

# The Role of Wildlife in Sustainable Forest Management

## Part 3. Wildlife and its wider role

**Jonathan Spencer** and **Andrew Stringer** conclude this three-part series explaining why wildlife diversity matters to foresters.

This is the third in a three-part series exploring the role of wildlife in supporting sustainable forestry in UK forests and plantations. Part 1 (Spencer and Tew, 2021) looked at nutrient flows as illustrated by ospreys in northern plantations, highlighting the flow of nutrients as a critical part of forest function. Part 2 (Spencer and Elliott, 2021) explored the importance of wetlands and water courses, and the importance of beavers in promoting biodiversity and the natural management of water within forests. This article looks at the wider role of wildlife in forests whose primary role is timber and fibre production. Biodiversity is the key 'regulating and maintenance' ecosystem service (Dasgupta, 2021) that imparts productivity, resilience, functionality and diversity to forest ecosystems. We focus here on both the unseen, largely unsung biodiversity of soils, small invertebrates and plants, as well as the more enigmatic wildlife, especially those that may be rare or missing in our present-day forests, such as martens, migratory fish and minor tree species. We explore the varied roles they might play in sustaining forest productivity and resilience in the future. The reinstatement of missing ecological processes into manmade forests is likely to prove of considerable importance in securing long-term forest resilience and productivity allowing forests to thrive in an uncertain future.

Many species have limited individual impact on forests as producers of timber, fuel and fibre. It is difficult to see how the chequered skipper (*Carterocephalus palaemon*) in the woods of the Midland clays makes a measurable difference to forest production or performance. Individually, species such as these are best regarded as 'cultural natural

capital', adding to our enjoyment of forests and their wildlife, and hence justifying their conservation or reintroduction. Collectively though, the diversity and abundance of species imparts enhanced functionality and an increased efficiency in key processes. These include harnessing or cycling of nutrients, the pollination of flowers or the distribution of seeds and fruits. Diverse species complexes compete with and predate pest and problem species, imparting resilience against damage and change. Conversely, in the face of structural simplicity and species uniformity, pest and disease outbreaks are inevitable. Individual species fall into functional categories that allow ecosystems to perform, as primary producers or decomposers, predators or prey, as pollinators or as critical elements in forest soils. Many species play several roles simultaneously or throughout their life histories; adult hoverflies, for example, (Figure 1) can be pollinators, while



Figure 1. Hoverflies play a very important role in forest ecology in both adult and larval forms. The hoverfly (*Dasysyrphus tricinctus*) is a common and widespread arboreal hoverfly. The adult, illustrated here, pollinates flowers of forest trees and vegetation while the larvae has been recorded as a predator of the pine sawfly (*Neodiprion sertifer*).

their larvae can be either predators or detritivores, enhancing the decomposition and recycling of rotting plant material (Ball and Morris, 2015).

With climate change and the biodiversity crisis looming, the restoration and enhancement of forest biodiversity, the

recovery of richer and more functional forest ecosystems and the enhancement of carbon capture both above ground and in forest soils should become key aims for 21st century foresters and placed on a more systematic footing (Thompson et al., 2009).

### Wildlife and Forestry Standards

An important driver for improving woodland wildlife values over the last 30 years has been the development of standards defining what constitutes sustainable woodland management.

In Helsinki in 1993 European Forestry Ministers adopted General Guidelines, and at Lisbon in 1998 they followed up by adopting the Pan-European Operational Level Guidelines (PEOLG). This led, in 1998, to the UK Government publishing a UK Forestry Standard (UKFS) to reflect these guidelines by setting out a vision for the UK's woodlands together with regulations and guidance for their management.

Separately, the 1990s also saw great interest in the development of non-governmental voluntary certification standards designed to verify whether individual woodlands were responsibly managed on the ground. The Forest Stewardship Council (FSC) and later the Programme for the Endorsement of Forest Certification (PEFC), developed global certification standards to be adapted for use at a national level.

Wood products certified through these schemes are in much demand as they provide a widely recognised way to inform customers that timber products come from responsibly managed sources. This prompted the development of the UK Woodland Assurance Standard (UKWAS) in 1999 as a bespoke UK certification standard based on the governmental and voluntary standards. By 2021, 1.41 million ha, 44% of the UK's woodland area, were independently certified to UKWAS.

Although not necessarily stated in terms of ecosystem processes, the role of wildlife in forestry is explicitly supported in both the UK Woodland Assurance Standard and the UK Forestry Standard adopted by the country Forestry agencies (Forestry Commission, 2017; UK Woodland Assurance Standard, 2020). Both standards are currently under review and biodiversity aspects are likely to be strengthened.

