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Towards ecosystem-based restoration of peatland biodiversity

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SUMMARY

Natural peatlands support rich biological diversity at the genetic, species, ecosystem and landscape levels. However, because the character of this diversity differs from that of other ecosystem types, the value of peatlands for biodiversity has often been overlooked. Fundamentally, this arises because peatland ecosystems direct part of the energy captured by primary production into long-term storage within a peat layer, and thus establish a structural and functional basis for biodiversity maintenance that is not found elsewhere. This article examines the far-reaching implications for the assessment of peatland biodiversity as well as for the drivers, methods and targets of peatland conservation and restoration initiatives. It becomes clear that a robust framework for the management and restoration of peatland biodiversity must be founded in structural-functional ecosystem analysis, and such a framework is developed. The authors draw on a broad base of historical and contemporary literature and experience, including important Russian contributions that have previously had little international exposure.

KEY WORDS: Aichi targets, habitat loss, mire landscape, mire massif, pattern, population, species

INTRODUCTION

According to Article 2 of the Convention on Biological Diversity (CBD), biological diversity (biodiversity) is "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine, and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems" (CBD 1992). The scientific community already understood in the late 1990s that biological diversity should be considered not only in terms of structure, but also at functional level (e.g. Mooney *et al.* 1996), and that structural and functional diversity can be described at all organisational levels from cell to biome. This led, ultimately, to the realisation that biodiversity contributes to the maintenance of resilience not only within individual ecosystems but also at global level, *via* relatively stable but dynamic equilibria. The social benefits of biodiversity may be expressed and valued by discarding the traditional resource-based ideology of direct and indirect incentives (McNeely 1988) in favour of the ecosystem services ideology (Perrings *et al.* 1997). This, in turn, created economic incentives for the conservation and restoration of biodiversity. At the tenth CBD Conference of Parties

(CoP) in Nagoya (Japan), a revised strategic plan for biodiversity was adopted for the period 2011–2020, incorporating the Aichi Biodiversity Targets which establish principles for action based on an understanding of ecosystem services.

Peatlands differ from all other ecosystems in the way that they accumulate energy, matter and information within a peat layer through geological time. This, in turn, defines structural and functional limits for maintenance of their biota that are not found elsewhere. They present limited species diversity but a high incidence of unique species, a broad spectrum of morphological forms, and a high diversity of ecosystem types at various scales reflecting a combination of geomorphological diversity and climatic zonation (e.g. Pfadenhauer *et al.* 1993). Their contribution to regional biodiversity is important both where they form the dominant land cover and where they are the rarest habitats or the only wetland habitats; for example, in arid climates and mountainous areas. In the former case they provide habitat for a majority of species and in the latter case they harbour locally or regionally rare species including relict species and those at the edges of their geographical ranges. And yet, in recent decades they have been categorised for international policy purposes as wetlands, along with a wide range

of natural habitats that lack peat layers such as marshes, lakes, rivers, estuaries, shallow sea, underground water bodies and man-made water bodies (ponds, irrigated land, *etc.*)¹. Amongst these habitats, biological diversity is maintained by a wide range of very different processes that can be expected to respond differently to both environmental (e.g. climate) change and human intervention. As a result, the specific contribution of peatlands to biodiversity has been undervalued in both research and practical conservation.

In recent years there have been substantial improvements in knowledge about the natural functions of peatlands. Since the mid-1980s, many reviews have been published on the variety amongst peatland ecosystems in general (Mitsch & Gosselink 2000, Succow & Joosten 2001, Chapman *et al.* 2003, Steiner 2005, Rydin & Jeglum 2006, *etc.*) and on regional aspects (Bellamy 1987, Rubec 1988, Steiner 1992, Vasander 1996, Manneville 1999, Tarnocai *et al.* 2000–2011, Warner & Asada 2005, *etc.*). Charman (2002) examined key aspects of the nature and development of peatlands in their environments, and a multi-author review about peatlands and climate change (Strack 2008) deals mainly with carbon and greenhouse gases. A comprehensive analysis of peatlands as natural and economic objects, including an assessment of biodiversity values and losses based on a unique synthesis of the opinions of peatland users and conservationists, was carried out by Joosten & Clarke (2002). There is also a set of publications devoted to biodiversity issues in natural and transformed peatlands and their restoration, mostly from the period 1990–2003 (Mulamootil *et al.* 1996, Vasander *et al.* 1997, Chapman *et al.* 2003, *etc.*) but continued more recently by M. Evans (2010), Littlewood *et al.* (2010) and Vitt & Bhatti (2012). A general account of peatland biodiversity appeared as a chapter (Minayeva *et al.* 2008) of the *Assessment on Peatlands, Biodiversity and Climate* (Parish *et al.* 2008), which is a comprehensive consensus review about peatlands and climate change prepared for CoP8 of the CBD (IX/16), and the topic has since been revisited more concisely by Minayeva & Sirin (2012). Both of these publications review aspects of peatland biodiversity that are relevant not only to environmental issues but also in the contexts of human disturbance and restoration. This recent literature provides a robust foundation for focusing more clearly on peatland biodiversity in terms of structural and functional features, values, losses, and

strategies for their conservation and restoration.

As our knowledge has improved, the need to differentiate between sub-sets of wetlands has gradually gained recognition in policy circles. Peatlands have been mentioned repeatedly by the Ramsar Convention as the most important wetland type for both the support of biodiversity and the regulation of natural processes, and they have been singled out for increased attention by both the CBD and the United Nations Framework Convention on Climate Change (UNFCCC). However, their value for biodiversity and the mechanisms by which peatland biodiversity is maintained are still poorly understood amongst many audiences across the globe.

Peatland ecosystems have traditionally been used by people for their fauna (hunting and wildfowling), flora (berries, fungi, rubber, timber), vegetation (grazing), land and soil (agriculture, forestry), water (irrigation and drinking) and to extract peat for use elsewhere (animal litter, soil conditioner, fuel, horticultural growing media). Although the resources that can be obtained from peatlands are often indispensable, they are easily used at a faster rate than they can regenerate. Destroyed peatlands are essentially non-renewable within human timescales because they accumulate peat so slowly. As a diminishing resource that has traditionally supported a wide range of social, scientific and commercial interests, individual peatlands often already have multiple stakeholders and potential users, whose needs must now be considered in conjunction with the Aichi goals for biodiversity as well as the inescapable backdrop of climate change. An outcome is the new availability of economic incentives for the maintenance and restoration of natural peatland features, such as European agri-environment schemes and the emerging global carbon market (Tanneberger & Wichtmann 2011). Thus, we can expect an increasing need for robust approaches to peatland management, without which irreversible losses of peatland and peatland biodiversity seem set to continue into the foreseeable future.

In order to restore biodiversity in peatlands, we need first to understand what has been lost and why. In other words, we need to know how to recognise peatland biodiversity, how it arises, and how it is maintained in natural peatland ecosystems. Once we fully appreciate the intimacy of relationships between the peatland soil, water and biota it becomes clear that attempts to restore any of these elements are unlikely to be successful unless their structural and functional interdependencies are taken into account.

¹ The term ‘wetlands’, as defined by the 1971 ‘Convention on Wetlands of International Importance Especially as Waterfowl Habitat’ originating from Ramsar, Iran (the so-called Ramsar Convention, www.ramsar.org), refers to a broad spectrum of objects where water is the primary factor controlling environmental conditions and determining the habitats of plants and animals.

In this article we aim to compile key information about the biodiversity characteristics of peatlands, and on this foundation to build generic options for peatland management that are driven specifically by biodiversity objectives. To this end we first review the singular (and yet complex) contribution of peatlands to local, regional and global biodiversity in terms of the diversity of their habitats, species and landscapes; and how this is seated in ecosystem function. We then consider how human activities can lead to the loss of functionality in peatlands and, therefore, to loss of biodiversity; and how peatland biodiversity might be measured; before turning to the development of ecosystem-based principles for its restoration.

BIODIVERSITY IN NATURAL PEATLANDS

Characteristics of the peatland environment

Peatland habitats

Natural peatlands have a unique structural and functional integrity. Excess water promotes the dominance of mire plants and impedes decomposition of their dead remains which, consequently, accumulate as peat. The singular physical properties of peat enable it to retain and store a mass of water dozens of times that of its structural matrix, such that it can support subsequent generations of living organisms even through droughts with long return periods. This makes peatland a unique ecosystem type in terms of the role that the biota plays in its maintenance. Living organisms create and maintain specific abiotic conditions which, in turn, support specialist organisms that are an integral part of, and highly dependent upon, the ecosystem that is formed. Thus, the peatland ecosystem achieves self-perpetuation on a timescale that is tens to thousands of times the lifespan of any of the individual organisms involved, and peatlands present the longest direct successions of natural plant communities in the world. This, in turn, gives rise to a high level of integrity within peatland ecosystems, not only on account of the local relationships between plants, water and peat by which the cycling of matter and energy is achieved, but also between spatially separated parts of the mire. The directions of links between different parts of the mire may vary, and these connections may articulate with one another in a variety of ways, but they should always be taken into account.

Thus, in peatlands we see in the most obvious way how the biota create suitable conditions for their own self-maintenance. The peat layer is formed by the vegetation and this directly creates both the natural

habitats and the ecological conditions presented at the mire surface. In other words, the peatland biota determine the unique character of the biological diversity of peatlands through the phenomenon of peat formation. Regardless of the ecology of their surroundings, peatland massifs form distinct 'islands' of 'soil' characterised by high water level and moisture content, considerable fluctuations and vertical gradients of surface temperature, low oxygen content, accumulation of toxic substances and gases sequestered from the atmosphere, limited availability of nutrients and, in most cases, high acidity (Rydin & Jeglum 2006). These conditions place severe abiotic restrictions on living organisms and create intense competition for space and nutrients, even between plants with different life forms. For example, vascular plants risk being engulfed if the moss carpet in which they are rooted grows too rapidly, and the mosses may be shaded out of existence if the vascular plants become too luxuriant.

Influence on other habitats

Similar considerations apply at landscape level and beyond. The specialised peatland system influences driving factors such as water level, microclimate, matter and water balance, gas exchange *etc.*, that affect habitat conditions (and thus biodiversity) in non-peatland ecosystems nearby or downstream. The importance of peatlands for the conservation of biodiversity in other ecosystems arises largely from their environment-forming functions. Peatlands on high mountains and other uplands generate the headwater streams of rivers; arctic peatlands support the existence of permafrost and hence entire landscape features, whilst subarctic peatlands may even create permafrost; most peatlands regulate the hydrological regimes of adjacent areas through groundwater levels and runoff; peatlands create macro-climates, and they affect the climates of their surroundings.

Peatland plants

Biological characteristics

Peatland plants have some distinctive features that are independent of their positions in taxonomic classifications. The vascular plants may have particularly effective photosynthesis (Yumagulova 2007), often of the C4 type exemplified by many aquatic species (Nekrasova *et al.* 2003, Sheremetiev 2005); although no advantage can be traced through to ecosystem-level gas exchange measurements (Frolking *et al.* 1998). In many of the vascular plants and bryophytes the processes of growth, spread and matter accumulation are not highly seasonal, but start in early spring and continue until at least late autumn.

