology well beyond beaver ponds and show significant potential to support wetland restoration and rewilding (e.g. by helping to restore hydrological conditions to headwater streams and floodplains that have been artificially drained). (van Biervliet, 2024).

Other Ecosystem Functions and Services: ongoing research studies and monitoring are investigating the combined and interacting effects of beaver ecosystem engineering on both physical and biological components of the wetland ecosystems and the multiple opportunities for using beavers as a ‘tool’ in wetland restoration and maintenance of ecosystem health and function. Beaver dams can increase physical and biological diversity and biological ‘responses’ (e.g. increased aquatic plant biomass). Restoration of local ecosystem processes can also lead to wider scale ecosystem benefits such as nutrient retention in beaver ponds and flood attenuation (Law et al, 2016; Law et al 2017). Twenty years of data from Bamff WL (and other sites) are under review in 2025 and many ongoing studies are building on this. See other headings below (Nutrient Cycling; Herbivory), published studies and ‘List of Ongoing Research’ in References.

A current PhD study is assessing long-term biodiversity changes associated with cascades of beaver dams in Bamff WL. Dams create ponds, regulate flows, increase sedimentation, decrease shading and increase emergent vegetation which, alongside ongoing maintenance and herbivory by beavers, creates dynamic habitat heterogeneity of a type and scale that human intervention cannot replicate. The study will determine whether functional diversity and redundancy provided by disparate freshwater habitats enhance the resilience of a rewilded freshwater landscape. Preliminary findings showed an increase of 21.8% in macroinvertebrate species richness over 10 years (Dunleavy et al, 2023 and poster - see Annex).

2. Nutrient Cycling

Beaver Dams and Nutrients

Comparison of beaver-modified and unmodified sites on headwater streams draining 13 ha of pastureland in eastern Scotland showed that organic matter retention and aquatic plant biomass were higher in beaver ponds (7- and 20-fold higher respectively) than in unmodified channels. The beaver-modified habitat on Bamff WL consisted of a series of interconnected dam pools created by 10 in-stream dams constructed by beavers. Growing season concentrations of extractable P and NO₃ were on average 49% and 43% lower respectively below the series of dams than above, although colour and suspended solids concentrations increased below the dams. (Law et al 2016). There is also some recent evidence from Bamff of the ability of beaver ponds to act as sinks for microbial pollution derived from livestock waste, especially during episodes of high loading, providing an additional dimension to their role in water quality enhancement in agricultural landscapes (White et al, 2025 *In Press*).

Freshwater ponds, (in particular beaver ponds), are unique ecosystems with significant greenhouse gas (GHG) storage potential relative to their footprint on the landscape, (which accounts for <10% of global water bodies). Ongoing research on Bamff WL includes assessment of beaver ponds as sediment and vegetation carbon sinks and studies of how sedimentation rates affect storage of carbon and nitrogen, along with investigation of greenhouse gas (GHG)

storage, fluxes and emissions from beaver ponds relative to other freshwater habitats in the same landscape. Preliminary results suggest that animal behaviours and interactions in beaver ponds affecting mixing and stratification may differ from other ponds, which could impact the rate of GHG formation and release. Findings will be scaled-up to landscape and national scales to provide the first evidence base of the overall role of beavers in carbon cycling and climate. (Simpson, E (2024)).

3. Mediating Cross-Ecosystem Linkages

Water-Terrestrial Interface

Beavers manage this interface in various complex and ecologically beneficial ways, such as felling trees into watercourses, creating large woody structures and food caches, and drowning trees to create standing deadwood habitats. The physical and hydrological impacts of these activities (including water storage) may be significant at floodplain and landscape level, well beyond the created beaver ponds themselves (see 1. Water levels/ fluxes and storage above). Sediments held back by beaver dams store carbon, contributing to nutrient cycling; beavers also introduce significant quantities of nutrients via food caches and defaecation. Raised water levels may also aid seed dispersal and influence riparian vegetation development and spread.

Several ongoing research programmes at Bamff WL are investigating the interactions and interfaces between the aquatic and terrestrial environments and the impacts of beavers, other wild animals and their interactions in shaping these. A study using novel bioacoustic and ecoacoustic techniques, is assessing and monitoring biodiversity via soundscape analysis, at 5 beaver ponds on Bamff WL and 5 comparable non-beaver sites, to investigate how beaver engineering affects freshwater ecosystems in an agricultural landscape and the degree to which these impacts extend into the surrounding terrestrial habitat. Preliminary findings (based on bird and bat recordings) found some consistent differences between beaver and non-beaver ponds, potentially related to differences in availability of bat roosts (standing dead wood) and food availability (aquatic invertebrates). An acoustic classifier for freshwater invertebrates is being developed, to aid identification of sources of aquatic biophony (Adams, A et al, (2024)). Separately, stable isotope studies are being conducted to understand how beavers modify energy flows between terrestrial and aquatic systems via changes in aquatic vegetation, the detrital food base and invertebrate consumers. See also 5. Habitat modification for other organisms, below.

4. Herbivory and Vegetation Management

Beaver Grazing

Beaver grazing increases the diversity of wetland plant species and habitat heterogeneity (see 1. Ecosystem Engineering, above). Long-term studies and monitoring on Bamff WL and other sites in eastern Scotland have also shown that tree felling by beavers promotes riparian woodland regeneration and diversity of woodland composition and structure (Wilson, K (2022)). Studies

have also investigated the role of beaver herbivory in riparian woodland regeneration and the interactions and impacts in relation to other wild animal herbivores, notably roe deer (*Capreolus capreolus*), which readily exploit the regenerating secondary shoots produced after tree felling by beavers. A particular focus has been to understand why deer are attracted to this novel food resource and whether availability of beaver-browsed trees may enhance habitat quality for browsing deer and thus affect deer distribution and feeding habits. Sixty-two per cent (62%) of beaver-felled trees produced secondary shoots available to browsing deer and regenerating beaver-felled trees had 18% more secondary shoots than standing trees. The shoots were significantly higher in nitrogen content (+13%), but similar in carbon content and concentrated closer to the ground. The results showed that beaver herbivory can promote riparian woodland regeneration and heterogeneity by creating a mosaic of mature and multi-stemmed coppiced trees, even in the presence of other browsers (deer) whose browsing behaviour and movements may also be affected by the availability of the beaver-browsed trees. (Wilson, K (2022); Wilson et al, (2024)). Data analysis is underway to examine links between tree growth, deer browsing and beaver flooding and associated terrestrial invertebrate fauna in the same beaver wetland areas (Alan Law, *pers. comm.*).

Roles and impacts of other grazers in vegetation management and ecosystem restoration

Investigation of the impact and roles of Luing-cross cattle, Tamworth pigs, and Exmoor ponies in shaping wetlands in Bamff WL (alongside beavers and wild deer) and helping sustain the provision of ecosystem services is just beginning. Introduced in small numbers (between 2021-24), for natural grazing and ecological impacts, these species interact with the beaver wetlands as proxy wild herbivores helping to recreate complexity and diversity. There are many demonstrations of the use of large herbivores to replicate the impacts of their long-lost wild counterparts and support ecosystem restoration, regeneration of soil health and biodiversity. However, this combination of wild beavers, deer and other wild fauna, with proxy cattle, pigs and equines interacting in beaver wetlands (underpinned by 20+ years of monitoring and research data and experience) offers unique possibilities for new research and experimentation to help drive forward rewilding best practice and knowledge. Planned future studies include investigations of the interactions and impacts of 'hoofed animals as agents of rewilding', their combined impacts on soil structure, vegetation, carbon, biodiversity, wetland and woodland development across the Wildland and on ecosystem function, resilience and supply of ecosystem services.



Figure 6: Exmoor pony herd on Bamff Wildland in winter (photo credit @Dave Maric)

5. Habitat Modification for other organisms

One of the key roles that beavers play as ecosystem engineers creating and restoring wetland ecosystems is the modification of habitats (through changing water levels, impacts on vegetation etc.). This can provide opportunities for other animals (vertebrate and invertebrate) and plant species to establish or return to sites from which they may have been lost. The interactions with and between species lead to a continuous, dynamic process of change and renewal, increasing ecosystem complexity and resilience across landscapes. “Nothing is static when beavers are around” (Alan Law, *pers. comm*). The Bamff WL Monitoring Plan (WLMP) is designed to monitor long-term changes across the Wildland (and the impacts of occasional interventions) and to support adaptive management where necessary. The approach is one of ‘catalysed rewilding’ and minimal human intervention. The WLMP includes systematic recording of breeding bird assemblages, amphibia, pollinating insects and other invertebrates, habitats (flowering plants and woodland extent) and soil structure and composition using specific methodologies and technologies (e.g. trail cameras, fixed point and drone video photography) across the Wildland (wetlands, old agricultural and pasture ‘fields’ and woodland). (See *example video links below*). Over time this will form the basis for understanding landscape-scale habitat changes across Bamff WL and adjacent land and the roles that beavers and other animals play in this. Specific research studies complement and add to this ‘baseline’ monitoring

and help to understand the multiple interactions between beavers, habitats and many other organisms.

Emergent insects and birds

A study on Bamff WL which investigated insect emergence and related bird feeding activity found that both abundance and biomass of insects were higher at beaver-modified sites (compared with unmodified habitat). Linked to this, there was increased bird feeding activity at beaver sites. Peak insect emergence was positively linked to increased water temperature at beaver sites. This suggests that, in addition to restoring habitat connectivity, beavers can be very effective in increasing the availability of aquatic insect prey to bird communities foraging in wetlands. (Sanders, 2019).

Pollinators and other insects – farmland and wetland landscapes

A long-term study of invertebrate fauna and plants as (terrestrial) biodiversity indicators compares rewilded farmland (on Bamff WL) with adjacent conventionally farmed areas and is monitoring changes in relation to changing land use (i.e. the first few years of ‘full’ rewilding on what was previous farmland). This will provide an evidence base on how rewilding agricultural landscapes may affect biodiversity and ecosystem service potential at larger spatial scales and help to inform future land management decision making. Invertebrate sampling (beetles, spiders, butterflies, bees, hoverflies and moths) is taking place across the Wildland. Analysis of pollinator data, from beaver wetlands and other ponds shows that beaver wetlands are uniquely important for supporting high hoverfly species diversity and abundance. (Cook, P. (2023)).

(Small) mammals

Monitoring includes regular deployment of trail cameras and systematic drone footage. These reveal the impact that beaver dams and activities have in creating habitats for other species and the multiple interactions between beavers, their dams and other animals (predators such as otters, pine martens; small mammals/ prey; waterbirds; other herbivores including introduced proxy cattle, sheep and ponies); other animals using dams as useful structures for crossing streams or hunting prey). See links below: ‘*Drone footage of Bamff’s main wetland area*’ and ‘*Video footage from Beaver Dam*’.

- ‘*Drone footage of Bamff’s main wetland area*’ (July 8, 2024) – credit @Dave Maric: <https://www.facebook.com/watch/?v=459790910127487>
- ‘*Video footage from Beaver Dam*’ (July 1, 2024) - credit @Dave Maric <https://www.facebook.com/watch/?v=7987026288018453>

Beavers, migratory fish and conservation priority mammals

eDNA analysis and other methods are being used to investigate vertebrate communities, the differences and changes occurring above and below series of beaver dams on Bamff WL.

Twenty-eight vertebrate taxa have been detected across 4 sites using eDNA (4 fish species, 4 amphibian species, 9 mammal species and 11 bird taxa), with notable differences between the 4 sites and upstream/ downstream sampling results; probably due to the impact of beaver dams and other modifications increasing water retention, habitat availability and quality (e.g. extent of lentic habitats for waterbirds) and food availability. More detailed studies, especially on migratory fish (Atlantic Salmon *Salmo salar*, Brown Trout, *Salmo trutta*, European Eel, *Anguilla Anguilla*, Lamprey spp (*Lampetra*)), will investigate other aspects in relation to beaver dams and beaver-modified habitats (e.g. growth rates, community composition). (Macarthur, J (2024)). See Figs. 6i & 6ii: Photos of 2 Bamff WL (beaver pond) study sites, below.