The UKWAS requires that 15% of the forest management unit is managed with conservation and the enhancement of biodiversity as the primary objective and seeks to ensure that biodiversity and other values are enhanced across the woodland.

The UKFS specifically requires:

- A maximum of 75% allocated to any one single tree species, promoting tree species diversity.
- 10% of other timber producing tree species.
- 5% native broadleaved trees or shrubs.
- 10% open ground or ground managed for the conservation and enhancement of biodiversity as the primary objective.

Both standards require the retention and accumulation of deadwood and the protection of forest soils, water courses, existing wildlife habitat, ancient and veteran trees, protected areas, long term retentions and rare species.

Adoption and implementation of standards has raised the quality of management in UK woodland and continues to provide an excellent platform upon which to build biodiversity and its recovery into managed woods and forests.

*Peter Wilson (Chair, UKWAS Review and Revision Working Group) & Jonathan Spencer*

## Why wildlife diversity matters to foresters

### *Maximising productivity*

As an 'enabling' ecosystem service, biodiversity is essential to forest ecosystem function. Five key trophic levels interact: soil biodiversity, plants and plant diversity, herbivores, carnivores, and the detritivores and decomposers that break down and recycle all back into the system. All are critical to the efficient capture of light, water and nutrients, generating the highest net primary productivity (Borer and Gruner, 2014).

This effect goes far beyond simply reducing competition – the higher the plant species diversity, the higher the net primary productivity, with each species efficiently exploiting their place within an ecosystem (Gamfeldt et al., 2013). We have known for many decades that individual plant growth in monoculture is much slower than in a diverse species mix (Tilman, Wedin and Knops, 1996). Different species utilise different forms of nitrogen, have roots reaching to different depths, and use soil water at different times. Positive interactions may include better rainfall capture by mixtures or nutrient cycling at faster rates (Brockhoff et al., 2017). Plant communities that have co-evolved over millions of years show better niche partitioning, more mutualisms, and higher overall productivity (Flombaum and Sala, 2008). These principles are now being utilised directly in productive forestry through Forest Development Types (Haufe, Kerr and Stokes, 2021). A global meta-analysis found that on average mixtures were 15% more productive than their equivalent monoculture. Interestingly, this effect increased in areas with higher rainfall (Jactel et al., 2018).

### *Redundancy and resilience*

Resilient ecosystems harbour species 'redundancy', where suites of less common species provide spare capacity and the ability to respond swiftly when ecological conditions change. These species increase in prominence due to changes in the environment such as increases in temperature, drought, waterlogging, nutrient status or disturbance. This redundancy can be found at all trophic levels, from the many thousands of species of fungi and bacteria in forest soils to the much smaller suite of mammalian and avian predators once found in our forest ecosystems. The presence of these minor species offers the ecosystem what Elmqvist et al. (2003) have dubbed 'response diversity', which is defined as the range of reactions to environmental change among species contributing to the same ecosystem function.



*Figure 2. With their recovery and increase in larger woods and forests across the UK, goshawks (Accipiter gentilis) are beginning to have a significant impact on grey squirrel numbers through direct predation. In concert with other predators, notably pine martens but also polecat and wild cat, in the future, the impact of grey squirrels on forestry interests are likely to be minimal. The image is of a captive bird; photographing the wild bird is exceptionally difficult. (Photo: Larry James)*

### *The importance of predators*

Predators can naturally cap abundant prey populations. When predators are lost, single species can become hyper-abundant, leading to negative impacts for both foresters and wider ecosystems. Indeed, the presence of predatory species, of all sizes, increases plant biomass relative to the same community lacking predators (Borer and Gruner, 2014). This is largely due to changes in herbivore abundance and behaviour. A suite of such predators is more effective at dampening down outbreaks of prey species than just one species.

The trend towards the recovery of all the major predators of grey squirrels illustrates this well and is supported by emerging anecdotal evidence from woods with significant numbers of these critical predators, notably goshawk (Figure 2) in southern broadleaved woods (such as Bentley Wood in Wiltshire) and the increasing number of martens in the New Forest and the Forest of Dean. It is widely thought that had the grey squirrel been met by a complete suite of smaller forest predators on its introduction, such as goshawk, marten, polecat and wildcat, it may well have failed to become so widely established. As we know it was met with a complete absence of such species as a result of Victorian and Edwardian keepers eliminating these species from the landscape (Spencer et al., 2018).