For these reasons, peatland plants have unexpectedly high annual production rates. Their typical structural and functional features include: high morphological variability; aeration tissues in vegetative organs and diaspores; extraction mechanisms for toxins and excesses (formation of idioblasts, cystoliths and druses); and special strategies and mechanisms for nitrogen and mineral uptake (insectivory, symbioses with nitrogen-fixing soil micro-organisms and mycorrhizae, and excretion of phenol acids as solvents). They are distinguished by their ability to pollinate and disseminate diaspores in open areas by the agency of wind (anemophily, anemochory; Sundberg 2013) and with a high water level (hydrochory); and to compete with fast-growing *Sphagnum* mosses (rhizome and tussock-forming plants, vegetative reproduction). The predominant vascular plant species have K-strategy features; i.e. they are relatively large and long-lived plants that develop slowly, reproduce at later development stages, produce few offspring, have limited dispersal potential, and so generate populations with stable structure and size. Stable multilayer symbiotic relationships, often involving irreplaceable partners, are typical (Masing 1969).

Diversity of species

Most species that are permanently associated with peatlands have developed adaptive strategies during the course of evolution (Rydin & Jeglum 2006). This pronounced specialisation increases the probability of extinction should their peatland habitats be lost. Indeed, the peatland environment creates conditions that lead to high specialisation of living organisms, regardless of whether they are permanently or temporarily related to the habitat. Numerous studies have shown that their ability to adapt arises mostly from genotypic variation (Crawford 2008). Consequently, the range of plants inhabiting peatlands is limited to highly specialised species and those with strong adaptive capacity. Taxonomic species diversity is typically low (on average no more than 15 % of local floras and faunas) (Minayeva *et al.* 2008); and although it can vary with environmental characteristics even within the same mire type (Glasier 1992), it is always relatively low. Species diversity is higher amongst older and more primitive taxonomic groups (bacteria, fungi, spore plants) and highly specialised species predominate, with 5–25 % of peatland species being ‘endemic’ to their habitats across the world. Even though the total number of species is comparatively low, peatland species diversity is significant when consideration is given to the high representation of unique or highly specialised endemic species for the habitat. To

describe specialised peatland plants, the term ‘obligatory helophytes’ was introduced by Bogdanovskaya-Guenef (1946). The typical plants of mires (K-strategy species of older origin with discontinuous ranges, cosmopolitan distributions and numerous highly specialised symbiotic relationships) form closed communities that are generally resistant to invasions of alien species (Minayeva & Cherednichenko 2005). Exotic invasives can be successful in natural peatlands only if they have some specifically advantageous biological features like those of the American and Australian insectivorous species found on peatlands in England and Switzerland (Minayeva *et al.* 2008). The few specimens of the North American pitcher plant *Sarracenia purpurea* (Figure 1) that were first recorded on Wedholme Flow, Cumbria (UK) in 1976 (believed to have been planted by a botanist) have now spread dramatically to cover an area of around one hectare, and are regarded as a threat not only to invertebrate populations but also to native mire vegetation due their dense growth habit (S. Evans 2009).



Figure 1. The pitcher plant *Sarracenia purpurea* growing in its native habitat on a *Sphagnum* mire in eastern Canada. Photo: O.M. Bragg.

Diversity within species

The sharp boundaries of peatland massifs and the often large distances separating them promote the operation of selection mechanisms and enhancement of micro-evolution processes. Principles of island biogeography may be applicable (Istomin & Vagin 1991). In this rather isolated and highly variable environment, the relatively low taxonomic diversity is counterbalanced by morphogeny. A classical example of phenetic diversity in peatland plants is provided by the ecological forms of Scots Pine (*Pinus sylvestris*) described in the early 20th century by C.A. Weber (Couwenberg & Joosten 2002), Sukachev (1905, cited after Sukachev 1973), Abolin (1915) and others. Subsequent studies have shown that the forms *pumila*, *willkommii*, *litwinowii* and *uliginosa* are genetically identical (Tyuremnov 1949). Considerable variations in the morphology of non-woody plant species have also been described. For the pod grass *Scheuchzeria palustris* (also known

as Rannoch rush), differences in morphometric characteristics between plants of different coenopopulations and their loci reached 500 % for shoots (Minayeva 1997) and 300 % for seeds (Minayeva 2010) (Figure 2). Indeed, intraspecific diversity expressed as morphogeny is one of the most pronounced aspects of diversity in peatland plants. It is also a key factor for their functional and structural maintenance.

Animals

Animals usually occupy peatland habitats only at certain stages of their life cycles or during particular seasons, but have also developed adaptations such as resistance of amphibian and bird egg shells to the aggressive acidic environment, specific colouring of fur and plumage, parental care strategies, and adaptive synchronisation of life cycles with phenological and meteorological phenomena. The

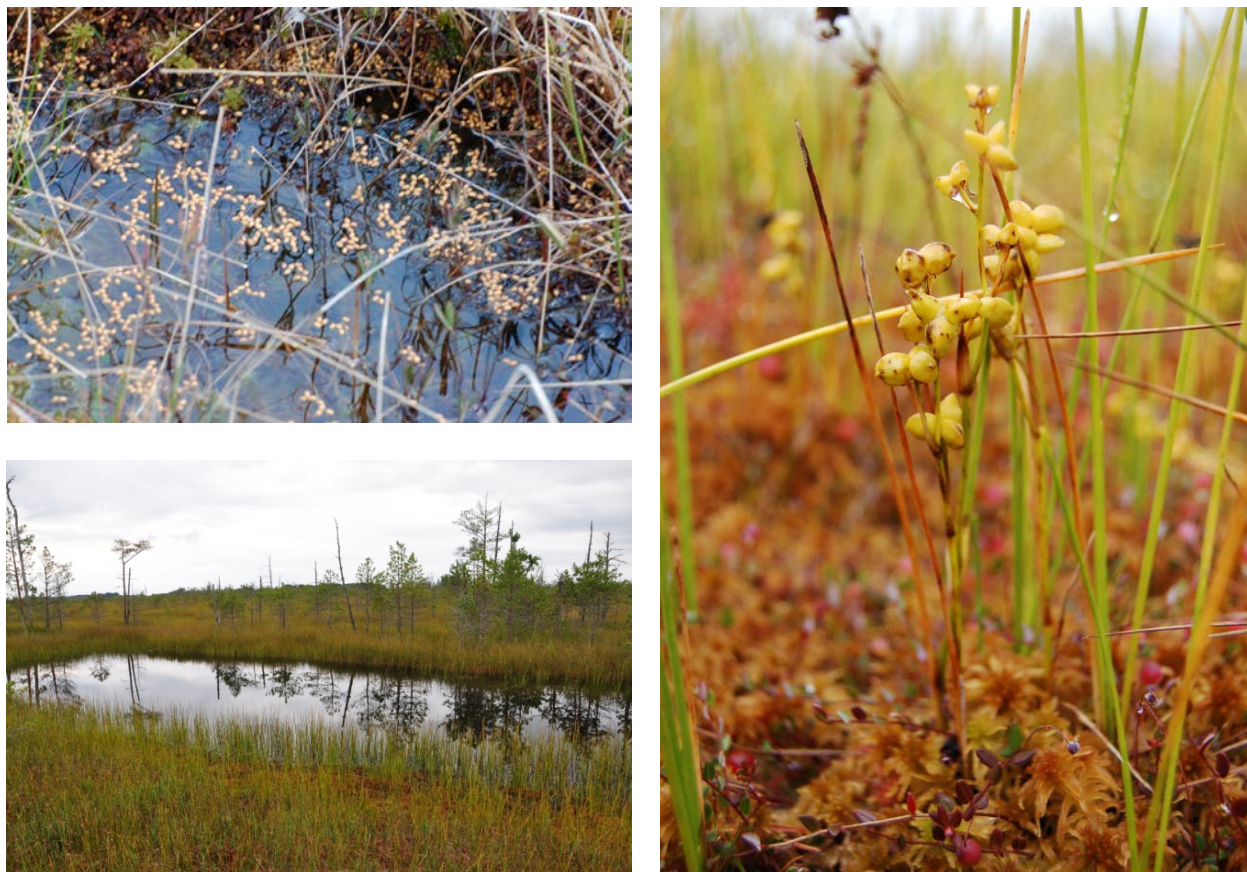


Figure 2. On the raised bog “Staroselsky Mokh” (temperate Southern Taiga zone, Tver region, European Russia), seeds of *Scheuchzeria palustris* are carried across the whole peatland by spring floodwater (top left), but develop into stands with different morphology and population structure depending on habitat type. On well-drained slopes this species forms a high-density carpet of small plants (up to 25 cm tall) with high reproductive potential (right); whereas around an oligotrophic mire pool (bottom left) it grows up to 50 cm tall but much more sparsely, although again achieving high reproductive potential. Photos: T. Yu. Minayeva.

movements of animals make peatlands important for preserving and maintaining not only their own unique species-level biodiversity, but also the biodiversity of other habitat types. The different types of interactions are outlined below.

Temporary use or partial replacement of reduced or transformed habitats

Peatlands provide temporary habitats for many animal species that use them only intermittently and for particular reasons, or have been forced to make increased use of peatlands because their original habitats have disappeared. For example, Spitzer & Danks (2006) report the survival in bog refugia of vulnerable insect species that were formerly widely distributed (tyrphoneutral), and name the phenomenon “induced tyrphophily”. There are similar reports for birds, such as the Skylark (*Alauda arvensis*), which are normally characteristic of open habitats (V. Nikolayev pers. comm.). Frogs cannot reproduce on raised bogs because the environment is too acidic for their eggs, but they use them as temporary refuges during drought (Minayeva *et al.* 2008). Large vertebrates tend to avoid mires and yet are frequently found there in hot weather, in the berry season, or when biting-insect populations peak in the surrounding forest. Many animals that spend most of their lives in other habitats have obligatory relationships with peatlands (Minayeva *et al.* 2008).

Support of breeding birds

The peatland avifauna of European Russia comprises around 180 species, of which 146 (16 orders) breed on peatlands. The relatively few that are specifically associated with peatlands throughout their seasonal and life cycles are conspicuous members of the orders Gaviiformes (loons and divers), Anseriformes (waterfowl), Falconiformes (diurnal birds of prey), Galliformes (game fowl) and Ciconiiformes (stork-like birds). The remainder are able to use other habitats but choose peatlands so frequently that peatlands are often their principal regional breeding grounds (V. Nikolaev pers. comm.). Many birds also use peatlands during chick-rearing periods that are timed to coincide with the population peaks of various insect groups, such as saprotrophs (flies, mosquitoes) that use the peat layer during their annual life cycles and water-related invertebrates (e.g. mayflies, caddis flies, dragonflies and beetles) for which peatlands often provide aquatic habitats. After the hatching and chick-rearing period, insect numbers decline sharply and birds such as waders move to more abundant feeding grounds. Cranes have a more complicated spatial and temporal relationship with peatlands. When they arrive in

spring, they feed in raised bogs on the rhizomes of mire plants and in small areas of floodplain mire where moor frogs are congregating to spawn at that time of year. In later months, when the frogs have dispersed, they become much less important in the diets of the cranes.