Proxy (large) herbivores and soils

The impacts of introduced proxy herbivores and their interactions (with beavers and other wild animals in beaver wetlands) are being monitored across Bamff Wildland. Particular areas of ongoing research include individual and combined impacts (in the wetlands and adjacent 'farmland' pastures now under rewilding) of herbivore trampling/ rootling, grazing and defaecating on soil 'health', structure and nutrients, carbon and nitrogen fluxes; vegetation diversity and the spread of riparian woodland through natural regeneration. All will contribute new knowledge on the management of wild and proxy grazing herbivores in combination, to support effective rewilding and achievement of carbon/ climate change and biodiversity objectives in beaver-modified wetlands in Scotland. In addition, the Exmoors are an endangered breed, possibly an endangered primitive archetype. As well as using their eco/ engineering function to support rewilding, another objective of keeping a free-living herd on Bamff is to help in maintaining a balance of founder bloodlines in a herd subject to natural environmental pressures in order to ensure a genetically healthy population for the future.

Figure 7i: i Bamff WL Dam 1 Upstream
 (@James Macarthur, 2024)

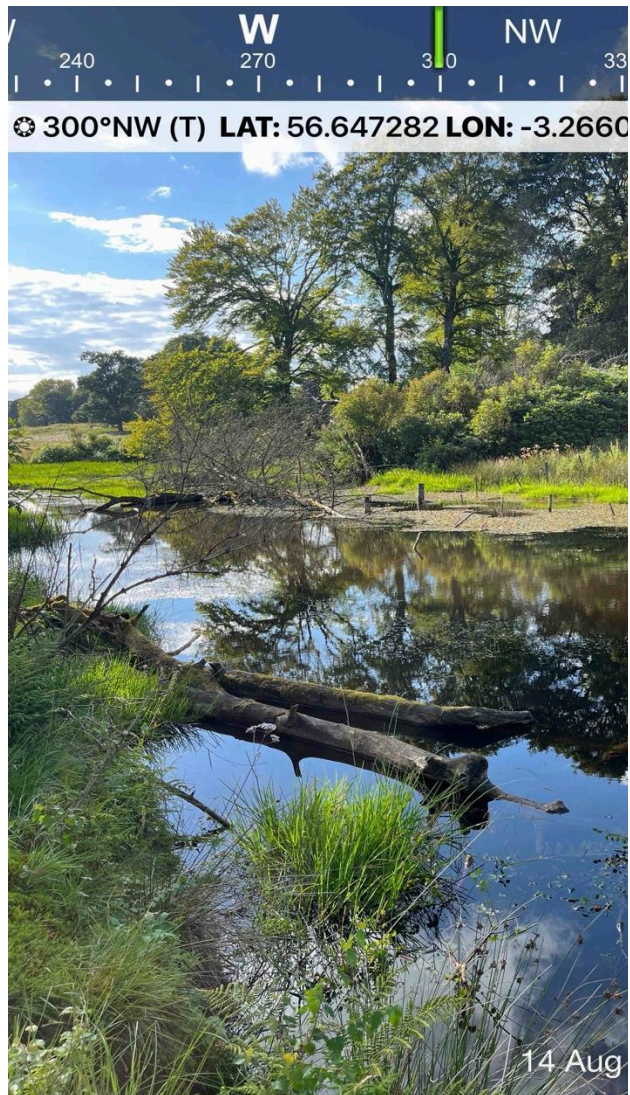


Figure 7ii: Bamff WL Dam 2 Upstream
 (@James Macarthur, 2024)

6. Human influences, attitudes and perceptions

Humans are of course the most influential and impactful animals in relation to the question of ‘How animals help shape wetlands (and restore ecosystem functions)’ – especially in the context of a site like Bamff WL which is relatively small (compared with other global ‘wildlands’ and other case studies in this report). It is also heavily affected by both past agricultural practices on what is now ‘Bamff Wildland’ and current surrounding land uses (agriculture, forestry, shooting and other) in the same catchments, which are also densely populated by humans, leaving little ‘space’ for nature.

In order for rewilding to be achieved successfully and to try to scale up positive rewilding impacts across wider landscapes, it is essential to understand these contexts and to involve, inform and educate people to support and implement necessary changes in human behaviours relating to wider land use and wild animals. Bamff WL has a very good track record in community engagement, the promotion of science and best practice and working with neighbours to try to achieve wider landscape impacts (e.g. see the ‘Braes of Alyth’ initiative - <https://bamff.land/braes/>). Ongoing socio-economic studies in support of these approaches include investigation of the impacts of people’s behaviour (and human disturbance to beavers) in relation to beaver welfare and social behaviours and other human-nature interactions and perceptions in relation to human wellbeing (Turner, et al (2024)). Plus, a sociological study of attitudes to beaver-modified landscapes and the cultural ecosystem services they may provide (Webb, et al (2024)).

Conclusions – Bamff Wildland

- The reintroduction of Eurasian Beavers at Bamff WL has had significant positive impacts on wetland ecosystems, demonstrating the species’ role as an ecosystem engineer and important keystone species in freshwater wetlands.
- There is a multiplicity of other animal impacts and interactions between wild animals, proxy (rewilding) herbivores, plants, other organisms and physical components (soils, water), which contribute to creating and maintaining diverse, dynamic and resilient wetland ecosystems and ecosystem functions – many of these are the subject of ongoing investigations and opportunities for learning and sharing of knowledge
- The increase in biodiversity and habitat complexity, alongside ongoing research into nutrient cycling, the roles of other grazing species, interactions at the terrestrial-aquatic interface and many other aspects highlights the importance of continued monitoring and study.

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Webb, S, Law, A, Anderson, D, Wartmann, F (2024) '*Beavers in Britain: what cultural ecosystem services do beaver-modified landscapes provide?*' BES conference POSTER, Liverpool UK December 2024.

Further References - review/ database:

CREW/ JHI/ NatureScot

The Centre of Expertise for Waters (CREW) and James Hutton Institute (JHI) carried out a 2020 review for NatureScot of available evidence relating to beaver activity and impacts on the functioning of rivers and streams for water resource management in Scotland:

"Establishing the potential influence of beaver activity on the functioning of rivers and streams and water resource management in Scotland".

See main and summary reports, *References, Annexes, Policy paper etc.*

<https://www.crew.ac.uk/publications/the-influence-of-beavers-on-freshwater-processes-and-resources>

Conservation Evidence database

The Cambridge Conservation Evidence resource (<https://www.conservationevidence.com/>) is an Open-Source database (and journal) designed to support anyone making decisions about how to maintain and restore biodiversity through documentation and making available (global) evidence for the effectiveness of conservation actions. The database can be searched (for example a search on {Studies/ [key word: **Species**] and [habitats drop-down list: **Wetlands**]} – gives the following list of 200 relevant published reference

Case Study #5: The Ecological Roles of Crocodylians

Chloe Eckert, Global Rewilding Alliance

(images provided by Ruchira Somaweera, School of Biological Sciences, University of Western Australia, Crawley, WA, 6009 Australia)

A significant body of literature shows that in terrestrial and marine ecosystems large predators can play important roles in ecosystem structure and functioning. By contrast, the ecological role and importance of large predators within freshwater ecosystems are less well understood.

Conservationists frequently promote the ecological roles that crocodylians are assumed to fulfil, but on what basis? A recent [study](#) reviewed the available information on the ecological importance of crocodylians. The order Crocodylia includes 27 species of [true crocodiles](#) (family [Crocodylidae](#)), [alligators](#) and [caimans](#) (family [Alligatoridae](#)), and the [gharial](#) and [false gharial](#) (family [Gavialidae](#)).

Known Knowledge

Global Distribution and Size: Most of them are confined to lowland rivers, streams, estuaries, mangroves, swamps, and lakes in the tropics, subtropics, and certain temperate regions in around 100 countries. Their dependence on terrestrial habitats for nesting make them the only aquatic predator group with extensive cross-ecosystem linkages.

- At least eight of 27 species grow over 5 meters long and weigh more than 500 kg, making them the largest predators in these environments, eclipsing the largest freshwater predatory fishes (e.g., giant catfish, river sharks, and rays) and carnivorous mammals (e.g., river dolphins, giant otters).

Habitat Modification – Ecosystem Engineers:

- Crocodylians alter habitats by digging holes, dens, and tunnels and building mound nests, impacting local biodiversity and habitat structure.
- These modifications provide refuges, affect water flow, and create breeding, feeding, and drinking sites for a wide range of other animals as well, benefiting various other species (fish, reptiles, amphibians, aquatic invertebrates, wading birds & mammals).
- However, it is not known to what extent these other species are dependent on these habitat modifications.



Figure 1. Images left to right: In salt marsh ecosystems, American alligators (*Alligator mississippiensis*) can trigger trophic cascades via their consumptive and non-consumptive interactions with a key mesopredator, the blue crab (*Callinectes sapidus*) (photograph: T. J. Dunkerton). In the marshes of Louisiana, American alligators frequently feed on lower trophic level species like apple snails, which are significant grazers within the ecosystem. This is evidenced by the discovery of numerous snail remains in the stomach contents of an alligator (photograph: R. Elsey). Crocodylians occasionally hunt large prey, especially when their typical food sources are scarce. This includes an Australian freshwater crocodile (*Crocodylus johnstoni*), normally a small-fish eater, capturing a large freshwater sawfish during the dry season in the Kimberley, as documented by the WA Department of Biodiversity Conservation and Attractions. Similarly, Nile crocodiles (*Crocodylus niloticus*) prey on zebras during migration periods in Kenya when large prey are abundant (photograph: M. Kirubi).



*Figure 2. Images left to right: In the Florida Everglades, the health and condition of American alligators (*Alligator mississippiensis*) serve as indicators of water levels and the availability of resources (photograph: M. Vieira). Assessing the body condition of crocodylians involves taking morphometric measurements of individuals in their natural habitats, such as these head measurements recorded from a black caiman (*Melanosuchus niger*) in Guyana (photograph: J. C. Nifong). The physiology and condition of developing embryos are commonly used as indicators of environmental contaminants in scientific research, exemplified by these American alligator eggs collected for analysis in Florida. (photograph: J. C. Nifong). Crocodylians are resilient creatures, capable of enduring severe physical conditions and generally recovering swiftly from illness and injury. Therefore, signs of poor body condition and potential illness in this American alligator, may suggest broader environmental issues (photograph: J. C. Nifong).*

Ecological Indicators:

- In the Florida Everglades, the American alligator and American crocodile serve as indicators of ecosystem health. Their population changes reflect water management and hydrological conditions, providing valuable data for ecosystem restoration.

- Overall, however, it is still too early to promote crocodylians as indicators of ecosystem health, but most species probably meet the criteria of responding to habitat change through reproductive output, body conditions, and abundance.

Cross-Ecosystem Movements:

- Studies using telemetry and stable isotope analysis show that crocodylians move between freshwater, brackish, and marine environments.
- These movements suggest that crocodylians could facilitate nutrient and energy transfer across different habitats, linking otherwise separate ecosystems. However, no studies have yet estimated the amount of resources translocated and their significance to recipient ecosystems.

Speculative Claims

Apex Predator Role:

- The role of crocodylians as apex predators is based more on assumption than solid evidence. Their diet is difficult to study due to their elusive and infrequent feeding behaviors.
- While they eat a variety of prey, their ability to survive on minimal food, and their irregular feeding capable of surviving for months without food, complicates their classification as apex predators.
- As opportunistic, generalist predators, there are no empirical studies that define how crocodylians impact on their prey populations and their trophic position, like those for other predators.
- Crocodylians can survive on significantly smaller amounts of food relative to their body size than are large endothermic predators.