### *Soil health, drought survival, tree stress and disease vulnerability*

Biodiversity in forests supports soil and tree health in very diverse ways. These can be direct, through the activities of mycorrhizal species, or indirect, through the activity of resource competition from species of soil fungi and



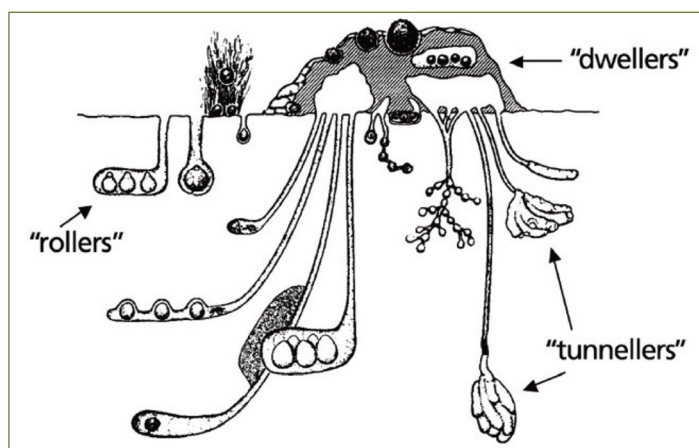


Figure 3. Diversity in dung beetle species. Though superficially very similar in appearance dung beetles deal with animal dung in a wide variety of ways and in different states of decomposition, aerating and fertilising soils as they do so and greatly enhancing soil drainage. (From Floate, 2011)

invertebrates. Moles, earthworms and dung beetles are all important in creating, aerating and draining forest soils, and consuming fallen leaves or animal dung that harbour plant and animal pathogens. All three promote the recycling of nutrients from forest litter but are constrained by the absence of larger herbivores generating dung, or within monocultural stands of trees that generate mor humus layers (notably in beech, spruce, and other conifer species) whose litter is characterised by an absence of earthworms.

By comparison tree species such as holly, hornbeam and lime generate mull soils (Langenbruch, Helfrich and Flessa, 2012). The activities of voles and other small mammals facilitate soil aeration and drainage and fungal spore dispersal (Terwilliger and Pastor, 1999). The presence of dung beetles can have a range of positive effects (Figure 3). In one study, their presence “enhanced soil water retention by 10% and promoted growth in plants subjected to drought by 280%, relieving the impacts of water stress on plants. Under drought conditions, plants grown with dung beetles had c.30% more leaves and were over twice as tall as those without dung beetles” (Johnson et al., 2016). A variety of pressures including climate change, drought and decreasing soil health can all lead to increasing tree stress levels, declining timber yield and lower biomass accumulation rates.

Tree associations with mycorrhizal fungi are of particular importance to foresters. It is now widely recognized that mycorrhizal fungi are in large part responsible for delivering

carbon (C) into soils. They can also improve the nutrition of host plants that need to cope with low nitrogen (N) and phosphorus (P) supply. Mycorrhizas benefit plants by helping them tolerate drought stress, heavy metal pollution and pathogens, via both nutritional and direct effects (Smith and Read, 2008). Trees benefit from associations with more than one mycorrhizal species and many trees may be associated with more than one fungal species. However mycorrhizal fungi in particular can suffer from excess nitrogen deposition and this can have a critical impact on both tree performance and the active sequestration of carbon into forest soils (Suz et al., 2022). The diversity of mycorrhizal species in forest soils itself imparts efficiency of resource use from soils and underlying minerals. This diversity of biochemical capabilities is illustrated in Figure 4.

#### Nutrient cycling throughout the forest

A key determinant of tree growth rate is nutrient availability. Wildlife plays an important role in husbanding, recycling and redistributing important nutrients around the forest on a far larger scale than is widely appreciated. It is now recognised that in the past large mammals once drove nutrient flows across whole landscapes and promoted access to recycled nutrients in dung and other wastes in very significant amounts, sometimes on a continental scale.

### “Wildlife plays an important role in husbanding, recycling and redistributing important nutrients.”

This process worked against the flow of nutrients from weathering continents to oceanic sediments in an interlinked system “with whales moving nutrients from the deep sea to surface waters, anadromous fish and seabirds moving nutrients from the ocean to land, and terrestrial megafauna moving nutrients away from hotspots, such as river floodplains, into the continental interior... Larger animals are

disproportionally important in transferring nutrients across landscapes, acting as “arteries” that increase nutrient diffusion rates by at least an order of magnitude” (Malhi et al., 2016).