Stopover sites, feeding stations and short-term refuges for birds

Peatlands play a special role in the support of global flyways. The availability of intact peatlands for staging and feeding on migration routes determines bird population numbers in parts of their ranges that may be distant from their breeding grounds, for example in Africa or central Asia for species that breed in the Arctic (E. Strelnikov pers. comm.).

Ecosystem diversity

The combination of structural (spatial) heterogeneity and functional integrity at various levels is common to most peatlands, and ecosystem diversity at all scales from the macrolandscape to the nanotope (Figure 3) is one of the crucial factors for maintenance of their biodiversity. It is extremely important to differentiate between these spatial levels when considering mire ecosystem diversity in the context of planning peatland management, conservation and restoration, because the heterogeneity at different spatial levels is driven by different natural factors.

The concept of spatial differentiation within mire landscapes was introduced by Abolin (1914), then developed further by Galkina (1946, 1959), Bogdanovsakaya-Guenev (1949) and Lopatin (1954), and was actively used by Russian scientists to create multi-level mire classifications that could be portrayed on maps. It was subsequently systematised by Pyavchenko (1974) and Masing (1974). Contemporary Scandinavian researchers were using mire types in the sense of mire massif types and differentiated areas within mire massifs (Cajander 1913, Melin 1917, Osvald 1923, Sjörs 1948, Ruuhijärvi 1960). Since the 1950s peatland has also been typified at the ecosystem level using mixed approaches (Ratcliffe & Walker 1958, Euroala 1962, Goode & Lindsay 1979, Euroala *et al.* 1984, Lindsay *et al.* 1985). However, following publication of the English translation of a book by K.E. Ivanov who used the spatial differentiation approach for hydrological studies (Ivanov 1975, 1981), Lindsay *et al.* (1988) chose to follow the Russian school when they came to describe the diversity of the extensive Flow Country peatlands in northern Scotland.

Nowadays, peatland researchers may be embarking unwittingly on a repeat of this cycle. It

seems that anyone wishing to typify mires at the ecosystem level arrives, sooner or later, at an approach that involves the classification of landscape units at different spatial levels. The scheme presented in Figure 3 is compiled from Masing (1974) and Lindsay *et al.* (1988) with modifications. It embodies thinking that began a century ago, evolved through the work of dozens of Russian and Scandinavian mire scientists over several decades, and was already fully formed 20 years before Masing (1974) developed it, in the most logical way, into a system for describing the diversity of mires. It is recommended to new generations of mire researchers as a paradigm that is worthy of study and consideration, in the interests of avoiding further confusion arising from unnecessary reinventions. Aware that Russian language publications are not accessible to all, and that the concepts and terminology are once again beginning to slip out of general knowledge, we provide a short explanation below.

○ The top (largest-scale) level is the **macrotope** - the level of river basins (catchments) and mire massif systems (several connected mire massifs) covering areas ranging from several square kilometres to

thousands of square kilometres and sometimes more - for example, the >55,000 km² Vasyugan Mire, which occupies the interfluvium of the Ob and Irtysh Rivers in the central sector of the West Siberian Plain (UNESCO 2016). The only higher spatial level (than the macrotope) at which mire ecosystem diversity can be described is the level of biogeographic zones.

○ The next level down from the macrotope is the **mesotope**, which is related to the “mesolandscape” (valley, hill, *etc.*) of classical landscape ecology and, in this case, is the **mire massif**. The scale can vary between several hectares and tens of thousands of hectares

○ Within the mire massif, the next level of heterogeneity is the **microtope** level. This relates to the different morphological parts of the mire, which also have distinctive vegetation. For example, the microtopes of a ‘generalised’ raised bog would be lagg, rand, sloping mire expanse with hummock-hollow complex, and watershed with hummock-pool complex; whose areas might range from dozens of square metres to thousands of

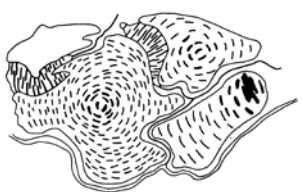

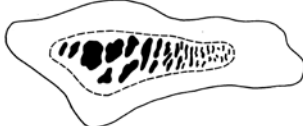
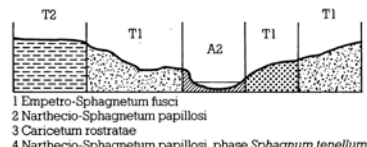
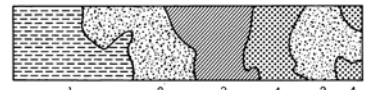
The landscape		Description	Vegetation unit	Scale (m ²)
	Macrotope	The mire complex (or system; several merged mire massifs)	Biogeographic zone	10 ⁵ –10 ⁹
	Mesotope	The mire massif (separate raised bog, fen, <i>etc.</i>)	Mire massif type	10 ² –10 ⁷
	Microtope	Homogeneous element of landscape heterogeneity within the mire massif (hummock-hollow complex, margin, sedge mat, <i>Sphagnum</i> carpet)	Complex of phytocoenoses	10 ² –10 ⁶
	Microform (nanotope)	Hummock, hollow, pool, ridge	Phytocoenosis	10 ⁻¹ –10 ¹
	Vegetation mosaic	Microcoenosis, tussock, <i>etc.</i>	Microcoenosis	10 ⁻² –10 ⁻¹

Figure 3. The elements of hierarchical mire classification (after Masing 1974 and Lindsay *et al.* 1988).

hectares. Their vegetation is represented by complexes of phytocoenoses and classified on the basis of complexes of associations.

- The next level down is the **nanotope** or **microform** (hummock, ridge, palsa, lawn, hollow, pool, *etc.*). Microforms host vegetation units at phytocoenosis level which are usually represented by phytosociological associations or subassociations. In this case the spatial scale ranges from square metres to tens of hectares.
- The lowest spatial level is the **vegetation micromosaic**, which is driven mainly by variations in plant population structure within the phytocoenosis. The units of vegetation classification here will be microcoenoses (singular: **microcoenosis**), whose extent may range from square centimetres to square metres. Some researchers call these units 'synusia', but they correspond to only one type (synusia of the 3rd order) from the classical concept of Gams (1918). According to Rabotnov (1983) it was Sukachev who developed the concept of the synusia in the sense of the microcoenosis, a part of the phytocoenosis. Lavrenko (1959) introduced a term 'microphytocoenosis' with similar meaning. In the current usage of phytocoenological concepts (Rabotnov 1983, Mirkin & Naumova 1998), the synusia is more a functional (than a structural) unit of the phytocoenosis, for which some scientists use the term 'parcella'. To avoid further confusion, we propose that the name 'microcoenosis' should be used for a vegetation unit, i.e. an element of the vegetation micromosaic.

Thus, ecosystem diversity in peatlands may be present at all levels from the peatland system as a whole down to individual microcoenoses, and biodiversity assessment at the ecosystem level can be carried out within each level of this hierarchy.

Ecosystem diversity at large scale

The GIS archive "Peatlands of Russia" (Institute of Forest Science, Russian Academy of Sciences) can tell us that the country's peatlands comprise more than 20 % permafrost (polygonal and palsa) mire, about 30 % transition mire, 18 % raised bog, 18 % fen, and less than 14 % ridge-hollow and ridge-pool complexes (Vompersky *et al.* 2005). The feature upon which this assessment of diversity is based is the relative dominance of particular mire massif types within the specified geographical zone. Similar assessments can be carried out using other features - for example, the occurrence of different life forms (mosses, forbs, shrubs, trees). Such an assessment, based on the same GIS, is that 62 % of the total

peatland area in Russia is treeless, 21 % has open woodland and 17 % is covered by forest (Vompersky *et al.* 2011). Both of these accounts are general descriptions of the diversity of peatlands occurring within the vast territories of northern Eurasia but, because they reflect different approaches and refer to different ecosystem levels, they will support different analyses of ecosystem diversity at the spatial level of the biogeographic zone. Various analyses at these large scales are needed for purposes such as the development of national wise use, conservation and restoration strategies for peatlands; and for national reporting to the Ramsar Convention and UNFCCC. However, such analyses are of limited relevance to local-scale scientific or practical work, and would require very careful interpretation and application in that context.

Diversity of mire massifs (mesotopes)




























Each peatland massif is a complex entity that has been individually shaped by the unique combination of conditions experienced during its lifetime. This results in enormous ecosystem diversity at macro- and meso-landscape scales, which has generated many approaches to describing the variety amongst peatlands including regional ones (e.g. Katz 1971, Galkina 1967, Botch & Masing 1979, Ivanov 1981). The principles of mire massif classification, as systematised by Galkina *et al.* (1974), are presented (in Russian) in the publication "*Mire Types of the USSR and Principles of their Classification*" (Abramova *et al.* 1974). This book is further commended as a unique collection of studies which together provide a comprehensive overview of the diversity of mire massifs throughout the former Soviet Union, from the Baltic countries to the Far East, together with example applications of mire massif classification to land use planning. However, the most sophisticated classification of mire massifs was developed by Tatiana Yurkovskaya (Yurkovskaya 1992), who used it to map mires in the European part of Russia. The mire features she employed were hydrological mire type, morphology and vegetation (dominant life form and regional variations in species composition).

Being landscape focused, classical Russian mire science has given priority in choosing attributes for mire massif classification to geomorphology, position in the macrolandscape, hydrology, and genesis. There are several classical schemes, due to Galkina *et al.* (1949), Tyuremnov & Vinogradova (1953), Ivanov (1953, 1975, 1981), Romanova (1961), Galkina (1964), Kirushkin *et al.* (1967), Masing (1968) and Kirushkin (1980), which describe a matrix of mire massif types distinguished mainly on

the basis of geomorphology and hydrology (Figure 4). This approach later provided the background for development of the hydrogenetic mire classification of Succow & Jeschke (1990).

Thus, the mire massif has proved to be a very useful unit for describing mire distribution and

diversity at local and regional scales. It is often adopted as the basic unit for spatial planning of peatland use and conservation (Cajander 1911, Yampolsky 1979, Tanovitsky 1980). It is also the key unit for peatland management, conservation and restoration.

Position in the landscape		Mesostructure: simple mire massif (mesotope)				Complex mire massif	Combination or system of mire massifs	
		Limnic stage	Minerotrophic stage		Ombrotrophic stage	Ombrotrophic stage		
		Lakewater fed	Groundwater fed	Mixed water supply	Precipitation fed	Precipitation fed		
In topographical basins	Closed (endorheic) bowl						Plan shape of mire massif, arrangement of mires in the landscape	isodiametric
	Open (exorheic) bowl							
								
Headwater channel							Mire massif systems of varying complexity can cover large areas	linear
On flat watersheds and coastal lowlands	In shallow depressions							
	In lake basins							
	On gentle slopes							



Matrix of mire massif development patterns

- 1 - Outline of topographical depression, 2 - Primary and secondary pools, 3 - Rivers, streams, 4 - Secondary endotelmic streams, 5 - Lake sediments, 6 - Peat deposits, 7 - Minerotrophic mires, 8 - Ombrotrophic mires

Figure 4. Example of a matrix for identifying mire massif and mire system types, redrawn from Masing (1968).