*Figure 3. Images left to right: Many crocodylians, including the American alligator (*Alligator mississippiensis*), create shallow ponds and construct substantial mound nests, as exemplified by this nest and nursery pond in Louisiana (photograph: R. Elsey). Crocodylian nests and their adjacent areas function as egg-laying sites for various reptile species, such as these skink eggs discovered within the cavity of an American alligator nest (photograph: R. Elsey). Crocodylians build above-ground nests by piling up vegetation and soil; these nests can be substantial, measuring up to 7 meters in diameter and 1 meter in height, as seen in this American alligator nest (photograph: J. Nifong). Beyond nursery ponds and nests, some crocodylians also create and sustain intricate burrows and dens, such as those excavated by Nile crocodiles (*Crocodylus niloticus*) (photograph: A. Kilpin). These burrows serve as shelters for various animal species, including smaller crocodylians, protecting them from extreme environmental conditions or predators.*



Figure 4. Images left to right: In salt marshes, American alligators (*Alligator mississippiensis*) can initiate trophic cascades through both their direct and indirect interactions with a key mesopredator, the blue crab (*Callinectes sapidus*) (photograph: T. J. Dunkerton). In the marshes of Louisiana, American alligators frequently prey on lower trophic level organisms like apple snails, crucial grazers in the ecosystem, as indicated by the numerous snail opercula found in an alligator's stomach (photograph: R. Elsey). Crocodylians occasionally consume large prey, especially when their regular food sources are limited. For example, the Australian freshwater crocodile (*Crocodylus johnstoni*), typically a small-fish eater, was observed capturing a large freshwater sawfish during the dry season peak in the Kimberley (photograph: WA Department of Biodiversity Conservation and Attractions), or when large prey are seasonally abundant, like these Nile crocodiles (*Crocodylus niloticus*) preying on zebras during the migratory period in Kenya (photograph: M. Kirubi).

Keystone Species Impact:

- The idea that crocodylians are keystone species lacks strong empirical support. There is little evidence that their presence or absence significantly alters ecosystem dynamics.
- Only one species of crocodylians – the American alligator in the Florida Everglades - has been proven playing a keystone role. It has been experimentally shown that the alligators can reduce the abundance of prey (blue crabs & apple snails) and modify

their behavior (blue crabs). The blue crab is an important 'mesopredator' in saltmarsh food webs, and in its absence keystone grazers (periwinkle snails & ribbed mussels) increase, generating a trophic cascade within the saltmarsh habitats.

- Generally, claims about their keystone status are often based on anecdotes rather

Recommendations for Future Research

Evaluating as Ecological Indicators:

- Comprehensive studies are needed to assess the effectiveness of crocodylians as ecological indicators in various ecosystems beyond the Florida Everglades.
- These studies should include a wider range of species and environments to see if these indicators apply generally.

Understanding Ecosystem Engineering:

- Future research should examine the wider ecological impacts of crocodylian habitat changes, including their effects on biodiversity, habitat structure, and ecosystem processes.
- Long-term and large-scale studies are crucial to understanding the full extent of these impacts, including the creation of microhabitats and their effects on plant community composition.

Clarifying Trophic Interactions:

- Detailed studies on crocodylian diets and their trophic interactions are essential to understand their role as apex predators. This includes examining their feeding habits, prey selection, and the impact on prey populations.
- Techniques like stable isotope analysis, genetic analysis, and long-term monitoring could provide valuable insights into their trophic roles and interactions with other species.

Assessing Population Dynamics:

- Research on the effects of crocodylian population declines and recoveries on ecosystem structure and function is vital for informed conservation efforts. This includes understanding demographic changes, population growth, and resilience to environmental changes.
- Studies should also consider the impacts of global threats such as climate change, invasive species, and habitat loss on crocodylian populations, and how these factors interact to influence their ecological roles.

Measuring Cross-Ecosystem Linkages:

- Studies are needed to measure how much nutrients and energy crocodylians move between different ecosystems and the impact on those ecosystems.
- These studies could help us better understand how crocodylians connect different habitats and support ecosystem health, especially in terms of nutrient cycling and primary productivity.

Conclusion

Although crocodylians are often believed to have significant ecological roles, much of this is based on limited evidence. Many claims about their roles as apex predators, keystone species, ecosystem engineers, and nutrient transfer agents are speculative. Future research should focus on filling these gaps with targeted, hypothesis-driven studies.

Irrespective of the true ecological roles of crocodylians, there is a clear moral imperative to conserve these species for their intrinsic values alone!

Case Study #6: Rewilding Apennines, White-Clawed Crayfish

Mario Cipollone, Rewilding Apennines, Italy

Introduction

The Central Apennines in Italy are home to diverse ecosystems, including streams and rivers that support native species like the white-clawed crayfish, a key species native to peninsular Italy. Crayfish play an essential role in maintaining the health of aquatic ecosystems by providing food for animals like otters, fish, and birds, and by keeping waterways clean through their consumption of decaying organic matter. Their ability to regulate invertebrate populations ensures the stability of the ecosystem. However, the crayfish's sensitivity to chemical pollution also makes it a valuable bioindicator for water quality. Over recent decades, the white-clawed crayfish has experienced a significant decline, particularly due to habitat loss, invasive species, and water pollution. The species is now listed as endangered by the IUCN and under Annexes II and V of the EU Habitats Directive, reflecting the need for urgent conservation action.

This case study explores the ecological role of the white-clawed crayfish in the Central Apennines, the factors contributing to its decline, and the conservation actions taken by Rewilding Apennines (RA) to restore its populations through breeding centers and habitat rehabilitation.



***Figure 1:** Biologist and river expert Tommaso Pagliani showing the sex of a just captured crayfish (©Bruno D'Amicis)*

Known Knowledge

Ecological Role

The white-clawed crayfish is a crucial species in the conservation of Apennine ecosystems. It provides an important food source for higher trophic levels, including otters, fish, and birds. The crayfish also actively contribute to maintaining the balance of invertebrate communities by preying on smaller animals. As ecosystem engineers, their consumption of decaying matter helps clean watercourses, ensuring that the aquatic ecosystem remains healthy and supports a diverse range of species. This species is also highly sensitive to chemical pollutants, making it an excellent bioindicator for monitoring the quality of freshwater environments.



Figure 2: A crayfish in the Verde River, Central Apennines (@Bruno D'Amicis)

Why the Crayfish Has Declined

The white-clawed crayfish has faced a dramatic contraction in its native range due to several key threats. Over the past 50 years, increasing exploitation of water resources for agricultural, industrial, and urban uses, alongside pollution and climate change, have severely degraded freshwater habitats. In Italy alone, crayfish populations have declined by 74% in the last decade. The introduction of invasive crayfish species such as red swamp crayfish (*Procambarus clarkii*) and spiny-cheek crayfish (*Orconectes limosus*) intensified the problem, as these alien crayfish species outcompete native crayfish for resources and often carry diseases such as crayfish plague (*Aphanomyces astaci*). This disease devastated many native populations in the Central Apennines, including a major outbreak in 2013 that wiped out crayfish in the Verde River, one of the region's largest populations.

Action Initiated and Planned

Rewilding Apennines has made significant efforts to conserve and restore the white-clawed crayfish. Key actions include the establishment of breeding centers and reintroduction programs. In 2020, RA signed an agreement with the Municipality of Borrello to manage a local crayfish breeding center that had been operated voluntarily. This center, along with two others later established in Monteferrante and Pettorano sul Gizio, aims to restock and reintroduce crayfish populations into the Apennine watercourses. Breeding centers follow the natural reproductive cycle of the crayfish, ensuring successful mating, egg incubation, and the release of juveniles back into the wild. Between 2014 and 2023, over 5,000 juvenile crayfish were released into the Verde River as part of the restocking efforts, with surveys showing a gradual increase in population and signs of natural reproduction.

In addition to breeding efforts, RA has focused on habitat restoration, particularly by removing weirs and other barriers that degrade stream ecosystems. Long-term plans include purchasing and protecting wetlands to secure the future of the crayfish and its habitat.



Figure 3: *The cycle of activities in the breeding centers (@Bruno D'Amicis)*

Conclusion

RA's reintroduction efforts have shown encouraging preliminary results, with increasing populations of native crayfish in some rivers, including the Verde River. The effectiveness of the program has been evaluated through field observations and surveys, with clear signs of natural reproduction emerging as a positive indicator of long-term success. However, challenges remain, particularly the continued threat of invasive species and the need for further habitat

restoration. RA's commitment to purchasing key wetland areas and strengthening protection measures is essential to ensure the sustainability of these efforts. Continued monitoring and adaptive management are necessary to maintain the momentum of this successful conservation initiative.



***Figure 4:** Tommaso Pagliani catching river invertebrates to carry out biotic index to estimate habitat suitability for the white-claw crayfish (©Bruno D'Amicis)*

Case Study #7: Potential influences of Sarus crane recovery on the wetland ecosystem services in eastern Uttar Pradesh, India

Samir Kumar Sinha, Wildlife Trust of India



Figure 1: Sarus Crane ([Image source](#))

The Ganges River basin is home to diverse natural inland wetlands—lakes, swamps, river floodplains, oxbow lakes—and man-made rice paddies, providing essential habitats for a wide range of biodiversity, particularly resident and migratory bird species. The Sarus Crane (*Antigone antigone*), a "vulnerable" species protected under India's Wildlife (Protection) Act of 1972, inhabits open wet and dry grasslands, agricultural fields, marshes, and pools throughout India, often utilizing both natural and artificial wetlands during the non-breeding season¹⁶. Due to the degradation and destruction of its natural wetland habitat, however, the Sarus Crane increasingly resorts to suboptimal rice paddies as breeding grounds^{17,18}. The species faces multiple threats, including habitat loss, wetland degradation, and a shift in traditional rice-wheat cropping systems to sugarcane farming, which fails to provide suitable habitats.

Despite the Sarus Crane's cultural significance in the region, it faces direct threats such as egg poaching, chick and adult mortality, and electrocution from power transmission lines. Wetland ecosystems support a rich diversity of bird species, which are highly sensitive to human

¹⁶ Archibald, G. W., K. S. G. Sundar, and J. Barzen. 2003. A review of the three subspecies of Sarus Cranes (*Grus antigone*). *Journal of Ecological Society (India)*, 16:5–15.

¹⁷ Meine, C. D., and G. W. Archibald. 1996. *The cranes: status survey and conservation action plan*. IUCN, Gland, Switzerland.

¹⁸ K. S. Gopi Sundar. 2009. Are Rice Paddies Suboptimal Breeding Habitat for Sarus Cranes in Uttar Pradesh, India?, *The Condor*, 111 (4), 611-623.

disturbances and serve as early indicators of wetland ecosystem health¹⁹. The Sarus Crane relies on crop fields, particularly rice paddies, and wetlands for nesting and roosting. In areas without a year-round water supply, these cranes migrate locally. Their flocking behavior is closely tied to water availability, with stable water conditions supporting regular flock sizes, while dry seasons result in large congregations at select wetland sites²⁰ (Vyas, 2002).

The Sarus Crane is an essential indicator of wetland ecosystem health due to its sensitivity to ecological and environmental changes within its habitat²¹. The crane's population is closely tied to the quality and availability of wetland areas. Research shows that alterations in wetland use lead to habitat loss and fragmentation, impacting not only Sarus Cranes but other crane species as well²². Breeding success in suboptimal habitats, like rice paddies, is slightly lower than in natural habitats; however, in parts of India, rice fields can still serve as viable nesting sites thanks to supportive farmers who permit cranes to nest in their paddies^{23,24}. Leveraging this local support can improve the species' breeding success.