In the rather simplified forest ecosystems found in much of Britain we encourage nutrient loss from the system (in the form of leaching, timber extraction and the export of deer carcasses), and this is only just in balance with nutrient imports from soils and biotic drivers such as birds (Spencer and Tew, 2021). Enhancing the natural input and cycling of forest nutrients (from soil fungi and the weathering of underlying rocks), while husbanding their loss from the

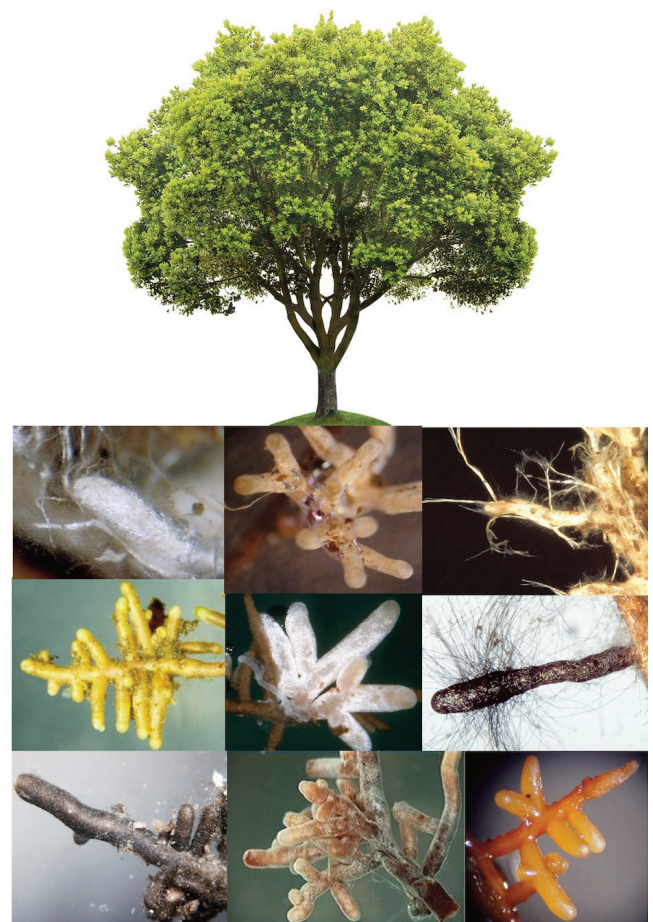


Figure 4. The range of mycorrhizal fungi and the wide array of biochemical capabilities they demonstrate in extracting nutrients from weathering bedrock and other materials is compared here to the capabilities of an electric drill and the wide array of attachments capable of undertaking very different tasks. (Illustration courtesy Professor Martin Bidartondo. Root and mycorrhizal images thanks to [www.deemy.de](http://www.deemy.de))

system, by restoring biodiversity, is critical to the recovery of forest function and ecology.

#### Natural regeneration

Natural regeneration has long been promoted as an effective way to establish trees. More recently its use has been advocated to promote genetic diversity within tree stands to enhance forest resilience and to establish extensive new woodlands on former arable or other open land (Woodland Trust, 2020). However, the reliability of natural regeneration can be variable, particularly in the establishment of timber stands of desired density and form. Erratic recruitment, variable spacing, and the problem of recording and reporting success when in receipt of state support are all cited as challenges.

The role of wildlife in both enhancing or suppressing natural regeneration is also complex. Wildlife can be useful in increasing the reliability of natural regeneration through dispersing seeds across landscapes (e.g. jays and wood mice), assisting with tree recruitment (e.g. wild boar rootling, cattle suppressing competitive grasses), as well as predator suppression of seed predators (e.g. small mammal suppression by foxes, martens, polecats and wildcats). However, there are also potential negative impacts on natural regeneration and tree quality by larger herbivorous mammals when at high density, notably deer.

#### Overall principles

The critical influence of biodiversity on forest ecosystem function is summarised below (based on Cardinale et al., 2012):

- The functional traits of organisms are very varied and collectively have large impacts on ecosystem processes.
- Species diversity at all trophic levels increases the efficiency with which plant and animal communities capture essential resources (nutrients, water, sunlight, prey), recycle them within the plant and animal community and produce biomass. As an example, a diversity of plant litter enhances decomposition and recycling rates of biologically essential nutrients. Biodiversity loss at all levels reduces this efficiency.
- Diverse communities contain key species that have a disproportionately large influence on productivity and contain species with varying functional traits between organisms, increasing total resource capture.
- The influence of biodiversity on ecosystem processes is non-linear; productivity declines at an accelerated rate as biodiversity loss increases.