Diversity of microtopes

The most obvious source of information about heterogeneity within the mire massif is the aerial photograph (Galkina 1937). The first mire scientists to work with the aerial images that became available after World War II (e.g. Galkina 1946, Galkina *et al.* 1949, Sjörs 1948, Galkina 1953) produced sketch maps showing the mire massif as a clearly delineated area containing homogeneous patches that were distinguished from one another by differences in microrelief and vegetation. The sketch maps were accompanied by vertical profiles indicating the geomorphological part of the peatland to which each patch belonged, the depth and type of peat beneath it, the average water level, and other characteristic features.

Theoretical discussions about the difference between the biogeocoenosis and the mire microtope culminated in the genetic approach. Thus, the microtope was characterised as an entity having common genesis and a long-term history, which is integrated by a wide range of natural factors and unified by their unique combination.

The indicator value of microtopes was described during the 1970s in the practical contexts of predicting berry productivity (Elina 1972) and planning road construction (Shaposhnikov 1974, 1978). However, the description of mires in terms of the diversity of their microtopes has been driven mainly by hydrologists. Because the different parts of the mire massif play unique roles in the formation and maintenance of the hydrological regime of the whole mire, the management of hydrology at microtope level (Ivanov 1953, Romanova 1961, Bogdanovskaya-Guenef 1969, Novikov 2009 *etc.*) is especially relevant to land use. For example, Usova (2009) developed a hydrological classification of mire microtopes as a basis for the spatial planning of oil and gas facilities and infrastructure in West Siberia, while K. Lopatin and colleagues used an integration of all characteristics of microtopes for the same purpose (Lopatin 2012). The latest approaches to planning both peatland development and the restoration of industrial sites have used microlandscape maps (Kosov & Panov 2001). Indeed, the management of mire massifs for all purposes, including restoration, is very often planned at microtope level.

Diversity of nanotopes

A classical example of the small-scale complexity of mires is provided by ridge-hollow microrelief. A ridge and a hollow, situated just a few centimetres apart, differ from one another in both their structure and their functions. For some purposes it is

convenient to distinguish between them, and they have been termed ‘nanotopes’, ‘microforms’ and, most recently, ‘microstructures’ (by Pouliot *et al.* 2011). The vegetation of the nanotope is the phytocoenosis. The structural heterogeneity at this level is usually described by large-scale mapping combined with vertical profiles. In some cases, differences and boundaries have been registered statistically, using a set of criteria that includes autecological features (Botch *et al.* 1979, Botch & Vasilevitch 1980). Fine-scale analyses of community succession and hummock-hollow dynamics in bogs are presented by Karofeld (1986), Ilomets (1988) and Zobel (1989).

The structural diversity may reflect long-term processes of mire genesis or current ecological processes. This is particularly well illustrated by the superficially similar appearance of the ridges in raised bogs and aapa mires. Whilst the raised bog ridge has been developing as an oligotrophic element of pattern for several thousand years, the building-up of oligotrophic vegetation to form the aapa ridge reflects a reaction to recent changes in ecological conditions (Figure 5). Another case of ridge nanotopes reflecting different ecological processes can be observed in the large valley fens of Western Siberia, where ridges known as ‘veretji’ have formed over mineral ridges at the base of the peat. To distinguish between different hummock-ridge complex types, especially when undertaking air-photo interpretations, it is more informative to consider vegetation in conjunction with the structural configuration than to observe structure only (Botch 1972).

An understanding of the nature, origin, structure and function of nanotopes (microforms) is crucial for the management and restoration of mire habitats as well as entire mire massifs.

Diversity of vegetation micromosaics

The vegetation micromosaic encompasses the diversity within microforms; in other words, it reflects the heterogeneity of vegetation within the phytocoenosis.

Microcoenoses were used to describe the horizontal structure of facies (a synonym for ‘microtope’ or ‘microlandscape’ which is used by the Karelian mire school) on oligotrophic and aapa mires in Karelia by Elina *et al.* (1984). In other studies (Yurkovskaya 1983, Antipin 1991, Blagoveschensky 1992, Yurkovskaya 1992), the features used for typology and mapping were structural heterogeneity and other ecological characteristics of microtopes. Sjörs (1948) adopted the microcoenosis as the basic unit of spatial and typological variability.

The ecological drivers of mire vegetation micromosaics have been studied very actively in Estonia (Loopman & Paidla 1981, Ilomets 1988, Loopman 1988). Zobel (1988) described the role of the micromosaic in autogenic mire vegetation dynamics. The leading role of the vegetation micromosaic in supporting species and structural diversity has been demonstrated at the level of microcoenosis dynamics by Masing (1982, 1984, 1994). On the other hand, microtopographical variety can occur in highly uniform vegetation such as the extensive *Sphagnum magellanicum* carpets of Andorra Mire in Tierra del Fuego (Couwenberg & Joosten 2005, Grootjans *et al.* 2010) and highly diverse vegetation may exhibit no microrelief as on the Ispani 2 Mire in Georgia (H. Joosten pers. comm.) as well as on various sedge fens. Several studies have demonstrated the importance of vegetation successions in the formation of spatial structure at the level of the vegetation micromosaic (Sjörs 1990), and elements of spatial heterogeneity in the context of long-term dynamics (Foster & Wright 1990) or even palaeoecology (Svensson 1988, Antipin & Lopatin 1989). The importance of population dynamics in creating spatial heterogeneity at the level of the vegetation micromosaic has also been studied by recording, instead of the cover of each species, the numbers of shoots belonging to classes reflecting their ontogenetic status (Minayeva 2010). Structural diversity at the level of the vegetation mosaic can also

influence structure at larger (nanotope and microtope) scales, as described for *Sphagnum* carpets (including palaeoreconstructions) by Smolyanitsky (1977) and Panov (1991, 2006, 2012).

An understanding of the spatial structure and dynamics of the vegetation micromosaic provides a basis for planning the conservation and restoration of mire habitats, species and populations.

Diversity of the wider landscape

Peatlands tend to be the best conserved and least transformed ecosystems in modern landscapes. This arises from a combination of natural and anthropic causes such as longer natural successions, delayed reactions to environmental changes and lower historical human impacts; and is confirmed by palaeoecological data, which shows that the composition and structure of peatland ecosystems has remained fairly stable in comparison with their constantly changing surroundings. Peatlands are assured quiet zones with relatively natural habitats where many species (including azonal, intrazonal and relict species as well as those at the edges of their ranges) can find short-term or long-term refuge if displaced from their original habitats as a result of increasing human impact, climate change or any other environmental change (Minayeva *et al.* 2008, Minayeva & Sirin 2012). Examples from the temperate zone are the presence of a stable group of arctic-alpine species in oligotrophic mires, and of

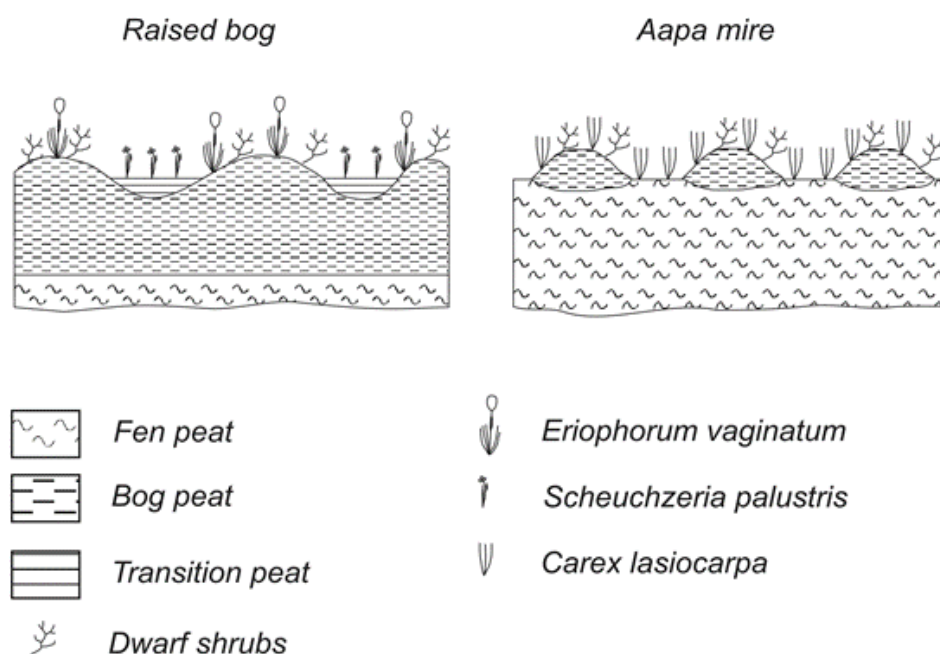


Figure 5. Comparison of the structures of raised bog and aapa mire microtopes (Tatiana Minayeva and Oxana Cherednichenko, after Katz 1971). All of the raised bog microforms are underlain by a thick layer of bog peat, whereas only the ridges in the aapa mire are composed of bog peat.

subtropical species in fens (Kuzmičyov 1992), which can be explained by historical changes in the vegetation cover of adjacent areas. One example of more recent change is the observation that some passerines, small waders, gulls and raptors that used to be associated with meadow vegetation have moved onto peatlands due to gradual loss of their original habitats (Nikolayev 2000).

Due to their relative naturalness, preservation and stability, peatlands play a key role in the support of landscape connectivity. Watershed and floodplain peatlands form corridors and refuges for biological species; while peatlands in intermediate positions within river basins provide functional connections across the landscape *via* flows of water, minerals and other substances, and contribute to the stabilisation of temperature regimes. A study of lepidopteran species composition in the Meshchera Lowland (Russia) by Butovsky *et al.* (2004) demonstrated the importance of discrete peatland massifs as nodes in a habitat network supporting invertebrate diversity. Indeed, the establishment and management of ecological networks in which peatlands function as nodes and corridors (e.g. floodplain mires) is regarded as the most effective available approach to nature conservation for densely settled regions, especially under conditions of limited humidity such as those encountered in the steppe and forest steppe regions of Eurasia, as well as in the American prairie. The capacity of peatlands to maintain 'biodiversity-friendly' habitat conditions across the whole landscape makes them especially valuable for nature conservation, and this emphasises the need to specifically distinguish peatlands from other (dryland and wetland) habitats when developing landscape-level conservation strategies.