In northern India's eastern Uttar Pradesh, the Wildlife Trust of India has been working across ten districts to conserve the Sarus Crane within a mosaic of wetlands and agricultural lands. Conservation efforts focus on enhancing breeding success by protecting nests in rice paddies and small wetlands, where human activities threaten nest stability. Additionally, the project aims to secure wetland habitats through legal protections and community-based conservation initiatives. Local communities have committed to safeguarding wetlands and combating bird and animal poaching. The project has also trained community members in monitoring biodiversity, particularly Sarus Cranes and other wetland species vulnerable to poaching. Presently, efforts are underway to protect approximately 2,600 hectares of wetlands and around 20,200 hectares of catchment area, promoting biodiversity conservation and ecosystem services based on protection and sustainable use principles. Over the past decade, more than 700 Sarus Crane nests have been safeguarded, achieving an average hatching success rate of over 90%. This success has led to an annual population growth of about 8%, increasing from 650 in 2013 to over 2,600 in 2024 across more than 75 wetlands and surrounding agricultural areas.

¹⁹ I, Kabore., Lallébila, Tampo., Victor, Bance., Clément, Daboné., Komandan, Mano., Halamoussa, Joëlle, Ayoro., Adama, Oueda. (2022). Preliminary biological data of Sahel wetland ecosystems in Burkina Faso: Implications for ecological health assessment. *Frontiers in conservation science*, doi: 10.3389/fcosc.2022.913333

²⁰ Vyas, R. 2002. Habitat utilization by Sarus Crane *Grus antigone* and the importance of man-made wetlands in its conservation. In: Rahmani, A. R. and Ugra, G. (eds.) *Birds of wetlands and grasslands: Proceedings of the Salim Ali Centenary Seminar on conservation of avifauna of wetlands and grasslands*, Mumbai, India. PP. 35-40.

²¹ Harsh, Gulati., Sarita, Rana. (2022). Habitat Preference and Current Threats to The Sarus Cranes *Grus Antigone* (Aves: Gruiformes: Gruidae) In Important Bird Areas of Haryana, India: Implications for Determining Effective Conservation Actions. *Journal of Advanced Zoology*, doi: 10.17762/jaz.v43i1.110

²² OU, Wei-xi. (2014). Wetland Use Change and Its Impact on Wintering Habitats of Red-Crowned Crane in Yancheng Coastal Wetland. *China Population, Resources and Environment*,

²³ MUKHERJEE, A., C. K. BORAD, AND B. M. PARASHARYA. 2002. Breeding performance of the Indian Sarus Crane in the agricultural landscape of western India. *Biological Conservation* 105:263– 269.

²⁴ K. S. Gopi Sundar. 2009. Are Rice Paddies Suboptimal Breeding Habitat for Sarus Cranes in Uttar Pradesh, India?, *The Condor*, 111 (4), 611-623.

The conservation of wetlands and the Sarus Crane has provided direct benefits to a species that serves as a vital indicator of wetland health. Birds fulfill diverse roles in ecosystems, acting as predators, pollinators, scavengers, seed dispersers, pest controllers, nutrient cyclers, and ecosystem engineers²⁵. Aquatic birds, particularly waterfowl, are valuable bio-indicators of heavy metal pollution in wetlands, underscoring the essential ecosystem services they offer, which benefit both the environment and human communities²⁶. With the growing global interest in nature tourism, wetlands that support rare or threatened bird species contribute crucial cultural services, enhancing local community earnings²⁷. These services support nature-based solutions to ecological issues and improve human well-being.

Cranes, as a group, provide essential ecosystem services such as habitat support for aquatic flora and fauna, nutrient cycling, and biodiversity conservation. The Black-necked Crane, for instance, interacts closely with local farmers, which can lead to human-wildlife conflicts. However, it also offers ecosystem services like aesthetic value, recreation, ecotourism, and therapeutic benefits. In China's Caohai Wetland, these benefits are recognized by farmers as a form of ecological compensation, helping to reduce conflicts²⁸.

The restoration of Sweden's Lake Hornborga, which enabled the return of the Eurasian Crane (*Grus grus*), exemplifies how species conservation contributes to cultural ecosystem services. The lake, now a popular springtime destination, attracts thousands of tourists drawn by the cranes' iconic dancing displays, creating new economic opportunities for local communities. This demonstrates how cranes contribute to both biodiversity and cultural enrichment²⁹.

The Sarus Crane holds significant cultural value throughout its range in India. Known for forming lifelong monogamous pairs, these cranes are symbols of marital fidelity. In some regions, newlyweds are encouraged to observe a pair of Sarus Cranes, as sightings are considered omens of good fortune and harmonious marriage³⁰. The crane is also featured in the Jataka tales, a collection of stories depicting the Buddha's past lives and emphasizing moral and ethical conduct³¹. In one tale, the Sarus Crane embodies wisdom and nobility, reinforcing the bird's

²⁵ Mariyappan Mathialagan, Meena Rajendran, Sarathkumar Velu, Alfred Daniel Johnson, G K Dinesh, Kumaravel Solaimuthu, Maheshwaran Kaliyappan, Mangayarkarsi Sankar. Ecological Role and Ecosystem Services of Birds: A Review. *Int. J. Environ. Clim. Change*. 2023;13(6):76-87. DOI: 10.9734/ijec/2023/v13i61800

²⁶ Zhang WW, Ma JZ. Waterbirds as bioindicators of wetland heavy metal pollution. *Procedia Environmental Science*. 2011;10:2769-2774.

²⁷ Sujata, Deori., Niranjana, Das. (2013). Ecotourism in wetland environment: a case study of Deepar Beel Wildlife Sanctuary (Ramsar site) of Assam (India) *Ecoturismo em ambiente de pantanal: um estudo de caso no Deepar Beel Wildlife Sanctuary (sítio Ramsar), Assam (Índia)*.

²⁸ Lanyan, Zhong., Yanhua, Li., Yalong, Li., Tongxiang, Zou., Tailin, Yu., Chuanyin, Dai. (2023). Local farmers' perceptions of ecosystem services and disservices provided by the Black-necked Crane (*Grus nigricollis*) and their conservation implications. *Global Ecology and Conservation*, doi: 10.1016/j.gecco.2023.e02614

²⁹ Margaryan, L., Prince, S., Ioannides, D., & Röslmaier, M. (2018). Dancing with cranes: a humanist perspective on cultural ecosystem services of wetlands. *Tourism Geographies*, 24(4–5), 501–522. <https://doi.org/10.1080/14616688.2018.1522512>

³⁰ **Johnsgard, P. A. (1983). *Cranes of the world*. Indiana University Press.**

³¹ Fausbøll, V. (1883). *Jataka Tales: The Buddhist Legends of the Buddha's Previous Lives*. Royal Asiatic Society.

cultural importance. Such cultural associations foster positive attitudes among farmers, supporting the crane's survival in agriculture-dominated landscapes where it frequently nests³².

With their large bills, Sarus Cranes are expert diggers, using their powerful mandibles to unearth tubers and roots from muddy wetlands. This foraging behavior disturbs the soil, creating “ploughed” patches that increase environmental diversity and support the growth of less dominant plant species. Artificially disturbed soil effectively increases environmental heterogeneity and provides establishment microsites for subordinate plant species³³. Similar to the Eurasian Crane (*Grus grus*), the Sarus Crane's digging activities produce vegetation patches that differ from undisturbed areas in structure and species composition, leading to nearly twice the plant diversity in disturbed areas³⁴. These crane-foraged patches also prevent the spread of invasive species and sustain floral resources longer, which in turn supports insect diversity, particularly pollinators and pollen-feeding species³⁵. This ecosystem service is particularly valuable in grass-dominated habitats, contributing to conservation.

Sarus Cranes prefer open habitats for nesting, relying on wetland plants, rice or other crops, and local food sources like mollusks and aquatic arthropods. Their nests, located in marshy areas within agricultural fields, benefit farmers. As the seasonal marshes dry after breeding, the nests provide a foundation for pioneer grasses, skipping the typical reed and sedge stages of natural succession. This process accelerates land formation, allowing farmers to till, plow, and sow Rabi crops earlier, enhancing agricultural productivity in these shared landscapes³⁶.

³² Sundar, K. S. G. (2009). *Are rice paddies suboptimal breeding habitats for Sarus cranes in Uttar Pradesh, India?* The Condor, 111(4), 611-623.

³³ Limb, R. F., Engle, D. M., Bidwell, T. G., Althoff, D. P., Anderson, A. B., Gipson, P. S., & Howard, H. R. (2010). Restoring biopedturbation in grasslands with anthropogenic focal disturbance. Plant Ecology, 210(2), 331–342. <https://doi.org/10.1007/s11258-010-9760-7>

³⁴ Valkó, O., Borza, S., Godó, L., Végvári, Z., Deák, B. (2022) Eurasian crane (*Grus grus*) as ecosystem engineer in grasslands – conservation values, ecosystem services and disservices related to a large iconic bird species. Land Degradation and Development, 1–11 <https://doi.org/10.1002/ldr.4314>

³⁵ Bátori, Z., Kiss, P. J., Tölgyesi, C., Deák, B., Valko, O., Török, P., Erdős, L., } Tothmérész, B., & Kelemen, A. (2020). River embankments mitigate the loss of grassland biodiversity in agricultural landscapes. River Research and Applications, 36(7), 1160–1170. <https://doi.org/10.1002/rra.3643>

³⁶ Sushil, Kumar, Upadhyay., Shiv, Ji, Malviya., Dheer, Pal, Singh., Raj, Singh. (2018). Hydrosere Succession Model of Marshy Wetland Mediated Nesting Behavior of Sarus Crane, *Grus antigone* (*Aves: Gruidae*). doi: 10.5958/2320-3188.2018.00006.2

Case Study #8: Ecological processes and functions maintained by large fishes, reptiles, birds, and mammals in India's riverine, estuarine, and wetland ecosystems, with a focus on Ramsar sites.

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Overview

The ecological functions and processes maintained by freshwater 'megafauna' have not been studied in detail, with studies typically dominated by aquatic plants, microbes, invertebrates, and fishes in India. However, a growing body of global research is providing evidence about the key roles played by freshwater megafauna (He et al. 2024, Malhi et al. 2016, Froyd et al. 2014). In India, riverine, wetland, and estuarine ecosystems support several species of endangered megafauna or 'wildlife', many of them endemic to the Indian subcontinent. In this overview, I include large fishes, reptiles, birds, and mammals under the umbrella of 'megafauna', and summarize some points on their ecosystem functions, trophic position and interconnections, and contributions to ecosystem processes in the face of severe declines in populations and habitat loss over the last century. The present summary is based on field observations and studies on threatened species such as Ganges and Indus river dolphins, three species of crocodiles: the gharial, marsh crocodile, and saltwater crocodile; three species of otters: Eurasian otter, smooth-coated otter, and small-clawed otter; ~20 species of freshwater turtles and aquatic birds, large catfish and carp species (> 1 m in captured size), and other carnivore and ungulate species that depend on wetlands and rivers significantly (Sinha et al. 2014, WII-GACMC 2018). As of 2023, of India's 865 non-marine protected areas (PAs), 743 are terrestrial PAs, 93 are wetland, 14 are riverine PAs, and 15 are estuarine PAs (WII-ENVIS database: [Source](#)). Overall, these protected areas cover a very small proportion (~5%) of the total extent of riverine, wetland, and estuarine systems. The list can be expanded further by including 85³⁷ Ramsar sites declared on wetlands across 23 of India's 36 states and union territories (Farheen et al. 2022). As the designation of Ramsar sites was focused on waterfowl and wading bird conservation, Ramsar sites may not always have significant populations of other threatened species. Therefore, while the PAs may be important for the protection of threatened species, the extant abundances of these species may not always translate to maintain ecosystem functions in the same manner as historical abundances might have done, prior to steep declines (see He et al. 2019).