**Table 1. Wildlife and Forests; Ecosystem Services and Ecological roles**

	<b>Example species</b>	<b>Ecological and ecosystem service role</b>	<b>Forestry benefits</b>	<b>Forestry issues</b>
Timber trees	Oak, ash, spruce, pine.	Provisioning role; timber woodfuel and fibre. Above ground carbon sequestration. Dominant vegetation; structural determinant for forest ecosystem. Main determinant of forest ecology & function.	Timber provision and income source.	Establishment and management to ensure timber quality.
Minor trees and other vegetation	Lime, hornbeam, willows, hazel, aspen, rowan.	Provisioning role; timber, woodfuel, fibre. Regulating and maintenance services. Diversity of resource use (light, soil water and nutrients) within forest, above and below ground. Above ground carbon sequestration. Supporting service in pollinators and insect diversity.	Wood fuel and fibre provision  Understorey establishing timber quality in main stand. Soil improvement via leaf fall. Supporting resilience through support of insect and fungal diversity.	Competition for space and nutrients for other more valuable timber tree species.
Small herbivores	Voles, squirrels, rabbits, caterpillars, sawfly larvae.	Regulating and maintenance services. Nutrient cycling, vegetation cycling, nutrient dispersal. Seed and spore dispersal. Supporting predator populations at higher trophic levels.	Nutrient cycling within forest. Supporting predator and parasite diversity.	Damage to tree establishment, tree growth and tree quality.
Large herbivores	Deer, cattle, ponies, wild boar.	Regulating and maintenance services. Some provisioning services via harvest of meat and venison. Generate structural and species composition diversity in vegetation. Nutrient cycling, vegetation cycling, nutrient dispersal. Cycle key forest nutrients on larger scale. Recycling cellulose grass thatch into insect diversity and abundance via dung.	Nutrient cycling within forests and reduction in vegetation competition.	Damage to tree establishment and tree quality.
Detritivores and saproxylic invertebrates	Soil fungi, woodlice, beetles and earthworms, deadwood fungi and invertebrates.	Regulating and maintenance services. Recycling of dead and decaying material, organic wastes and deadwood.	Promotion of healthy forest soils	Some loss of productivity from deadwood materials and maturing trees (as future veterans) retained on site.
Meso predators	Martens, polecat, wildcat, goshawk.	Regulating and maintenance services. Control of small mammal populations notably grey squirrel.	Control of small mammal populations notably grey squirrel.	None
Larger predators	Lynx, wolf.	Regulating and maintenance services. Potential control of larger mammal populations.	Potential control of deer and promotion of tree recruitment. Cycling of key nutrients notably calcium and phosphorous in prey carcasses.	Relationships with farming neighbours.
Large soil organisms	Worms, moles and dung beetles.	Regulating and maintenance services. Recycling of dead and decaying material. Soil drainage and aeration, and hence promotion of soil fungal activity.	Promotion of healthy forest soils.	None
Fish; migratory fish	Trout, salmon, eels.	Regulating and maintenance services. Recycling of nutrients from ocean to water courses.	First stage in recovery of biological productivity to forests, especially in upland locations.	None

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- An accelerated rate of productivity decline in response to greater biodiversity loss may amount to major regime shifts (from forest to grassland or heath, for example).
- Loss of diversity across trophic levels (e.g. loss of top predators) has the potential to influence ecosystem function even more strongly than diversity loss within trophic levels, due to the loss of the functional group.

Cardinale et al. (2012) lists four further effects of biodiversity that are becoming increasingly evident:

- The impacts of biodiversity loss on ecological processes may well rival the impacts of the other major global drivers of environmental change, such as fires, eutrophication of soils and rising carbon concentration in the atmosphere.
- The influence of biodiversity grows over time and increases with scale. Small-scale studies over limited periods may underestimate the significance of biodiversity on ecosystem function.
- Maintaining ecosystem processes at many places and over longer timescales requires far greater biodiversity than does a single process at a single place and time.
- Biodiversity is thus an enabling service of ecosystems, promoting and supporting the other more self-evident services of importance to society such as clean water, timber production, fuel and climate mitigation.

The varying roles played by forest biodiversity in supporting forest ecosystem services and function are presented in Table 1.