FROM HUMAN ACTIVITIES TO BIODIVERSITY LOSSES

Human activities create environmental hazards which may result in impacts on ecosystems that lead to biodiversity losses, according to a chain of causality (Figure 6). Whatever human activities take place, the hazards for a target process or component of a peatland ecosystem will be changes in environmental driving factors such as hydrology, climate, relief, bedrock, peat deposit, vegetation cover, species composition and connectivity, that affect processes which sustain or influence the target. Impact occurs when the hazard causes the target to change. The change may, in turn, have direct or indirect consequences for biodiversity. In the present context, any changes in the biodiversity characteristics of the peatland amount to departures from the natural condition and are regarded as biodiversity losses. For example, the construction of a road through the catchment of a peatland may create a hazard for that peatland by altering the pattern of water supply from upslope, either by diverting water that would otherwise enter the peatland or concentrating the inflow around the outfalls of culverts (Grootjans *et al.* 2010). In either case, an impact on the water table regime within the peatland can be expected. This, in turn, can alter the habitat conditions for trees growing on the mire expanse sufficiently to cause changes in growth forms (von Sengbusch 2015). As a rule, each human activity will generate several types of impact. There may be scale changes across the structural hierarchy; for example, a microtope-level activity such as waste disposal may upscale to a chemical hazard at mesotope or even larger scale (Figure 7). The effects are often

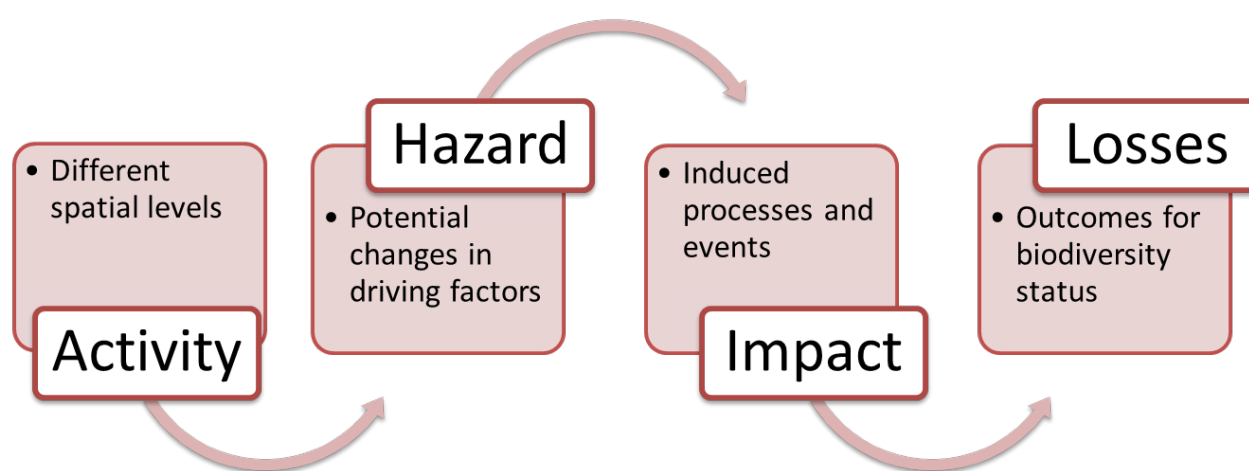


Figure 6. The sequence of causality from human activity to biodiversity losses.

cumulative, and biodiversity losses resulting from different impacts may be reversible or irreversible. Although it may be difficult to trace the impact that resulted in a specific loss, a specialist can always associate the loss with its driver (the hazard), which can then be addressed through management intervention. Thus, the evaluation of biodiversity losses should follow the causality chain, be undertaken at different spatial levels, and take account of cumulative effects and biogeographical variability. Once causality is fully understood, it can be used as a basis for identifying the restoration measures that are most likely to be effective.

The most extensive biodiversity losses are induced by “macro-level” activities; and these losses are the least amenable to regulation, mitigation and restoration. Some examples of macro-level activities on peatlands are: the creation of extensive linear structures, such as roads and railways crossing the arctic tundra; the construction of large dams and reservoirs; the exploitation of oil sands (as in Alberta, Canada); peat extraction or ploughing for agriculture at large scale (on mire massifs >3000 ha in the temperate and boreal zones, and at catchment level in the tropics—e.g. the million-hectare Indonesian “Megarice” project); catchment-level overgrazing of

high-altitude peatlands; and large-scale construction (of airports, *etc.*). These activities create hazards such as loss of landscape connectivity and significant changes in climate, hydrology, bedrock, relief, soil (peat), vegetation and species complement; which, in turn, impact on natural processes with repercussions that include melting of permafrost, water shortage or flooding, shifts in seasonality, and the disappearance of vegetation cover or even of the peat layer. The resulting losses might be described in terms of: smaller differences in biodiversity characteristics between peatland and its surroundings; change in the number of mire massif types represented; smaller patches and variability of mire complex types; fewer peat composition types and mire vegetation communities; changes in productivity; loss of habitats; changes in species composition including establishment of alien and invasive species; and indirect effects on populations, forms and genotypes.

Examples of meso-level activities are: drainage/flooding of whole peatland massifs; water discharge from peatlands (e.g. in South Korea); small-scale peat extraction (from just part of a mire massif); linear constructions (e.g. roads, pipelines) passing through peatlands; surface pollution and contamination; small-scale constructions such as oil

<i>Aspects of biodiversity affected</i>	<i>Spatial level of human activity and impact</i>		
	<i>Macro</i>	<i>Meso</i>	<i>Micro</i>
biodiversity of adjacent land and catchments			
mire massif types			
area/variability of mire complex (pattern) types			
diversity of microform patterns			
peat composition types			
present vegetation communities			
productivity			
diversity of habitats			
native species composition			
alien and invasive species composition			
structure of populations			
morphobiology and forms			
genotypes			

Strength of relationship between impact and loss:

Strong		medium		weak	
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Figure 7. The strength of correlation between different types of biodiversity loss and the spatial level of human activity and impact.

wells and houses; and the conversion of adjacent peatlands into semi-natural landscapes (e.g. arable land, as in western Europe and the 'brown lands' of the Canadian boreal forest zone). The associated hazards include shrinkage and compaction of peat; alteration of hydrology affecting water level and water quality; and changes in mesorelief and microtopography, peat depth and quality, vegetation, species composition, and connectivity. Impacts may be expected at all scales from micro-level to macro-level; and again to cause changes in such attributes as productivity, habitat diversity, microform patterns, species composition, population structure, and the representation of different morphs and genotypes.

Micro-level activities might include: small-scale peat extraction without drainage; dumping of waste; pumping-in of polluted water; local water discharge; the installation of infrastructure for birdwatching, hunting and tourism including permanent walkways; industrial berry picking; and local drainage of the mire expanse or the lagg. These activities alter hydrology including water quality, relief, vegetation cover and microtopography. Even if primary impacts occur at

micro-level, there may be secondary scaling-up to meso-level and above. Biodiversity losses arise from the resulting changes in species composition, productivity, habitat diversity, microform patterns, biology and morphology of species, and population structure including genotype diversity.

The vegetation or the water regime of a peatland may be changed directly by natural events such as extreme weather and climate change; as well as by human activities including burning, afforestation, drainage and peat extraction. Because of the close linkages between plants, water and peat, any change in one of these components usually affects the others and can ultimately lead to degradation of the peat layer and, indeed, of the peatland as a whole. The principles, based in ecohydrological theory, were already well understood in the 1990s and a non-mathematical exploration of the implications for peatland restoration is given by Bragg (1995). Various authors have observed the expected consequences of different types of disturbance at individual sites. Some examples from literature are outlined in Box 1 and illustrated in Figure 8.

Box 1. Examples from literature of scale changes in the causality chain from human activities to impacts and biodiversity losses.

Kolomytsev (1993) reports examples from Karelia where small alterations to single components of the plant cover or to the water balance caused dramatic changes in the structure and functioning of the peatland ecosystem, which could lead to complete loss of the mire massif and its associated habitats.

At Kirkconnell Flow in Scotland, the excavation of a duck pond and a single drainage ditch in the central mire expanse, combined with removal of the uppermost 1–2 m of vegetation and peat from its periphery, created conditions that favoured the establishment of self-sown exotic conifer trees across the whole site (Bragg 2004).

During the first 30–40 years of the 20th century, the edges of many raised bogs in Europe were partially reclaimed (Figure 8A) and the upper reaches of streams rising there were canalised. Although only a small and peripheral part of each peatland was disturbed, the ecological consequences were far-reaching: the modified peatland edges developed uncharacteristically diverse habitats and species complements; the runoff regime was affected and the chemical composition of the streamwater supplied to habitats downstream was altered; and habitats on the mire expanse changed as the peat dome began to degrade (Lindholm & Heikkila 2006).

At Puergschachenmoos, a Ramsar site in Austria, the vegetation changed gradually over a period of decades despite the fact that there was no evidence of direct disturbance on the mire surface. A more in-depth study showed that the functional peatland unit was much more extensive than the designated area, and the remainder had been converted to agricultural use with concealed drainage (Figure 8B) (Bragg & Steiner 1995).

At Clara Bog in Ireland, drainage and the excavation of peat from the mire margins (Figure 8C) caused dramatic subsidence of the peat dome that fundamentally altered its drainage pattern, leading ultimately to changes in vegetation (van der Schaaf 1999).



Figure 8. Even very localised human disturbance can lead to serious changes in peatlands. The lags of many raised bogs in Europe were disturbed in the 1930s. Marginal drainage and peat extraction caused loss of the bog margins, their characteristic ecotopes, plant species and communities; and fundamentally changed the hydrological functioning of whole bog systems and their catchments. At Puergschachenmoos, a Ramsar peatland in Austria, old peat cuttings along part of the margin had been colonised by birch (*Betula*) woodland and dwarf mountain pine (*Pinus mugo*) was growing vigorously at the expense of *Sphagnum* on the adjacent uncut mire surface by 1992 (A). At this time, a concealed drainage pipe and gravel backfill (B) were being installed to impose a new artificial boundary in another part of the bog. Along the margins of Clara Bog in Ireland (C), turbarry rights (inherited entitlements to cut peat for fuel) are still exercised using tracked excavators, even though the peatland is protected as a natural mire ‘remnant’. Photos: O.M. Bragg (A, B) and A.A. Sirin (C).

MEASURING LOSSES OF PEATLAND BIODIVERSITY

Methods and criteria for the assessment of biodiversity status

Traditional methods for biodiversity assessment are based on: (a) research in population genetics from the 1940s (Simpson 1949), which proposed diversity indices for species; and (b) classical research in population and ecosystem ecology carried out between the 1950s and the 1970s, which gave rise to assessment methods for ecosystem diversity. However, because these methods are based primarily on structural attributes, they cannot access a number of the peculiarities of mire/peatland ecosystems. When they are applied to peatlands, both have shortcomings, as outlined below.