Very few river stretches now have intact assemblages of freshwater megafauna, which have remained so mostly due to some protection (Kelkar 2023, Nawab et al. 2016, Lang & Kumar 2013). Most stretches, however, have drastically altered species assemblages with many of the above key species missing, owing to severe long-term population declines and local extirpations due to hunting, fishing-induced mortality, species invasions, persecution, and breeding failures due to dams and barrages (He et al. 2019, Lang et al. 2019, BirdLife International 2020, Swain et al. 2021, Barcenás-García et al. 2022, Chen et al. 2023).

³⁷ At the time of writing this overview.



Figure 2: Many marsh crocodiles have been introduced into the wild as part of a restocking programme in India.. Image: Anish Andheria/Wildlife Conservation Trust (WCT), India

Ecological functions have been altered due to losses of faunal elements on the one hand, and by two key changes on the other: 1) biological invasions of wetlands by aquatic plants (e.g. water hyacinth), herbivorous or omnivorous fishes (e.g. Tilapia and common carp), and invasive predators (e.g. African catfish), and 2) conservation releases and restocking of captive-bred native (e.g. marsh crocodile) into rivers and wetlands. In the further sections, I first identify different protected areas and other sites that could be considered as “reference” or “benchmark” sites for evaluations on ecosystem functions maintained by megafaunal assemblages. Second, I comment on potential changes in ecological functions brought by species reintroductions, biological invasions, and losses of megafauna populations (e.g. see Khan & Panikkar 2009, Singh et al. 2013, Srivastava et al. 2014, Lundgren et al. 2018). Third, I summarize ecological functions across different freshwater ecosystems in India, in relation to megafauna species of conservation priority. I then conclude with a note on future directions and insights for ecosystem restoration and recovery of modified ecosystem functions and processes through effective protection of megafauna.

Protected rivers and wetlands in India as ‘reference sites’

The National Chambal Sanctuary that is designated on c. 425 km of the Chambal River in north-central India is probably the only river system in the Gangetic plains that still holds an intact assemblage of freshwater megafauna. The Chambal River supports almost 85% to 90% of the critically endangered Gharial in the world (Lang et al. 2019, Lourenco-de-Moraes et al. 2023), and probably 100% of the critically endangered red-crowned roofed turtle population (Praschag et al. 2019).



Figure 3: The National Chambal Sanctuary is one the most ecologically functional riverine areas of India, hosting a large set of key wildlife species.. Image: Anish Andheria/WCT

For many other endangered turtles, including the narrow-headed softshell turtle *Chitra indica*, the Chambal is one of the few last strongholds (Asian Turtle Trade Working Group 2000, Ahmed et al. 2021, Das et al. 2021). In addition, marsh crocodiles, smooth-coated otters, Ganges river dolphins, and Indian Skimmers also occur in stable populations in the Chambal (Nair & Krishna 2013). Ganges river dolphins, gharials, and river turtles of the genus *Batagur* and *Chitra* are obligate riverine species, while other species of softshell and hardshell turtles, marsh crocodile, and otters occur in a wide range of lotic and lentic habitats. Most of these species are predators. It is interesting how these diverse predatory species are ‘packed’ in the Chambal river, which has been well protected due to ravines along its banks and a history of control of the

ravine-scape by outlaws – which led to de facto protection until the turn of the 21st century (Nair & Krishna 2013). This assemblage may hold some clues on the nature of coexisting size-structured predator and scavenger guilds. The other riverscape that comes a close second as a ‘reference site’ is the Katarniaghat wildlife sanctuary on the Giruwa river near the India-Nepal border, upstream of the Ghaghra river barrage (Vashishtha et al. 2021). Although a part of this area is impounded by the barrage, one can see gharials, marsh crocodiles, Ganges river dolphins, turtle species, and otters in a fairly small area. Other key riverine protected areas in the Indus-Ganga-Brahmaputra plains such as the Kaziranga National Park, Vikramshila Gangetic Dolphin Sanctuary, and Hastinapur Wildlife Sanctuary, have good densities or stable populations of some species (e.g. Ganges river dolphins, smooth-coated otter) but have not managed to retain more diverse species assemblages (Kelkar et al. 2010, Kelkar et al. 2022, Khoo et al. 2021). In the Beas River Conservation Reserve in the Indus basin, 3-4 Indus dolphins remain in India (Braulik et al. 2024), at such a low density that their ecosystem functions may be treated as negligible. River turtles have been the worst impacted and have been extirpated from most of the region (Rao 2016, Mendiratta et al. 2017, Ramya Roopa et al. 2024), barring a few exceptions. In peninsular India, a few protected areas support river megafauna such as smooth-coated otters and marsh crocodiles, as well as relatively intact fish assemblages and critically endangered turtles (e.g. Moyar river in the Mudumalai and Sathyamangalam Tiger Reserves, Tamil Nadu; Satpura and Satkosia Tiger Reserves in Madhya Pradesh in central India, and protected areas along the Cauvery, Kabini, and Tungabhadra rivers). Among estuarine sites, the mangrove forests and estuaries of the Sundarbans, Bhitarkanika, and Coringa are a few examples of relatively intact megafaunal assemblages along the deltas of eastern India. In the Ramsar sites, apart from birds (mostly wintering ducks, waders, and some resident endangered species such as Greater Adjutant or Masked Finfoot), river and sea turtles/terrapins, dugongs, crocodiles, otters, river and estuarine dolphins, and some terrestrial wetland-dependent or wet grassland-dependent mammals such as tiger, fishing cat, swamp deer (also the hardground Barasingha subspecies of swamp deer), hog deer, and brow-antlered or Eld’s deer may occur (Table 1).

Table 1. Megafauna occurring in Ramsar sites of India.

State/UT	No. of sites	Names of sites	Species
Andhra Pradesh	1	Kolleru Lake	Birds (e.g. Pelicans)
Assam	1	Deepor Beel	Greater Adjutant
Bihar	3	Kanwar Lake, Nagi Bird Sanctuary, Nakti Bird Sanctuary	Birds (waterfowl), turtles, tortoise
Goa	1	Nanda Lake	Birds (waders)
Gujarat	4	Khijadiya, Nalsarovar, Thol Lake, Wadhvana Wetland	Birds (waterfowl, waders)

Haryana	2	Sultanpur National Park, Bhindawas Wildlife Sanctuary	Birds (waterfowl)
Himachal Pradesh	3	Chandra Taal, Pong Dam Lake Wildlife Sanctuary, Renuka Lake	Birds (waterfowl, waders)
Jammu and Kashmir	5	Hokersar Wetland, Hygam Wetland Conservation Reserve, Shallabugh Wetland, Mansar-Surinsar Wildlife Sanctuary, Wular Lake	Birds (waterfowl)
Karnataka	4	Ranganathittu Bird Sanctuary, Ankasamudra Bird Conservation Reserve, Aghanashini Estuary, Magadi Kere Conservation Reserve	Birds (storks, ibises, pelicans), marsh crocodiles, smooth-coated otters
Kerala	3	Ashtamudi Wetland, Sasthamkotta Lake, Vembanad-Kol Wetland	Birds, fishes
Ladakh	2	Tso Kar, Tsomoriri Lake	Birds (black-necked cranes, nesting sites of waterfowl, gulls, etc.)
Madhya Pradesh	4	Bhoj Wetland, Sakhya Sagar, Sirpur Lake, Yashwant Sagar	Birds (waterfowl, waders)
Maharashtra	3	Lonar Lake, Nandur Madhameshwar, Thane Creek	Birds (flamingos)
Manipur	1	Loktak Lake	Brow-antlered deer, birds (waders, waterfowl)
Mizoram	1	Pala Wetland	-
Odisha	6	Ansupa Lake, Bhitarkanika Mangroves, Chilika Lake, Hirakud Reservoir, Satkosia Gorge, Tampara Lake	Saltwater and marsh crocodiles, gharials, Irrawaddy dolphins, sea turtles, Eurasian and Smooth-coated otters, birds (waterfowl), king cobra
Punjab	6	Beas Conservation Reserve, Harike Wetland, Kanjli Wetland, Keshopur-Miani Community Reserve, Nangal Wildlife Sanctuary, Ropar Wetland	Indus dolphins, birds (rare waterfowl), gharials (reintroduced), turtles
Rajasthan	2	Keoladeo National Park, Sambhar Lake	Birds (waders, waterfowl, cranes), fishing cat
Tamil Nadu	16	Chitrangudi Bird Sanctuary, Gulf of Mannar Marine Biosphere Reserve, Kanjirankulam Bird	Dugongs, sea turtles, birds (pelicans, storks, ibises etc.)

		Sanctuary, Karaivetti Bird Sanctuary, Karikili Bird Sanctuary, Koonthankulam Bird Sanctuary, Longwood Shola Reserve Forest, Pallikarnai Marsh Reserve Forest, Pichavaram Mangrove, Point Calimere Wildlife and Bird Sanctuary, Suchindram Theroor Wetland Complex, Udhayamarthandapuram Bird Sanctuary, Vadavur Bird Sanctuary, Vedanthangal Bird Sanctuary, Vellode Bird Sanctuary, Vembannur Wetland Complex	
Tripura	1	Rudrasagar Lake	Birds (rare waterfowl)
Uttar Pradesh	10	Bakhira Sanctuary, Haiderpur Wetland, Nawabganj Bird Sanctuary, Parvati Aranga Bird Sanctuary, Saman Bird Sanctuary, Samaspur Bird Sanctuary, Sandi Bird Sanctuary, Sarsai Nawar Jheel, SurSarovar, Upper Ganga River	Birds (cranes, waders, waterfowl), Ganges river dolphins, swamp deer, marsh crocodiles, gharials (reintroduced) in river sites
Uttarakhand	1	Asan Barrage	Birds (waterfowl), otters
West Bengal	2	East Kolkata Wetlands, Sundarban Wetland	Birds (waterfowl, masked finfoot, kingfishers), saltwater crocodiles, small-clawed otters, river terrapin, fishing cat, Irrawaddy dolphins, tigers, king cobra
Total	82*	—	

*Three Ramsar sites were declared only in 2024 August, at the time of preparing this report.

Of all Ramsar sites listed here, only a small proportion (~8.5%, n=7) appear to have near-intact megafauna assemblages. Interestingly, most of these sites are estuarine or brackish-water areas with mangrove forests, or relatively well-protected but small stretches of rivers. Bird and waterfowl-dominated wetlands, which are the bulk of the Ramsar sites, need to be surveyed fully for assessments of groups such as turtles and native fishes, for which comprehensive data are currently wanting. Turtles are highly diverse, greatly imperilled, and known to be a part of important wetland processes. Therefore, a Ramsar site-wide turtle species diversity and abundance assessment could enhance our understanding of the dominant trophic and nutrient processing pathways operating in those wetlands. However, with the levels of turtle hunting in many parts of India, combined with the impacts of invasive alien fish species, we may have

several Ramsar wetlands with altered ecosystem function, or indicate a “shifted baseline”. But stronger evidence and data are needed to verify this possibility of whether Ramsar sites may be considered just “altered” or “dysfunctional” on account of megafauna declines and local extirpations.