### The need for change

The UK is one of the most nature-depleted countries in the world, ranked 189th of 218 countries measured on a biodiversity intactness index (Scholes and Biggs, 2005). As such there are great opportunities within modern British forests and plantations to increase forest biodiversity, biological abundance, and the ecosystem services they provide. British forests, in particular the extensive plantations established over the last century, are often lacking in forest biodiversity. This is largely a feature of their very recent origin on nutrient poor and previously unforested ground, coupled with their history of establishment as extensive tracts of the most productive timber species suited to the site. Climate change and the steep increase in the occurrence of novel insect pests and fungal pathogens (Freer-Smith and Webber, 2017) now challenges these forests. Degraded and simple ecosystems are far more at risk from invasion by these novel pests than complex mixed stands (Elmqvist et al., 2003; Kimmins, 2004). Foresters have long been engaged in nature conservation and species recovery programmes within their forests (Dennis, 2021). It is now critical to their future as production forests yielding timber, fibre and feedstocks for the future low carbon economy, whilst sustaining forest soils, tree health and resilience.

**Table 1. Wildlife and Forests; Ecosystem Services and Ecological roles ...continued**

	<b>Example species</b>	<b>Ecological and ecosystem service role</b>	<b>Forestry benefits</b>	<b>Forestry issues</b>
Fish; coarse fish	Rudd, dace, perch, chub, tench.	Regulating and maintenance services. Recycling and husbanding of nutrients in water from leaching, silts, dead and decaying material and wastes.	Recovery and recycling of materials from surrounding forest.	None
Piscivores; birds and mammals	Osprey, herons, goosander, kingfisher, otter	Regulating and maintenance services. Chief means of transfer of nutrients from forest water bodies, and more distant water bodies, to forest and plantation ecosystems.	Maintenance of forest productivity, notably recycling of P lost in timber export.	None
Beaver	European beaver	Regulating and maintenance services, supporting biodiversity and flood regulation, water quality and carbon sequestration. Primary architect of wetland creation and maintenance. A keystone species cost effectively supporting considerable biodiversity and abundance.	Biodiversity, habitat creation and habitat quality maintenance; husbanding of forest nutrients; supporting forest productivity and soil health.	Flooding impact on access infrastructure e.g., culverts and bridges. Some loss of potential timber trees on edges of water courses outside UKFS buffer zones.



### Restoring species

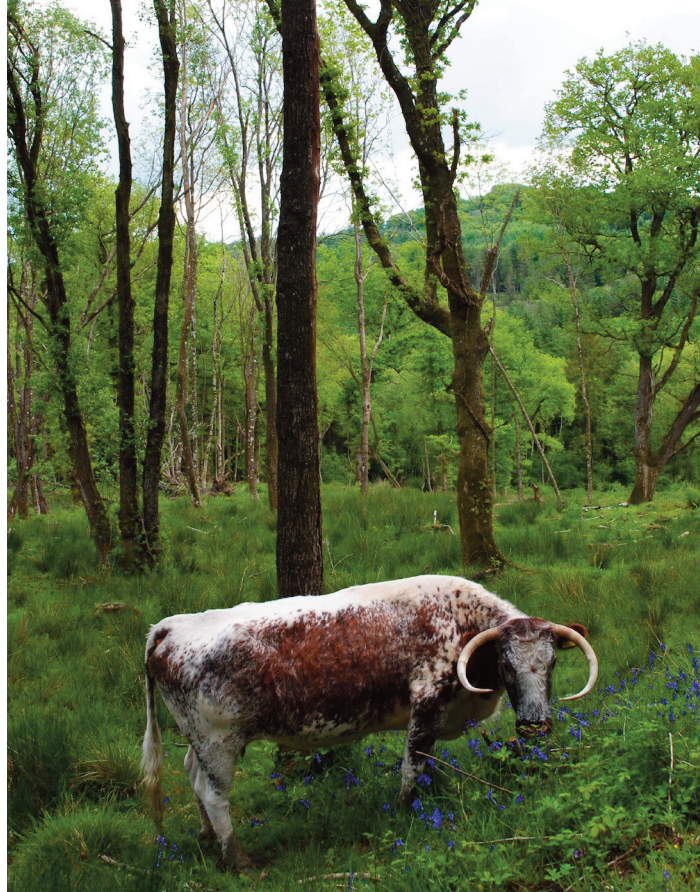
A select suite of species have ecosystem-wide impacts, and these are known as keystone species or ecosystem engineers. Many of these could be restored to our woodlands:

- All larger forests and wooded landscapes could support the recovery of avian raptors and the smaller mammalian predators, notably pine marten, polecat and wildcat.
- Most larger forests and woodlands will inevitably host and come to accommodate wild boar as they spread throughout the UK.
- All woods and forests with suitable water courses can accommodate beaver populations at some level as they recolonise the UK landscape.