- Introduction of the concepts of alpha, beta, and gamma diversity (Whittaker 1972) provided impetus for formalisation of the assessment procedure and for the development of some algorithms. The approach was expected also to form a basis for decision-making in environmental conservation. However, a recurring problem is that certain 'non-conformist' ecosystems, including peatlands, do not fit into the schemes proposed. By demonstrating that beta diversity provides the best representation of environmental variety in oligotrophic peatland, Bennie *et al.* (2011) effectively confirm that ecosystem diversity prevails over species diversity here. However, we suggest that the evaluation of alpha diversity could still be effective in some cases, if ecological morphs are treated as separate species.
- The evaluation of species diversity indices, even if adjusted for species distribution and predominance, results in under-estimation of the biodiversity value of peatlands for the reasons outlined above. To obtain more objective results, indices that reflect the uniqueness of communities (e.g. the uniqueness index) should be used. Phenetic diversity of forms within individual species should also be considered, because the extreme conditions in peatlands combine with the island effect to elevate intraspecific diversity, which is typical for all life forms of peatland plants and invertebrates, as well as for some other groups of organisms living on peatlands.
- Dominance-diversity curves for peatland communities resemble those of communities that have been anthropically transformed, except that the species list is dominated by K-species in peatlands and by r-species in transformed habitats. The evaluation of peatland biodiversity in terms of

alpha, beta, and gamma diversity is applicable not only at species level, but also at ecosystem and organism levels (phenetic and genetic diversity). For example, ridge and hollow microforms could be regarded as elemental units of ecosystem diversity. Then, in an ecosystem level assessment, alpha diversity would reflect the number of microform types in a single peatland massif, beta diversity would reflect differences in microform representation between different massifs, and gamma diversity would reflect the range of microform types found in all peatland massifs occurring within a specified area.

- None of these approaches offers definitive methods for assessing the role of a specific peatland or peatland type in maintaining the biodiversity of other ecosystems, so that this aspect can be evaluated only indirectly and in a rather speculative manner at the present time.

We aim here to develop a more effective approach to the assessment of both the status and losses of biodiversity in peatlands, by taking account of functional characteristics which can be translated into ecosystem services.

- In any other ecosystem type, the conservative energy exchange pattern found in peatlands would give rise to a high diversity of ecological niches occupied by different species or forms, all of which would be involved in numerous (strong and weak) interactions that combined to create functionality. This is not the case in mire ecosystems, where most of the conserved energy is stored in a form (peat) that is unavailable for re-mobilisation by living organisms and is instead utilised for structuring habitats. Under these conditions, the energetic potential is realised mainly *via* intimate biological connections and functionally optimal solutions, and functional effectiveness is often best expressed by the involvement of groups of very small biologically tuned species, such as insects or aquatic invertebrates, which can be used as indicators.

Therefore, for peatlands, it is of paramount importance to have an overview of all their components and species and to understand their natural ecosystem processes and functions. Only then can we hope to accurately evaluate their biodiversity status, estimate losses, and address the latter competently through restoration measures.

Quantifying biodiversity losses

Once the nature, origin and potential scale of biodiversity losses is understood, a quantitative

evaluation should be within reach. This is important not only for justification and planning of a restoration and/or sustainable management programme, but also to define the baseline condition for gauging its success. However, it is unlikely to be straightforward because the difficulties already identified for the assessment of peatland biodiversity itself apply. As a general principle, the measurements upon which the evaluation of biodiversity losses is based should reflect the actual biodiversity characteristics of the peatland in question. Some key examples from literature are summarised in Box 2.

Existing practice reflects three different

approaches to selection of the characteristics upon which the evaluation is based, namely: structural and compositional characteristics of biodiversity; functional characteristics of biodiversity; and the socio-economic consequences of biodiversity losses.

The first approach employs direct methods, based on the traditional biodiversity indices or on even simpler formal parameters, to evaluate losses within a clearly delineated area. It is used mostly in environmental impact assessments for industrial projects, as well as in planning decommissioning and restoration in the same context. In its most reduced form, it involves the compilation of an initial list of

Box 2. Example approaches to the assessment of peatland biodiversity losses from literature.

Impact of wind farm development on the biodiversity (vegetation) of blanket bog in Spain

Fraga *et al.* (2008) investigated the plant species and vegetation diversity of blanket bog on summits and slopes of the Xistral Mountains in north-western Spain, nine years after the installation of wind turbines and associated infrastructure. The area surveyed was covered mainly by the endemic *Carici durieui-Eriophoretum angustifolii* community, which usually forms very homogenous vegetation. Qualitatively, new communities (wet meadows, wet heath or humid grassland) were observed in disturbed areas. Quantitatively, data from 100 vegetation relevés (55 impacted and 45 non-impacted sites) were used to calculate five indices of α diversity (diversity within sites) and six measures of β diversity (species turnover between sites). The analysis showed that impacted areas had significantly lower α diversity and higher β diversity than non-impacted areas.

Functional evaluation of tropical peat swamp forest in Kalimantan, Indonesia

Dommain *et al.* (2010) identified ability to self-regulate as the most important functional characteristic of tropical peat swamp forest, and defined contributing processes and structures (e.g. evapotranspiration control, surface oscillation, intraspecific variety of growth forms, species changes, vegetation types, microform structure, microtope patterns, mesopattern, limit to dome size) whose evaluation should reflect both biodiversity losses and the success of restoration.

The socio-economic consequences of biodiversity loss in coastal peatlands of Maputaland

The southernmost tip of the Mozambique coastal plain (in Kwazulu-Natal) is a region of exceptionally rich biodiversity, where many tropical species reach their southernmost distribution limits in Africa. Maputaland contains 60 % of the peatlands and most of the coastal peat swamps in South Africa; but their vegetation, structure, functioning, and the nature and effects of exploitation are still poorly understood. Grobler *et al.* (2004) used a vegetation and environmental dataset from May 2003 to assess the impact of subsistence cropping of (predominantly) madumbes (*Colocasia esculenta*) and bananas (*Musa xparadisiaca*) on coastal peat swamps. This showed that the ecological functioning—and thus the continued existence—of these systems is critically threatened by the related changes in forest structure and peat hydrology, which impact negatively on habitats and biodiversity; and will eventually deprive the rural community of a sustainable gardening environment, alter the nutrient balance of the associated lake system, and reduce the availability of clean (fresh) water. The situation poses an urgent challenge for the conservation agency and, perhaps more significantly, for the local community whose livelihoods are intricately interwoven with their peat swamp dominated environment.

Integrative assessment of peatland biodiversity losses in Central Kalimantan, Indonesia

Page *et al.* (2009) based this assessment on structural, functional and socio-economic characteristics. The main field observations were of vegetation, water level and the livelihoods of local communities, which were interpreted in terms of (i) land-cover dynamics of degraded peatlands, (ii) vegetation rehabilitation, (iii) restoration of hydrology, (iv) reinstatement of carbon sequestration and storage, and (v) promotion of sustainable livelihoods for local communities.

species followed by identification, from repeat surveys, of those which disappear as the ecosystem is altered by use. Otherwise, it may involve repeat mapping of vegetation at habitat or community level as in, for example, the UK Habitat Survey (JNCC 2010) and National Vegetation Classification (NVC) (Rodwell 2006) methodologies.

The second approach is functional, and based on observations that reflect how well the ecosystem is working. The variables observed—for example water levels, humidity and temperature at the surface, carbon sequestration rates or GHG emissions—reflect the ‘health’ of the ecosystem and hence, indirectly, its capacity to maintain biodiversity. This approach may be applied at ecosystem level or at species level *via* the availability of habitat types.

The third approach involves evaluation of the economic consequences of biodiversity losses. The ecosystem services whose alteration is likely to have economic consequences for human societies, and which are potentially threatened by changes in biodiversity, include: the provision of food, fibre, medicines and fresh water; pollination of crops; filtration of pollutants; and protection from natural disasters. The portion of natural resources provided by peatland biodiversity is most often monitored in tropical countries, where livelihoods tend to be most directly linked to biodiversity status.

Thus, we see that it is possible to arrive at very different interpretations of a generally-stated aim to assess biodiversity-related losses of ecosystem services, depending on the scale of the peatland and the focus of the investigator(s). Most treatments in the scientific literature incorporate elements from more than one of the approaches identified above (see Box 2), and none of them is globally applicable alone. Therefore, whether the intention is to carry out a strategic evaluation at national level or to formulate a management plan for an individual site, we may expect that the appropriate methodology for evaluation of peatland biodiversity losses will often be based on a combination of structural, functional and socio-economic characteristics assessed at suitable scales, and the details will be case-specific.

RESTORING BIODIVERSITY IN PEATLANDS

Underlying concepts

When an understanding of a particular loss of peatland biodiversity has been developed, the possibilities for its restoration can be explored. The conceptual framework for our consideration of different approaches is close to that developed by the Society for Ecological Restoration (SER), who

define (ecological) restoration as “the process of re-establishing to the extent possible the structure, function and integrity of indigenous ecosystems and the sustaining habitats they provide” (SER 2004). Defined in this way, restoration encompasses the repair of ecosystems (Whisenant 1999) and the improvement of ecological conditions in damaged wildlands through the reinstatement of ecological processes. Such integrative approaches to restoration have been widely adopted over the last decade, and most authors suggest that an indicator of biodiversity status should be used to judge success (Van Andel & Aronson 2006). The strategy is process-oriented, and involves directing autogenic processes whilst taking landscape interactions into consideration (Whisenant 1999). Importantly, this means that if techniques for repairing abiotic factors and processes such as hydrology and carbon balance are implemented effectively, they will also contribute to biodiversity restoration.

In terms of ecosystem dynamics, the likelihood that biodiversity will be maintained or recover after an external disturbance will depend upon whether the disturbance is transient or a long-term chronic pressure; and the ability of the peatland to resist, adapt to, or recover from it (its robustness, adaptive capacity and resilience) (Dawson *et al.* 2010). Peatlands are equipped with strong feedback mechanisms that, within limits, tend to move the system back towards a stable state after disturbance; and the stratigraphical record suggests that these mechanisms have enabled peatland massifs to spontaneously adapt to, and thus to survive through, past changes in climate. In some cases, the same mechanisms may work to move the system back towards an equilibrium state after direct human disturbance, but because the changes that man can impose are more abrupt and usually more severe than climatic changes, some intervention—in other words, active restoration work—is often needed to assist the recovery, at least if positive results are to be seen within timescales that are relevant in human terms. The need to reverse the effects of direct disturbance becomes more pressing when considered against the current backdrop of forced climate change because the effects are potentially additive; thus, reducing human pressure will enable utilisation of more of the ecosystem’s stability-maintaining capacity for adjustments driven by climate (e.g. Bragg & Tallis 2001).

Choosing an approach

The restoration of peatland to a condition in which it regains its ability to deliver specific ecosystem services is often a highly ambitious task demanding

substantial (usually financial) resources. To justify such investment, each initiative should have a clearly formulated goal and an adequately developed strategy for achieving it. This must be based on a firm foundation consisting of three elements, namely: a statement of the drivers for financial investment; an understanding of the natural structure and processes of the ecosystem; and an assessment of the nature, origin and scale of previous losses.

The key drivers in selecting an approach to biodiversity restoration at a particular peatland site will be statutory (legal) requirements, policy objectives and finances. Any or all of these may influence the combination of methods that is chosen. The methods that are available can be roughly grouped under the headings of the sub-sections that follow below.

Do nothing: expect spontaneous recovery

Under favourable conditions, the peatland may begin to self-restore, but the degree of recovery achieved will depend on the situation. This approach has, in effect, been repeatedly adopted simply through inaction and/or the abandonment of peatlands that have been disturbed in various ways. It must always be worthy of consideration, if only for economic reasons, but in many instances only limited success can be expected.