Notably, some areas are not formally protected, but have significant populations of some threatened species, e.g. gharials in the Ghaghra and Gandak rivers of northern India, otters in rivers like the Tamiraparani, Irrawaddy dolphins in the Chilika lagoon and Hooghly estuary, and fishing cats in the multi-use wetland landscapes of West Bengal. The ecological functions of most of these megafauna species have not been systematically studied. With birds, trophic functions mostly include herbivory (waterfowl), predation on invertebrates and fishes (storks, flamingo, pelicans), scavenging (e.g. adjutants, vultures) and contributions to primary production by “guanotrophication” (Adhurya et al. 2020, Chatterjee et al. 2017, Roy et al. 2011). In southern India, many farmers protect nesting sites and heronries of pelicans, ibises, and storks, near irrigation canals, and use the guano-enriched waters in their fields (Kumar & Krishanan 1991, Menon et al. 2015, Adhurya et al. 2020). Birds may thus be strong contributors to nitrogen cycling and detrital processes in shallow wetlands that are well-protected Ramsar sites. In such sites, the functions of other species may be mostly linked to food webs composed of multiple interacting herbivores and predators (Woodward & Hildrew 2002, Hilker & Lewis 2010, Wesner et al. 2013). In the absence of information on these trophic linkages and temporal changes in them, a thought experiment is useful. Bird conservation in many Ramsar sites appears to have been quite effective. With stable or increased bird abundances at these sites, along with invasive alien carps, herbivory on aquatic plants may have intensified (for waterfowl-dominated wetlands without water hyacinth invasion). On the other hand, the loss of turtles, crocodilians, and carnivores from these wetlands may have reduced the importance of predation as a key determinant of trophic dynamics and energy flows. In water hyacinth-invaded wetlands, most native aquatic plants may be outcompeted, and aquatic plant herbivory by birds or carps may not even remain relevant, as detrital/decompositional pathways become dominant over and above herbivory and predation.



Figure 4: Three megaherbivores – Asian elephant, Asiatic wild buffalo & Greater One-horned Rhinoceros – that play an important ecological role in Indian wetlands. Image: Anish Andheria/WCT

While not represented well in Ramsar sites, terrestrial ungulates such as Asian elephants, Greater One-horned Rhinoceros, and Asiatic wild buffalo, and marine herbivores such as green turtles and dugongs may exert strong impacts on ecosystem function by channelizing most primary production through herbivory rather than detritus cycling pathways that may dominate in the absence of such species. Rhinoceros and elephants overlap to a very small extent with Ramsar sites in Assam. The ranges of Asiatic wild buffalo (or wild water buffalo) are highly restricted today, in contrast with a once-extensive distribution (Kaul et al. 2019). But in ecosystems such as Kaziranga National Park where the whole megaherbivore assemblage exists in good numbers, their persistent ecosystem functions and impacts may be extraordinary. Mungi et al. (2023) showed that herbivory by large terrestrial megaherbivores in India (elephant, gaur, rhinoceros, wild buffalo) can interact with ecosystem productivity, leading to suppression of alien invasive plant species in nutrient-rich systems and possibly, promotion of invasion in nutrient-limited systems. Such research is critical to emphasize the roles played by large herbivores in wet grassland ecosystem changes, for which Kaziranga can be a unique reference site.

Changes in animal assemblages and ecosystem functions

Plant and fish invasions in most Indian wetlands have characteristically altered both primary autotrophic production and herbivory/ detrital pathways of biomass decomposition (Thorp & Delong 2002, Suresh et al. 2019, Pandey et al. 2020). Productive tropical wetlands may either be dominated by autotrophic primary production from aquatic macrophytes and algae, or be dominated by heterotrophic food webs involving diverse predatory fish species (Kundu et al. 2014, Chakraborty et al. 2017). Invasion by species such as water hyacinth may have dramatically increased plant organic matter in many wetlands (Srivastava et al. 2014, Wang & Yan 2017). Due to carp culture, herbivory levels may have increased from enhanced native river carp and exotic carp abundances (e.g. *Gibelion catla*, *Labeo rohita*, *Cirrhinus sp.*, *Ctenopharyngodon idella*, *Hypophthalmichthys nobilis* and *H. molitrix*) in wetlands where they may not be present at such densities naturally (Singh et al. 2013, Tiwari et al. 2016, Chakraborty et al. 2017). Seasonal changes in assemblages of invasive carp species has been shown to negatively affect water quality and turbidity in diverse wetland systems (e.g. Koushlesh et al. 2023, Tiwari et al. 2016, Richardson et al. 1995). As compared to carps that are predominantly herbivorous and omnivorous, the culture of predatory large fishes has been relatively limited. However, increases in predation by invasive alien species such as African catfish (*Clarias fcareipinus*) may have led to diminished abundances of invertebrates, native fish species, and waterbirds (e.g. in the low-diversity manmade wetlands of Rajasthan, a semi-arid region in western India, or in other wetlands as well) (Thakur 1998, Anoop et al. 2009). Other predatory species such as *Pangasiodon spp.* and *Piaractus brachypomus* (redbellied pacu or Pirapitinga) are also increasing in culture-based fisheries and their impacts on ecosystem function may

become apparent over time (Anupama et al. 2021, Singh 2018). Sharma et al. (2021) documented the competitive effects of introduced brown trout on native snow trout in Himalayan rivers, but such studies remain few compared to the likely extent of impacts on native fish species.

Declines in native megafauna alongside intensive ecosystem invasions may have led to an imbalance with high-level trophic interactions rarefying and low-level trophic interactions intensifying (Chen et al. 2023). This may have implications for carbon storage, release, and decomposition rates, as well as greenhouse gas emissions from wetlands (Ramesh et al. 1995, Panner Selvam et al. 2014). Rivers with relatively intact flows can resist fish invasions and remain dominated by complex, multi-predator trophic webs, as seen in the lower Gangetic plains (Singh et al. 2013). The case of the marsh crocodile is an interesting one in this regard. A native species, this crocodilian has been re-stocked in several water bodies across India, including rivers, wetlands, man-made tanks, ponds, and dam reservoirs (Bors et al. 2024). A generalist and highly adaptable predator, such introductions may have led to positive as well as negative impacts on trophic interactions. On the one hand, crocodile introductions in reservoirs and ponds with culture fisheries may have intensified predation on non-native fishes, and on the other, it is thought that increasing marsh crocodile densities may have led to dampened



Figure 5: The Ganges river dolphin occurs in all perennial large rivers of the Ganga-Brahmaputra river systems but occurs in only one Ramsar site (Upper Ganga River) in the region. Image: Soumen Bakshi/WCT

recruitment of more sensitive species like gharials. There have also been socially negative outcomes of such reintroductions, seen in instances of human-crocodile conflicts after attacks on people and livestock, and killings of marsh crocodiles in retaliation or due to fear, or as ‘pest control’ by fisher folk (Bors et al. 2024). Gharials and turtles have also been reintroduced into river systems as part of conservation breeding, head-starting, and translocation programmes, but the success of these reintroductions in terms of establishment of breeding and self-sustaining populations in the wild has been doubtful. It can be assumed with certainty that,

unlike marsh crocodiles, these reintroductions would not have led to any alterations in ecosystem processes and functions. Apart from marsh crocodiles, no other major reintroductions of threatened riverine megafauna have taken place in India's waterscapes. Instances of conservation-aided population recoveries of water-dependent terrestrial mammals (notably the Indian Rhinoceros, Asian elephant, Gaur, and swamp deer) have not yet been empirically studied in terms of their impacts on aquatic ecosystem functions (but see Mungi et al. 2023). Many deer species (Sambar, hog deer, swamp deer) prefer wet grasslands for foraging on nitrogen-rich grasses and forbs, and their relative contributions also deserve study as do the larger and more charismatic herbivores.

Ecosystem functions and processes in relation to freshwater and estuarine megafauna in India

- *Predation: complex webs of multiple interacting predators*

Size-dependent predation surely marks the most important ecological function maintained by most species that WCT's Riverine Ecosystems and Livelihoods programme works on. Predator trophic levels are often marked by predator: prey size ratios rather than species identity in aquatic systems (Gutierrez-Canovas et al. 2021). In river systems in particular, the diversity of apex predators is high, which may form multi-predator, heterotrophy-dominated food webs, and involve complex facilitation and competitive interactions between predator guilds (Wesner et al. 2013, Banerjee et al. 2016) and impacts of predation may also cascade onto primary producers (e.g. Beschta & Ripple 2012). These have not been studied in detail, but there are some functional aspects that make this an interesting problem to unravel. Most specialized predators feed on small-sized fish and shrimp prey, without any apparent preference for species. Here, gape limitation and eco-morphological constraints appear to dictate size limits in feeding on prey, coupled with morphological constraints on prey handling and manipulation (Kelkar et al. 2010, 2018). Ganges river dolphins, Gharials, Indian Skimmer, and some river turtles such as *Chitra indica* are predators of small-sized prey. Large predatory catfishes also prey on small-sized fishes, and in some cases, on birds and young turtles. Marsh crocodiles (due to jaw strength, bite force, and better capacity to manipulate prey before feeding) and smooth-coated otters (due to pack hunting: Nawab & Hussain 2012, Anoop & Hussain 2005) may be able to predate on large-sized fish and other vertebrate/invertebrate prey, including young turtles and gharials in case of marsh crocodile (Cuff et al. 2013, Hocking et al. 2017). Going by prey sizes, these species are generalist apex predators in water bodies across India. No confirmed instances of predation on river dolphins have been reported, although we have heard of one unsubstantiated anecdote of a massive, >2.5m long Goonch catfish (*Bagarius yarelli*) that was allegedly found with a dolphin calf in its stomach. Other predators such as fishing cat and tigers (in the Sundarbans estuary) may take large-sized fish as prey. However, in estuaries and mangroves, it is quite clear that saltwater crocodiles, along with large sharks such as bull sharks or tiger sharks, may be apex predators, on account of feeding on large-sized aquatic and terrestrial vertebrates (see Adame et al. 2018).

- *Scavenging guilds*

Many river turtle and terrapin species are known to be regular scavengers and detritus feeders. Due to the loss of turtles from many rivers and wetlands due to incessant hunting, this function may be significantly altered and diluted in its importance (Lovich et al. 2018, de Mirands 2017). Scavengers may have once been a crucial trophic pathway for decomposition of decaying animal matter, in times of abundant fish and turtle densities. Turtles, especially Gangetic softshell *Nilssonina gangetica*, were known to be regular feeders on decaying corpses and carrion in rivers (Ahmed et al. 2021, Das et al. 2021). In many regions of India, it is also believed that the presence of flapshell turtles *Lissemys punctata* and Indian black turtle *Melanochelys trijuga* may keep water bodies clean, indicating their connections with detritus processing pathways (Rahman et al. 2021). Occasional scavenging has been reported in marsh crocodiles and gharials. Among birds, Adjutant Storks and vultures are known scavengers, but their abundances have also declined considerably. As such, the scavenging guild may now be dominated by different catfish and perciform fish species in rivers and wetlands, as it is by free-ranging dogs in terrestrial systems that have replaced scavengers such as vultures, wild pigs, and hyenas.

- *Herbivory*

As explained earlier, herbivory in freshwater and estuarine environments may be mostly limited to fishes, waterfowl (ducks and geese), and some turtle species, where they may still exist. Other than fishes (both native and exotic), geese and ducks are clearly the major herbivores in India's rivers and wetlands. Impacts of ungulates on aquatic vegetation may be non-trivial only in a few systems such as the Loktak Lake where brow-antlered deer occur on dense mats of aquatic vegetation, and in wetlands where swamp deer survive. In other areas, elephants, water buffaloes (wild and domestic both), rhinoceros, green turtles, and dugongs may be important as megaherbivores. In the Gulf of Mannar Biosphere Reserve or the Andaman Sea, dugong densities are quite low and ecosystem impacts of herbivory may not be likely (D'Souza et al. 2015). Green turtles, however, have shown global population recoveries due to a range of factors including reduction in abundances of sharks that predate on turtles (Heithaus et al. 2014). Intensive herbivory by green turtles has been documented to decimate seagrass meadows in regions such as India's Lakshadweep islands between 2005 and 2015 (Kelkar et al. 2013a, b; Gangal et al. 2021). Barring such exceptional situations, herbivory may generally be of low importance in natural riverine and estuarine systems, but where present, its impacts on plant communities are significant (Bakker et al. 2016a, b).