Large carnivores such as lynx and wolf are beyond the scope of individual forest management organisations to deliver. Their return, should they eventually be restored to the UK landscape, will be a societal choice taken at the highest levels. Their presence in forests with regard to deer control or nutrient flows within forest ecosystems should however be considered as potential benefits to UK forests and forestry interests.

Ecological 'replacements' for extinct keystone species can also be an option. For instance, domestic cattle (Figure 5), pigs, and Exmoor ponies can stand in for wild cattle (the aurochs), wild boar and wild horses, to a considerable extent replicating their ecological role and impact. The benefits would include:

- Improved soil drainage, function, and fertility.
- Improved access to plant nutrients by timber tree species.
- The generation of insect diversity and abundance from plant material, notably as animal dung converted into dung beetle abundance.
- The wider distribution of nutrients throughout the forest.
- The creation of warmer, sunny areas of shorter sward (to the benefit of insect and fungal diversity, grouse chicks and other bird species requiring shorter and drier turf).
- An increase in prey for bird species requiring larger insect prey such as nightjars, shrikes, small raptors and owls.
- The creation of habitats important for rarer plant species and fungi (notably *Boletus* spp) that require short, more tightly grazed swards.



*Figure 5. English longhorn cattle are now important components in the management of The Forest of Neroche in Somerset. Established in 2009 by Forestry England and the Blackdown Hills Trust, the core herd is owned by Forestry England while the support payments and surplus animals are retained by the Trust. Some 220ha is grazed by the cattle in some seven grazing units, soon to be merged into one larger extensive forest unit. This herd is confined within perimeter fences; other projects have successfully adopted the use of invisible 'no fence grazing technology' fencing systems to manage livestock. (Photo: Forestry England)*

Not all of our native wildlife can be fully restored to all our forests, nor can their domestic analogues, such as cattle or ponies, be fully integrated in all forest situations. However, an understanding of their role in forest ecology allows for a more complete exploration of potential opportunities, and for an appreciation of limitations in their absence.

### Conclusions and way forward

Species are interdependent. For example, to promote a diversity and abundance of dung beetles, we need a diversity and abundance of dung-producing species. We cannot support a full range of flowering plants in our forests unless there is a complementary range of pollinators that suit them. We cannot pick and choose parts of an ecosystem at random to promote, we either have a functioning community or a partially degraded and impoverished one. Some species or features, e.g. deadwood habitats and beavers, are particularly good examples, and are far more critical than others.

We should be evolving our existing forests to be resilient and adaptable, with:



- Diverse genetics (through planting choices and natural regeneration).
- Diverse stand composition (through the adoption Forest Development Types (Haufe, Kerr and Stokes, 2021)) and forest planning.
- Diverse within-stand age structure (through the adoption of CCF).
- Robust, intact and healthy soils.
- Abundant and diverse wildlife at each trophic level.
- An abundance of deadwood and woody debris, and veteran trees.
- Wetlands and watercourses, open habitats, and a variety of early successional growth.
- The recovery of ecological processes via the reinstatement of grazing, browsing and predatory mammals where possible (Figures 2 and 5).

The restoration of key biotic drivers – browsing cattle, beavers and ponies, predatory birds and mammals, a wide range of tree and plant species and an even wider range of insects and fungi – are all prerequisites to addressing both the biodiversity and the climate challenges facing our forests in the coming century.

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## References

- Ball, S. & Morris, R. (2015) *Britain's Hoverflies: A Field Guide*. Princeton University Press.
- Borer, E.T. & Gruner, D.S. (2014) III.6 Top-Down and Bottom-Up Regulation of Communities. In *The Princeton Guide to Ecology*, Princeton University Press.
- Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., Lyver, P.O.B., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I.D., van der Plas, F. & Jactel, H. (2017) Forest Biodiversity, Ecosystem Functioning and the Provision of Ecosystem Services. *Biodiversity and Conservation*, **26**:3005-3035.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity Loss and Its Impact on Humanity. *Nature*, **486**:59-67.
- Dasgupta, P. (2021) *The Economics of Biodiversity: The Dasgupta Review*