Cutover bog appears to re-vegetate spontaneously under some circumstances (e.g. Figure 9), but cases of incomplete recovery have been widely reported and studied (e.g. Lavoie & Rochefort 1996, Robert *et al.* 1999, Lavoie *et al.* 2003, Graf *et al.* 2008, Konvalinková & Prach 2010). The most recent comparative research indicates that spontaneous re-vegetation is more successful on block-cut than on milled areas (Triisberg *et al.* 2011), but even for the former there may be no clear resemblance to natural vegetation 70 years after abandonment (Pouliot *et al.* 2011). Thus, the resilience of these ecosystems to peat extraction by either method appears to be rather low. Observations of eroded blanket bog in Scotland suggest that it is possible for new *Sphagnum* carpets to develop spontaneously on bare peat, especially where patches of the underlying mineral surface are exposed (Birnie 1993, Lindsay & Freeman 2008). Vegetation can also recover surprisingly well after a one-off wildfire event (R. Lindsay, unpublished monitoring data, northern England). However, there are many other types of human disturbance and each restoration problem will be different in terms of the intensity and time course of impact, the characteristics of the peatland affected, and the exact way in which it responds.

The main point to be made here is that it is impossible to know whether spontaneous recovery is



Figure 9. Peat extraction is one of the most destructive human activities on peatlands, but the recovery of vegetation afterwards is strongly dependent on the extraction method used. Mire vegetation can re-establish quite readily after ‘wet’ peat extraction (excavation, ‘hydrotorf’ extraction, *etc.*). This peatland, 15 km from the city of Moscow, was excavated in the 1940s and now has typical bog vegetation with *Sphagnum* mats. Photo: A.A. Sirin.

in progress unless monitoring is carried out. Logically, establishment of a well-designed monitoring programme should be the first element of any peatland restoration initiative. If the data collected confirm that recovery of ecosystem functions is progressing satisfactorily, a substantial financial investment might be avoided. If a need for active intervention is demonstrated, the early monitoring data will provide a baseline against which the success of restoration works (and thus return on investment) can be measured. It is obviously expedient to delay active restoration until there is clear evidence of need, and this position will be reached only after sufficient information has been collected to build an understanding of trends in the unmanaged situation. Where practical interventions are dependent on funding opportunities that will expire before robust baseline data can be gathered, early attention to sourcing surrogate baseline information (for example, from a suitable control site) may help avert eventual difficulties in quantifying outcomes.

Habitat restoration for populations and species

In some cases, the goal of mire management is to restore the abundance or population structure of a single target species which has attracted the attention of stakeholders (and, consequently, funding) because it is rare or endangered. The outcome is usually evaluated in terms of reproduction success, population size and density, number and variety of individuals, genetic variability, or connectivity to other populations. For plants, there are two principal methods. The first aims to restore suitable habitats and often relies on natural recolonisation from available propagules to regenerate the population, but may also employ transplantation methods or the deliberate introduction of seeds, spores or vegetative propagules. The second involves transplanting specimens of the desired species into existing suitable habitats (Given 1994). For animals, habitat restoration is usually the more appropriate approach, although re-introduction might be considered in some cases.

The restoration of suitable habitat for a focus species may overlap with restoration of peatland vegetation, the mire ecosystem, the massif, or even the landscape. Since 2003, the conservation requirements for a single bird species, the Aquatic Warbler (*Acrocephalus paludicola*), have enabled the restoration of extensive tracts of peatland in the Pripyat river basin (central Europe); and it has recently been shown that the resistance to climate change of another bird, the Golden Plover (*Pluvialis apricaria*), is likely to improve as a result of peatland restoration in the UK (Box 3, Figure 10).

The appropriate management for a single species does not always align so satisfactorily with the objectives of ecological restoration, however. In some cases, such as the creation and maintenance of a wet patch hosting several plants of a rare orchid species, it may amount to an insignificantly small-scale exercise. In other cases it can negatively affect the natural diversity of the mire ecosystem and/or the biodiversity characteristics of adjacent areas. The simulation of historical flax and hemp processing activities (Martin & Robinson 2003) by repeatedly excavating pits on bogs to encourage colonisation by *Sphagnum* moss promotes the local cover of one group of mire species, but perpetuates the distortion of natural microtopography and water relations of the surrounding mire surface. Another example is the re-introduction of grazing or mowing on east European fen meadows with long histories of traditional extensive management (e.g. Bragg & Lindsay 2003) that are no longer required for agriculture. Whilst these practices may reinstate species-rich 'cultural climax' vegetation and/or valuable habitat for endangered birds, they could impair the recovery to 'natural' condition of functions such as peat formation (by removing biomass that may otherwise eventually be added to the peat deposit, or altering aeration conditions in the topmost layer of peat (Jeschke 1987, Schröder *et al.* 2015) and/or runoff generation (by compressing surface soil and thus altering its water storage and permeability characteristics). A study by Kotowski *et al.* (2013) at Biebrza National Park in Poland showed that mowing with tracked vehicles actually reduced the occurrence of rare plants and was generally detrimental to plant species diversity, although the outcome for target bird populations seemed promising. The reduction of plant species diversity was linked by these authors to compression of the mire surface by vehicle tracks and, specifically, to the resulting reduction of microtopography. The sustained application of 'artificial' conservation management measures on fens might be less controversial in cases where fen has, in effect, artificially succeeded bog as a result of peat extraction continuing until the residual layer consisted of fen peat only. An example is the Rivière-du-Loup peatland in eastern Canada (Cobbaert *et al.* 2004).

The species diversity of bird populations on peatlands often increases with disturbance of the habitat. For example, different species use intact and eroded parts of blanket mires in the UK (D. Jackson pers. comm.), and atypical species including Snow Bunting (*Plectrophenax nivalis*), raven, swallows and gulls move into oil and gas well sites in the arctic tundra. In other cases, disturbance promotes the

abundance of a single species. For sport shooting on some peatlands in the UK, rotational burning is deliberately practiced to increase habitat for Red Grouse (*Lagopus lagopus scoticus*), not only to the detriment of peatland vegetation, but also reducing carbon storage in the peat (Garnett *et al.* 2000) and possibly contributing to undesirably high colouration of the runoff collected by drinking water reservoirs

(Mitchell & McDonald 2002, C.D. Evans *et al.* 2005). Elsewhere in the UK, the conservation objectives set for wintering Taiga Bean Goose (*Anser fabalis fabalis*) preclude most restoration options for a degrading peatland that currently provides their favoured roosting habitat in flooded peat cuttings. In this example, higher value is assigned to a single species than to either the intrinsic characteristics of

Box 3. Two examples of peatland restoration to support vulnerable bird species.

The Aquatic Warbler Memorandum of Understanding (MoU) was finalised in Minsk (Belarus) under the auspices of the Convention on Migratory Species (CMS 1979), and became effective on 30 April 2003. It aims to safeguard the small migratory warbler *Acrocephalus paludicola* (Figure 10). This was the most widespread bird species of European sedge fens at the beginning of the twentieth century, but its world population had declined by 40 % over ten years due to drainage of the habitat. Therefore, it became a globally vulnerable (IUCN Red List) species. In 2010 the number of singing males in Belarus was 3,000–5,500, which is around 40 % of the world population. To meet the obligations imposed by the Memorandum, numerous projects were undertaken to restore Aquatic Warbler habitat, mainly on sedge fens. Under the auspices of an EU ‘LIFE’ programme, around 15,000 ha of peatland was restored in Belarus, along with similar habitats in Western Pomerania and Poland (Tanneberger *et al.* 2008). Restoration of a further 20,000 ha was completed in 2012 under a German government initiative driven by the new incentive of carbon trading opportunities (Tanneberger & Wichtmann 2011).

The Golden Plover (*Pluvialis apricaria*, Figure 10) is another bird species that benefits from peatland restoration. This wader reaches the southern limit of its global range in the United Kingdom (UK), where it breeds on upland heaths and bogs. Given the expected poleward shift in species distributions, the UK population is especially vulnerable to climate change (Pearce-Higgins & Green 2014). One potential source of risk is climate-related decline of this bird’s main food species, the crane-fly (*Tipula paludosa*). Pearce-Higgins *et al.* (2010) have demonstrated a negative correlation between Golden Plover numbers and August temperature, with a two-year lag, which is explained as follows. Adult crane-flies emerging from the surface layers of peat in May and June can provide a super-abundance of food for breeding birds, and more Golden Plover chicks fledge in years when crane-flies are plentiful (Pearce-Higgins & Yalden 2004). Crane-fly larvae suffer high mortality when the surface layers of peat dry out in hot weather. Consequently, in the following year, few adult crane-flies emerge and few chicks survive to fledge, resulting in a reduced Golden Plover population the year after that. This understanding can be used as a basis for developing appropriate management strategies. Because the density of crane-fly larvae increases with the moisture content of the peat, the negative effect of hotter summers on Golden Plover might be reduced by managing water levels on peatlands (Pearce-Higgins 2011). Peat wetness could be increased by blocking the drainage ditches (grips) that were dug across most UK uplands during the last century in a largely unsuccessful attempt to improve the quality of grazing for sheep (Stewart & Lance 1983). Several conservation organisations are already blocking grips for various purposes including biodiversity restoration, carbon sequestration and storage, amenity improvement and reduction of fire risk, and recent data show that crane-fly numbers increase significantly as a result (Carroll *et al.* 2011). This is one of the first studies to show how the resilience of an ecosystem to climate change might be improved through specific management practices. Importantly, although grip blocking is already beneficial for peatland conservation, the benefits for the wide range of bird species that feed on crane-flies are likely to increase as the climate changes in the future (Pearce-Higgins 2010). This study is also notable because it demonstrates a significant interaction between Golden Plover and crane-fly, reinforcing a recommendation that is common to all available reviews of ecological restoration, namely that species interactions should be taken into account whenever species restoration techniques are applied (Van Andel & Aronson 2006).

natural peatland or the medium-term sustainability of the whole ecosystem. Thus, the responses of individual bird species to human disturbance may enhance local species diversity and/or contribute to a national or global conservation target for a particular threatened species, but the management of peatland to support this facet of biodiversity alone may limit the potential for reinstatement of other ecosystem services. In such cases, a need for especially clear objective-setting is indicated.

For the most severely degraded peat bodies, the rehabilitation approach that is most often applied nowadays, especially in ‘green’ projects, involves restoration of their structure followed by planting to deliver alternative ecosystem services; for example, crops of cranberries, biomass or timber may be produced. These activities may be viewed as another type of species-focused restoration practice. Because they initiate unnatural successions and may involve non-peatland plants, such projects aim to create new ecosystem types rather than to restore natural peatland. However, some of the characteristic features of peatland ecosystems are still needed, such as peat soil, shallow water table and appropriate nutrient levels. A refinement of the approach is the principle of paludiculture (wet agriculture), which involves cultivating monoculture ‘crops’ of mire

species or artificial mixed plant communities in peatland habitats (Wichtmann & Couwenberg 2013, Schröder *et al.* 2015). The intention is to use the peatland for economic benefit whilst at the same time maintaining peatland ecosystem services such as carbon storage and the delivery of clean water to river systems. Crops are selected for their tolerance of the environmental conditions that prevail after re-wetting of the peat body, and are often obligate wetland species such as reeds or *Sphagnum* moss (Gaudig *et al.* 2014). In these cases, some peatland biodiversity value may be regained and maintained in conjunction with commercial use of the peatland, and there may be hydrological benefits to adjacent areas of semi-natural peatland.