- *Ecosystem engineering and habitat modification for other organisms*

No defining examples of ecosystem engineering or habitat modifications by freshwater megafauna species have been documented in India's aquatic ecosystems. Interestingly, domestic water buffaloes, which are frequent users of many wetlands on account of the local human livestock keepers, may play key roles in maintaining wetland productivity and wet grass abundance through herbivory (Furész et al. 2023). Trampling by buffaloes can lead to soil compaction over time, allowing water residence times to increase, which in turn can improve

wetland primary production and biodiversity supporting functions. A similar role may be played by domestic or feral pigs as well, in smaller wetlands.

- *Seed dispersal*

Crocodiles and turtles are known to be passive or active seed dispersers (Platt et al. 2013), however, no studies exist from India on riverine and wetland species. Freshwater fishes and birds may disperse seeds of aquatic and amphibious plants between water bodies where they may show local movements.

- *Nutrient cycling and cross-system linkages*

Predators that take terrestrial as well as aquatic prey may be critical mediators for cross-system linkages through nutrient cycling. Crocodilians may be important cross-system conduits for nutrients as they show movements between water bodies and over land. Crocodilians are known to be important agents driving nutrient cycling in aquatic ecosystems. Elephants may also be crucial contributors to nutrient cycling in wetlands due to their affinity towards water bodies for multiple social and physiological purposes.

Future directions

Understanding the trophic functions and linkages between size-dependent predation and scavenging in riverine and wetland ecosystems is a fascinating question, given the diversity of predator functional traits involved. In sites such as the Chambal River, nutrient cycling and trophic web models offer an exciting research topic for ecosystem ecologists. Such studies may also have great relevance in assessing wildlife contributions to carbon, nitrogen, and phosphorus fluxes in aquatic systems, and their importance in setting ecosystem recovery targets (Kumar & Das 2024). It is worth understanding the trophic and ecosystem function implications of the steep declines of freshwater megafauna and predators/ scavengers such as turtles in India. Another question of interest and importance would be the alterations in energy transfers and trophic linkages caused by biological invasions and declining functional diversity of native species in wetlands (Calizza et al. 2021, Chen et al. 2023). Studies on these aspects can provide interesting insights for river and wetland restoration (He et al. 2024). Protected areas appear to show a disproportionately positive effect on retaining closer-to-original megafauna assemblages and more intact ecosystem functions as compared to adjacent unprotected areas in general (Abell et al. 2007, Dudley et al. 2018). However, with the critical dependence of human communities on freshwater for basic survival and livelihood needs, large-scale protection may not be possible to achieve through policymaking (Hussain et al. 2020). Instead, working to ensure wide social support for wetland and river conservation remains far more important, even if slow in realizing their objectives (Anderson et al. 2019, Irvine et al. 2016). Further studies on ecosystem functions of megafauna may enhance the appreciation of values of freshwater protection and their spill-over effects across riverine networks. In India, commercial inland navigation and river interlinking (inter-basin transfers of water) are being

promoted and likely to cause irreversible damages to freshwater ecosystems (Grant et al. 2012). In this context the urgency of studying and documenting ecosystem-level impacts of conserving freshwater megafauna and restoring river-wetland ecosystems cannot be overstated.

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Case Study #9: The Rewilding of Iberá Wetlands, Argentina

Emiliano Donadio & Sebastian Di Martino - Rewilding Argentina

Introduction

The Iberá Wetlands, situated in the Iberá Basin of Corrientes province, northeastern Argentina, represent one of the largest freshwater subtropical wetlands in South America, covering approximately 1.3 million hectares. Rich in biodiversity, these wetlands consist of marshes, lagoons, small rivers, and forests, which support a wide variety of species. Despite appearing vibrant and healthy, Iberá has faced substantial ecological disturbances due to human activities like agriculture, cattle ranching, and exotic forestry. These activities have led to significant biodiversity losses, prompting extensive restoration efforts by Rewilding Argentina.

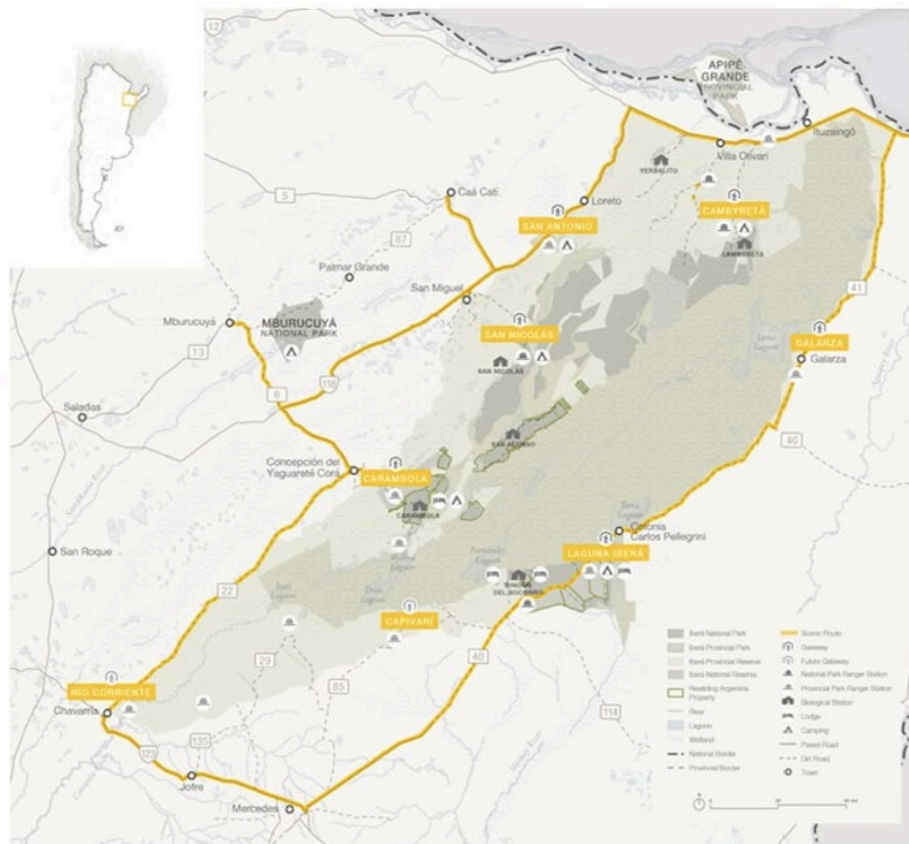


Figure 1. The Iberá Wetlands, in NE Argentina, encompass 1.3 million hectares and it is protected by a complex of federal (incl. Ramsar), provincial, and private parks and reserves.

Ecosystem Challenges

Historical exploitation of the land for rice farming, cattle ranching, and exotic pine plantations, coupled with intense hunting, has led to habitat degradation and a decline in native fauna, particularly large vertebrates.

Conservation and Community Engagement

Efforts to secure land for protected areas are paramount, involving the purchase of private lands deemed critical for conservation. Local communities are integrated into the conservation process, primarily through ecotourism, which provides sustainable economic opportunities.

Rewilding and Restoration Initiatives

Rewilding Argentina has initiated a comprehensive strategy focusing on species reintroduction and habitat rehabilitation. This includes:

- **Species Reintroduction:** Key species such as jaguars have been reintroduced, helping control the capybara population and restoring natural trophic cascades that balance ecosystem dynamics.
- **Infrastructure Development:** Development of ecotourism infrastructure promotes the area as a nature destination, engaging local communities economically.



Figure 2. Capybaras are the most abundant large herbivore in Iberá and preliminary data show that reintroduced jaguars heavily prey on them. Image: Sebastián Navajas/Rewilding Argentina

Current knowledge on the functional role of wildlife

1. Ecosystem Engineering

- **Caimans:**

- Influence spatial heterogeneity through nesting, feeding, and deposition sites.
- Increase habitat complexity and generate nutrient hotspots, benefiting plant communities and biodiversity.
- Create 'gator holes' which maintain water during dry periods, acting as refugia for various aquatic species and helping maintain the hydrological balance.

2. Nutrient Cycling

- **Giant River Otters:**

- Accumulate fecal material in latrines, creating hotspots of nitrogen and other nutrients benefiting terrestrial vegetation.
- Control fish populations, indirectly affecting aquatic vegetation and sediment dynamics, expected to restore balance to aquatic food webs and enhance biodiversity of primary producers and detritivores.

- **Jaguars:**

- Control capybara populations, indirectly affecting nutrient cycling by altering plant community structure and the decomposition rates of plant material.
- The reduction in capybara grazing alters species composition and increases vegetation height and biomass, which enhances landscape heterogeneity, modifies nutrient cycling, increases carbon sequestration, and may alter fire regimes.

3. Mediating Cross-Ecosystem Linkages

- **Giant River Otters and Caimans:**

- Act as vectors for nutrient and energy transfer between freshwater and terrestrial ecosystems, enhancing interconnectivity and ecological resilience.



***Figure 3.** A reintroduced female jaguar with two cubs roaming in the grasslands of Iberá. The restoration of this large predator started in 2021 and is still ongoing but their effects on capybara populations and grassland communities can be already observed in some areas. Image: Matías Rebak/ Rewilding Argentina*



***Figure 4.** The largest herbivore in Iberá, marsh deer is steadily recovering after a severe population decline caused by hunting and habitat degradation. Image: Matías Rebak/ Rewilding Argentina*

4. Herbivory and Vegetation Management

- **Capybaras:**
 - Impact vegetation through grazing, controlled by apex predators like jaguars to manage their numbers and influence on plant diversity, composition, and biomass.
- **Collared Peccaries:**
 - Facilitate seed dispersal and alter plant species richness and diversity through rooting behavior, which disturbs the soil and mixes in nutrients.
 - Their rooting behavior enhances plant species richness and diversity by turning over the earth and mixing nutrients.

5. Habitat Modification for Other Organisms

- **Caimans:**
 - Their 'gator holes' provide refuge for aquatic organisms during dry periods and maintain wetland hydrological needs.
- **Peccaries and Marsh Deer:**
 - Their trampling disturbs sediments, triggering the release of nutrients, creating habitat heterogeneity that enhances biological diversity and provides various ecological niches for other organisms.

Conclusion

The restoration of the Iberá Wetlands showcases a profound commitment to ecological integrity in one of Argentina's most diverse habitats. By reintroducing key species and involving the community in conservation efforts, Rewilding Argentina aims to establish sustainable coexistence between humans and nature. This project exemplifies the importance of integrating top-down and bottom-up processes in ecological restoration and serves as a vital model for similar efforts worldwide, emphasizing the critical roles that various species play in maintaining ecosystem health and functionality.

Case Study #10: Rewilding the Danube Delta

Mykhailo Nesterenko, Rewilding Ukraine

Introduction

The Danube Delta underwent significant changes in its ecosystems in the 20th century due to the decline of natural herbivores and the collapse of large-scale farming. This led to the spread of dense reed monocultures, causing a decline in biodiversity that had previously thrived in the delta's grasslands, meadows, and salt marshes. As the Danube Delta was declared a Biosphere Reserve, some feral herds of cattle and horses were left to roam in protected areas, showing a positive impact on biodiversity and vegetation in several regions of the delta. However, their influence remains debated in some areas.



Figure 1: Vision for restoration of Ermakov Island, Danube Delta, Ukraine (drawing by Jeroen Helmer)

Rewilding Efforts in Tataru-Daller

The Tataru and Daller islands have been part of an active rewilding initiative focusing on natural grazing systems. Introduced herbivores, including Ukrainian grey cattle and Hutsul horses, have significantly influenced the landscape. These animals prevent the encroachment of reed beds,

maintain riverine levees, and create meadow habitats by grazing on tall grasses, which reduces shrub and bramble encroachment, making the landscape more accessible for both wildlife and tourists.

Key Outcomes in Tataru-Daller:

- **Vegetation Management:** The grazing by cattle and horses prevents dense reed bed formation, promotes diverse meadows, and significantly reduced bramble grows and controls *Amorpha fruticosa*.
- **Tourism Impact:** Improved landscape passability and diversity attract more visitors, boosting local eco-tourism.
- **Challenges:** Prolonged flooding can lead to overgrazing on the remaining meadows, highlighting the need for balanced herbivore populations.