- Abridged Version. HM Treasury, London.
- Dennis, Roy. (2021) *Restoring the Wild: Sixty Years of Rewilding Our Skies, Woods and Waterways*. William-Collins, London.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response Diversity, Ecosystem Change, and Resilience. *Frontiers in Ecology and the Environment*, **1**(9):488-494.
- Floate, K.D. (2011) Arthropods in Cattle Dung on Canada's Grasslands. In *Arthropods of Canadian Grasslands (Volume 2): Inhabitants of a Changing Landscape*. Biological Survey of Canada.
- Flombaum, P. & Sala O.E. (2008) Higher Effect of Plant Species Diversity on Productivity in Natural than Artificial Ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **105**(16):6087-6090
- Forestry Commission (2017) *The UK Forestry Standard*. 4th ed. Edinburgh.
- Freer-Smith, P.H. & Webber J.F. (2017) Tree Pests and Diseases: The Threat to Biodiversity and the Delivery of Ecosystem Services. *Biodiversity and Conservation*, **26**:3167-3181.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusi ski, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J. & Bengtsson, J. (2013) Higher Levels of Multiple Ecosystem Services Are Found in Forests with More Tree Species. *Nature Communications*, **4**:1340.
- Haufe, J., Kerr, G. & Stokes, V. (2021) Forest Development Types, an essential tool for diversifying stands in Britain. *Quarterly Journal of Forestry*, **115**(3):175-182.
- Jactel, H., Gritti, E.S., Drössler, L., Forrester, D.I., Mason, W.L., Morin, X., Pretzsch, H. & Castagneyrol, B. (2018) Positive Biodiversity–Productivity Relationships in Forests: Climate Matters. *Biology Letters*, **14**:20170747.

- Johnson, S.N., Lopaticki, G., Barnett, K., Facey, S.L., Powell, J.R. & Hartley, S.E. (2016) An Insect Ecosystem Engineer Alleviates Drought Stress in Plants without Increasing Plant Susceptibility to an Above-Ground Herbivore. *Functional Ecology*, **30**(6):894-902
- Kimmins, J.P. (2004) *Forest Ecology – A Foundation for Sustainable Forest Management and Environmental Ethics in Forestry*. Prentice Hall, Upper Saddle River, New Jersey.
- Langenbruch, C., Helfrich M. & Flessa, H. (2012) Effects of Beech (*Fagus Sylvatica*), Ash (*Fraxinus Excelsior*) and Lime (*Tilia Spec.*) on Soil Chemical Properties in a Mixed Deciduous Forest. *Plant and Soil*, **352**:389-403.
- Malhi, Y., Doughty, C.E., Galetti, M., Smith, F.A., Svenning, J.C. & Terborgh, J.W. (2016) Megafauna and Ecosystem Function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America*, **113**(4):838-846.
- Scholes, R.J. & Biggs, R. (2005) A Biodiversity Intactness Index. *Nature*, **434**:45-49.
- Smith, S.E. & Read, D.J. (2008) *Mycorrhizal Symbiosis* (3rd Edn), Academic Press: San Diego and London.
- Spencer, J., Stringer, A. & Sheehy, E. (2018) Martens, Squirrels and Forestry. *Quarterly Journal of Forestry*, **112**(4):257-261.
- Spencer, J. & Elliott, M. (2021) The Role of Wildlife in Sustainable Forest Management Part 2. Beavers, Biodiversity and Forestry. *Quarterly Journal of Forestry*, **115**(4):269-76.
- Spencer, J. & Tew E. (2021) The Role of Wildlife in Sustainable Forest Management: Part 1. Ospreys and the Forest Nutrient Flux. *Quarterly Journal of Forestry*, **115**(2):130-137.
- Suz, M.L., Bode, J., Bryne, J.J., Van der Linde, S. & Bidartondo, M.I. (2021) Nutrients, Carbon, Mycorrhizas and Tipping Points in Forests. *Quarterly Journal of Forestry*, **116**(1):36-43.
- Terwilliger, J. & Pastor J. (1999). Small Mammals, Ectomycorrhizae, and Conifer Succession in Beaver Meadows. *Oikos*, **85**(1):83-94.
- Thompson, I., Mackey B., Steven McNulty S. & Mosseler A. (2009). *Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems*. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 43, 67 pages.
- Tilman, D.W. & Knops, J. (1996) Productivity and Sustainability Influenced by Biodiversity in Grassland Ecosystems. *Nature*, **379**:718-720.
- UK Woodland Assurance Standard (2020) UKWAS.
- Woodland Trust (2020) *Woods in Waiting*. Woodwise Autumn.

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