Figure 2: Release of Konik horses on Ermakov Island in 2020 (photo credit: Andriy Nekrasov / Rewilding Europe)

Rewilding Efforts in Ermakov-Chernovka

Ermakov Island has seen a wider variety of reintroduced species, including water buffalo, Konik horses, red deer, and fallow deer. These large herbivores create a mosaic of habitats by their grazing behavior, which includes maintaining meadows, suppressing reed beds, and opening up reed-dominated landscapes. This diverse natural grazing approach has a profound impact on vegetation and biodiversity, supported by ecological monitoring techniques like NDVI and SAVI, which show a positive trend in vegetation health.



Figure 3: Release of red deer on Ermakov in 2021 (Photo Credit: Andriy Nekrasov / Rewilding Europe)

Key Outcomes in Ermakov:

- **Vegetation and Biodiversity:** Grazing by water buffalo and horses has led to a significant increase in plant diversity and habitat complexity, creating favorable conditions for a wide range of insects, amphibians, and birds.
- **Economic and Ecotourism Benefits:** The presence of large herbivores like water buffalo and Konik horses has boosted tourism, making Ermakov a popular destination for wildlife enthusiasts.
- **Management Techniques:** Use of remote sensing for monitoring vegetation dynamics and assessing stress conditions in plants has provided valuable data to guide grazing management practices.



Figure 4: Introduction of water buffalo on Ermakov in 2019 (Photo Credit: Andriy Nekrasov / Rewilding Europe)

Comparative Analysis

Both Tataru-Daller and Ermakov-Chernovka islands demonstrate the importance of natural and semi-natural grazing systems in maintaining biodiversity and supporting ecosystem services. However, their approaches differ in scale and the variety of species involved:

1. Diversity of Herbivores:

- **Tataru-Daller:** Primarily uses grey cattle and Hutsul horses.
- **Ermakov-Chernovka:** Employs a wider range of species, including water buffalo, Konik horses, red deer, and fallow deer, enhancing its impact on habitat diversity.

2. Vegetation Management:

- **Tataru-Daller:** Focuses on meadow creation and control of reed beds, with occasional challenges of overgrazing during floods.
- **Ermakov-Chernovka:** Uses detailed monitoring tools to manage a diverse landscape that supports both dry and wetland habitats, resulting in a highly complex and resilient ecosystem.

3. Socio-Economic Impact:

- Both regions aim to boost ecotourism, but Ermakov-Chernovka has a more structured approach with active development of tourism infrastructure, thanks to its varied landscape and larger herbivore populations.

4. Impact on Wildfire Prevention:

- Both areas benefit from reduced fire risks due to grazing activities, but Ermakov Island's diverse herbivore population provides a more comprehensive approach to managing vegetation and preventing fires.



Figure 5: View from Tourism Infrastructure (Photo Credit: Kateryna Kurakina / Rewilding Ukraine)



Figure 6: Tourism Infrastructure (Photo Credit: Andriy Nekrasov / Rewilding Europe)

Conclusion

The rewilding strategies in Tataru-Daller and Ermakov-Chernovka islands highlight the effectiveness of reintroducing large herbivores in managing habitats and boosting biodiversity.

Ermakov-Chernovka's broader approach with diverse species and advanced monitoring techniques sets a stronger foundation for ecological restoration and sustainable tourism compared to Tataru-Daller's more limited but focused efforts on grazing management. Both areas, however, demonstrate the critical role of grazing systems in preventing habitat degradation, supporting local economies, and enhancing the overall resilience of the Danube Delta ecosystem.



Figure 7: Tourists watching water buffalo taking a bath in the Danube River (Photo Credit: Andriy Nekrasov / Rewilding Europe)

Case Study #11: U Minh Animals and Wetlands, Vietnam

Russell Gray, *Re:wild*

Introduction

The U Minh Wetlands in southern Vietnam are a seasonally inundated ecosystem within the Greater Mekong Subregion, historically dominated by *Melaleuca* forests, reed meadows, and swamps. However, landscape conversion due to forest fires, poor management, and human activities like agriculture and plantations have led to significant degradation. Efforts to control peat degradation and fire risk, such as canal systems, have disrupted natural hydrology, dried some areas and concentrated water in others, worsening fire risks. Native forests have largely been replaced by plantations of acacia, guava, and banana, with remaining *Melaleuca* forests recovering slowly and becoming fragmented.

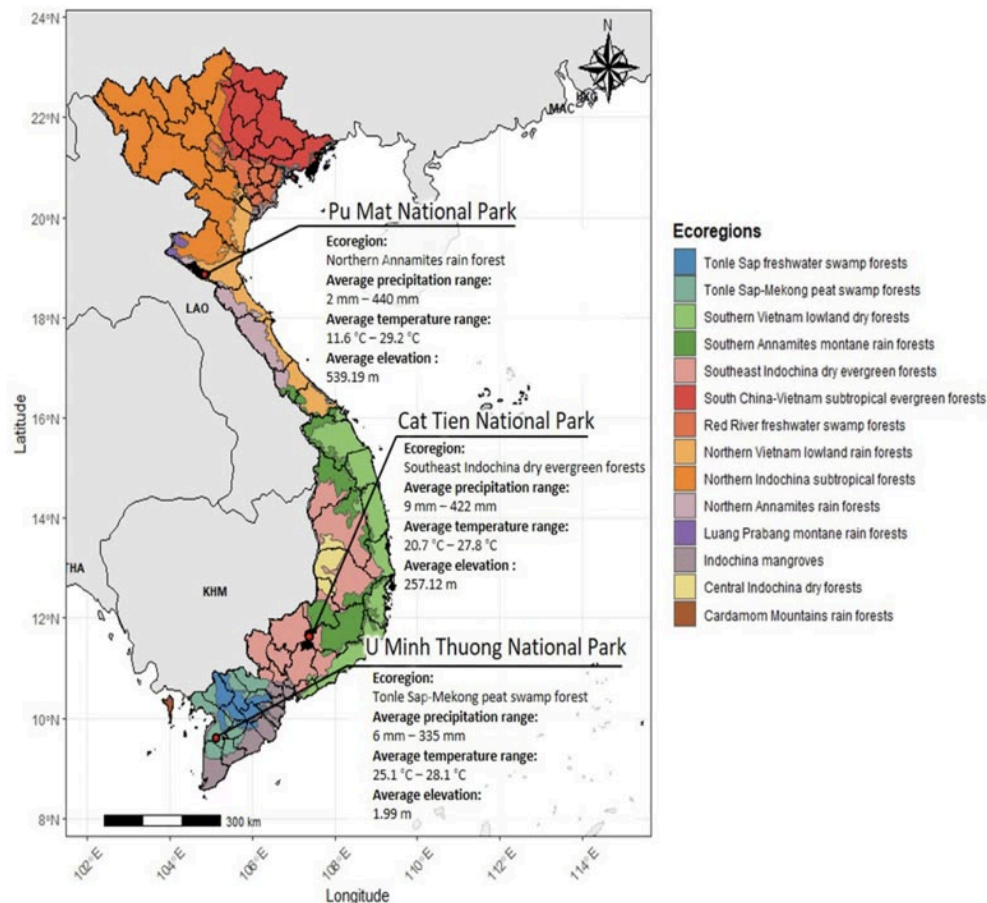


Figure 1. Map of study sites in Vietnam where pangolins were tracked, with an ecoregion shapefile (Dinerstein et al. 2017), and general information on climate.

The conservation and restoration efforts in the U Minh wetlands have been actively carried out through various ecological assessments since the 2000s, primarily focusing on species status, population distribution, and impact analysis. The unique wetland ecosystem, once heavily damaged during the American War and further threatened by human activities like shrimp farming, has gradually recovered.

Monitoring and research, while primarily conservation-based, have provided valuable insights into the role of key species in ecosystem processes. In this case study, the focus is on the wildlife commonly observed in U Minh Thuong and U Minh Ha, drawing from camera trap data and anecdotal evidence to understand their ecological roles.



Figure 2. U Minh Thuong National Park became the eighth Ramsar site in Vietnam and the 2,228th in the world in 2016. Image: VNA)

Known Knowledge

Ecosystem Engineering

Wildlife in the U Minh wetlands play various roles as ecosystem engineers, impacting habitat structure and nutrient cycling:

- **Waterbirds:** These birds create nesting sites that influence vegetation structure and contribute to nutrient cycling through defecation, enriching the soil.
- **Sunda Pangolins:** By foraging and burrowing, pangolins disturb the soil, potentially enhancing nutrient cycling. Their deep burrows serve as water sources during the wet season, benefiting other species and contributing to ecosystem dynamics.

- **Otters:** Their dens alter microhabitats, providing shelter for various species, and their presence may influence overall ecosystem cohabitation.
- **Civets:** These animals contribute to vegetation structure through their feeding habits and enrich the soil with their waste.
- **Turtles:** Turtles disturb sediment and aquatic vegetation, which impacts habitat structure and nutrient availability.
- **Long-tailed Macaques:** By foraging and dispersing seeds, macaques influence forest regeneration and structure.

Seed Dispersal

Various species aid in seed dispersal, maintaining plant diversity, though some also spread non-native species:

- **Waterbirds:** These birds disperse seeds through droppings, aiding in plant diversity as well as in the spread of invasive species.
- **Otters** Transport seeds unintentionally via fur or between water bodies
- **Civets:** Civets are significant seed dispersers in wetlands, as they consume large amounts of fruit and defecate seeds intact, aiding in plant regeneration and restoration. However, in areas like U Minh, where fruit plantations are common, civets may prefer non-native fruits, spreading invasive plant species and potentially harming native plant communities.
- **Turtles** Transport seeds through the gut or by carrying aquatic flora and seeds on their bodies.
- **Long-tailed Macaques:** Contribute to seed dispersal through their diet and behavior, though their preference for non-native fruits may also spread invasive species.

Nutrient Cycling

Several species contribute to nutrient cycling through their foraging and waste deposition:

- **Waterbirds:** Their droppings enrich the soil, benefiting wetland vegetation.
- **Pangolins:** Pangolins' burrowing and foraging mix the soil, contributing to nutrient cycling.
- **Otters, Civets, and Turtles:** These species also contribute to nutrient cycling through their feeding and waste.
- **Macaques:** Their diet and waste help cycle nutrients in the ecosystem, influencing forest regeneration.

Top-Down and Bottom-Up Processes

Species in the U Minh wetlands influence both top-down and bottom-up processes within the ecosystem:

- **Waterbirds:** As predators of small aquatic organisms and prey for larger species (like pythons), waterbirds play dual roles in regulating populations.
- **Pangolins:** They control insect populations while being influenced by the availability of insects.
- **Otters:** These predators regulate populations of fish and crustaceans, influencing aquatic dynamics.
- **Civets and Turtles:** Civets control invertebrate populations and spread seeds, while turtles regulate aquatic vegetation and invertebrates.
- **Macaques:** As seed dispersers and foragers, macaques influence forest dynamics and are affected by habitat conditions and food availability.

Speculative Claims

The extirpation of major carnivores, such as Siamese crocodiles and other large predators, likely has had long-term effects on the biodiversity and structure of the U Minh wetlands. The absence of these top predators has potentially altered prey dynamics, with unknown impacts on the broader ecosystem.

Conclusion

The wildlife of the U Minh wetlands plays critical roles in maintaining ecosystem balance through various processes such as ecosystem engineering, seed dispersal, and nutrient cycling. Although direct academic research on these functions is limited, camera trap data and field observations provide valuable insights. As conservation efforts continue, understanding the ecological roles of these species will be key to enhancing the resilience and biodiversity of the U Minh wetlands. Continued monitoring and focused research are essential to address the challenges posed by habitat destruction and invasive species.