Restoration of vegetation

Much of the biodiversity value of an undisturbed mire massif is concentrated in the surface layer or ‘acrotelm’ (Ingram 1978), which consists of living moss and slightly decomposed peat held together by the roots of vascular plants. The vegetation itself provides a significant fraction of the system’s species biodiversity, and furnishes the three-dimensional habitat mosaic that hosts other life forms ranging from birds and mammals to insect larvae and microbes. The acrotelm also has a pivotal functional



Figure 10. Two focus bird species for peatland restoration. Left: Aquatic Warbler *Acrocephalus paludicola* (photo S. Seyfert¹); right: Eurasian Golden Plover *Pluvialis apricaria* (photo Bjørn Christian Tørrissen²).
¹GNU free documentation license, version 1.2, <http://commons.wikimedia.org/wiki/Commons>; ²Creative Commons Attribution-ShareAlike 3.0 Unported Licence, <http://creativecommons.org/licenses/by-sa/3.0/deed.en>.

role in maintaining the stability of the massif. It receives and partitions rainfall so that, whether or not precipitation is the system's only water source, the peat layer is kept sufficiently wet to preclude aerobic decomposition and ensure that new peat continues to form; the water table remains sufficiently high to support specialised biota and maintain any aquatic elements of the micro-topographical mosaic; and water of appropriate quality is discharged to aquatic ecosystems downstream in sufficient quantities and with suitable timing to maintain their biodiversity in turn. Thus, if a degraded vegetation layer is restored, we can expect some recovery in all of these functions; and if the hydrological regime is restored, there will be benefits for vegetation and thus, again, for other ecosystem functions.

The requirements for peatland restoration set by environmental regulators in most countries are rather similar. As a rule, active intervention is expected. Even if the objective is to control fire or water colour, targets may be set for vegetation; for example, to achieve the presence of plant species that appear on a standard list, or to restore an appropriate assemblage of habitats. A typical restoration project is conceived as a single short phase of intervention that will halt degradation and set the system onto a course of recovery towards the equilibrium self-sustaining condition.

Usually, the vegetation is manipulated directly. This may involve the removal (physically or using herbicides) of undesirable species, such as the grass *Molinia caerulea* and invading trees on bogs, or planted trees on afforested sites (Brooks & Stoneman 1997, P. Anderson *et al.* 2009, R. Anderson 2010); or the re-introduction of desirable species, often onto bare peat where the primary surface has eroded or been removed, by spreading propagules or planting cuttings and seedlings (e.g. Quinty & Rochefort 2003, Carroll *et al.* 2009, Th  roux Rancourt *et al.* 2009). Thereafter, imbalanced competitive relationships may be controlled by ongoing vegetation management operations such as annual uprooting of saplings by hand, 'weed wiping' with herbicides, manual or machine mowing, or grazing (usually by sheep or goats on bogs, cattle or ponies on fens).

In most cases, manipulations of the vegetation aim to directly reinstate mire plant communities, with the expectation that this will promote recovery of the associated natural ecosystem features. Recent work in Canada has shown that a new *Sphagnum* carpet established on a milled peat surface takes 20 years to develop microforms comparable to those in natural bogs, and thus to reinstate the natural ecosystem

diversity at this level (Pouliot *et al.* 2011).

An alternative indirect approach to the restoration of mire vegetation has been adopted for sand-filled oil well platforms in northern Russia and some eroded peatland in England. Here, the bare surface is first stabilised by establishing a sward of grasses, with a view to either introducing or allowing natural recolonisation by mire species later. Especially where fertiliser is applied to promote establishment of the grasses, and the grasses are (at least locally) exotic species, the biodiversity benefits may be negative in the initial stages. It is too early to judge longer-term outcomes in general, although the expected replacement of sown Timothy grass (*Phleum pratense*) by a peatland species (the arctic cottongrass *Eriophorum scheuchzeri*) occurred in just four years at one oil well site in Nenets Autonomous Okrug, Russia (A. Popov, unpublished data).

In some cases, local microtopography may be adjusted in conjunction with the reinstatement of vegetation. Ditches on primary mire may (rarely) be filled completely or (more usually) dammed at intervals along their length, creating areas of open water resembling pools. On milled peatland in Canada, pools have been excavated specifically to introduce microtopographical diversity; but their biodiversity is still rather low after six years (Fontaine *et al.* 2007) and this may indicate a need for additional measures such as propagule manipulation to actively promote the establishment of appropriate species.

The intensity of the propagule supply is important not only for spontaneous re-vegetation, but also for active restoration techniques. The scientific literature reports many instances of seed-rain shortage constraining the success of restoration projects; for example, the small dispersal range of heather (*Calluna vulgaris* L.) seed was found to be a strong limiting factor for re-vegetation of bare peat in the UK uplands (Gilbert & Butt 2010). Especially comprehensive studies of seed dispersal potential in tropical peat swamp forest after fire have been carried out by Afriyanti & Simbolon (2004), and examples from other ecosystem types are described by Van Andel & Aronson (2006). One strategy that might be adopted to improve the situation (for example, where disturbance has resulted in local extinction of target species with limited dispersal ranges) involves the manipulation of propagule sources at both the primary and secondary stages of dispersal (Harper 1977). Another exploits existing seed banks by translocating topsoil from appropriate donor sites onto the restoration area; this technique has been used

for bogs (Rocheftort *et al.* 2003), fens (Cobbaert *et al.* 2004) and marshes (Brown & Bedford 1997). An alternative involves ‘sterilising’ the restoration area by removing a layer of topsoil containing an inappropriate seed bank (Klimkowska 2008). Many other techniques have been developed for various habitat types.

In view of the difficulties noted above, it is clear that good practice for any biodiversity restoration project should include a full evaluation of seed and propagule sources at an early stage. One of the baseline studies for restoration of the stream-valley fen “Drentse Aa” (The Netherlands) investigated the soil seed bank, the wind-blown seed rain, and the seed influx from the coats of animals as well as in their droppings; and the results sparked the idea that grazing animals could be used to carry plant propagules into areas undergoing restoration (Grootjans & van Diggelen 1998; see also Vander Kloet *et al.* 2012). An essentially similar strategy that has been applied on tropical peatlands directs avian vectors to deposit seed-laden droppings in areas under restoration by installing artificial bird perches (Graham & Page 2012). For non-peatland ecosystems, the success of restoration work has been enhanced by creating streams as a mechanism for propagule transport (Engström *et al.* 2009), and this technique might be considered for use in peatlands under some circumstances although hydrological aspects would need very careful attention. There have also been numerous studies of the role of floods in seed dispersal for riparian habitats which may be relevant to peatland restoration, especially for floodplain mire systems (Jansson *et al.* 2005, Groves *et al.* 2007).

Degraded peatlands have usually been drained. Therefore, almost universally, measures to reinstate species and habitat diversity are supported by hydrological manipulations that aim to improve habitat conditions by increasing surface wetness. The primary reason for damming drainage ditches is to raise the water table by retarding the discharge of surface water. The other main approaches involve the construction of surface bunds to contain or slow down runoff from bare peat surfaces (e.g. peat bunds on extracted peat fields, various types of obstructions in erosion gullies) and, where moss propagules have been spread, to apply straw mulch which tends to reduce evaporative water losses.

Apart from a few examples of species-focused conservation that intentionally prevent the system from returning to its natural condition, peatland restoration usually encourages the re-establishment of self-sustaining natural peatland communities (with associated biodiversity value), even if the policy

driver (e.g. water quality, fire prevention, coastal protection) is not specifically biodiversity orientated. This often requires manipulation of one or more abiotic factors including not only hydrology but also relief, nutrient availability and water quality. Occasionally, full ecosystem restoration has been attempted on very limited areas. Grootjans & van Diggelen (1998) identify a set of example projects where the management goal ‘restoration of vegetation’ was achieved by manipulating other ecosystem elements including: topsoil, seed and other propagule sources, biomass turnover (*via* grazing or mowing), water regime, and even microclimate (by felling adjacent forest).

Mire massif restoration

Where attempts to restore vegetation using the methods outlined above have failed, the cause is often to be found at a higher level of the structural hierarchy (Figure 3). Vegetation can re-establish successfully only if sufficient water of appropriate quality is available at the peat surface. This cannot be achieved if the rate of water loss from the peat body as a whole exceeds the rate of supply. Such imbalances can arise, for example, if the peatland’s footprint (the area of land that it actually covers) has been reduced, if its hydrological boundary has been altered by peripheral drainage, or if a groundwater supply has been diverted. In such cases, appropriate restoration measures will tackle the cause at mesotope level, aiming to stabilise the hydrology of the whole peat body in order to create suitable conditions for the reinstatement of mire vegetation on its surface.

If the peat body has been severely disrupted, restoration of the original vegetation may no longer be a viable proposition and the best that can be done is to establish an ecosystem type belonging to an earlier developmental stage; or, indeed, any peat-forming ecosystem type even if it did not feature in development of the disrupted peatland. For example, if a bog has been cut down to the fen peat layer, fen vegetation may establish more successfully than bog vegetation. At some Canadian sites where peat extraction had exposed minerotrophic (fen) peat, re-vegetation was relatively rapid but important genera (e.g. *Carex* and *Sphagnum* spp.) failed to colonise spontaneously (Graf *et al.* 2008) so that measures to artificially introduce these key species were still required. If the residual peat layer is very thin and flooding is a problem, lake or swamp may be the only viable target for restoration to a self-sustaining wetland ecosystem. This will at least set a course that could eventually result in the establishment of a new peat-forming ecosystem.

Landscape approach

In order to realise the full biodiversity potential of a restored peatland, it will be necessary to consider not only the massif itself but also its connections to other similar habitat patches, for example through reproductive and dispersal mechanisms (see, for example, Butovsky *et al.* 2004) whose ranges vary widely between different peatland species and life forms. If peatlands are too widely spaced within the landscape, recruitment may become impossible for some populations of mire species. This is the ecological networks concept of interconnectivity, which addresses the need to ensure free movement of wildlife between fragmented habitat patches and may also involve island biogeography theory. Its potential application in the present context is to determine which degraded peatland massifs should be afforded the highest priority for restoration in order to achieve a spatial distribution of mire habitat patches within the landscape that is optimal in terms of the interconnectivity requirements of at least the critical characteristic species.

A related consideration is the spatially varying capacity of the physical environment to support peatland systems, insofar as this will influence the degree of correspondence that can be achieved between a practically achievable distribution of massifs and the theoretical optimum. At landscape scale, there are similarities between peatland massifs that occupy similar geomorphological locations and have similar water supplies. For example, blanket bog is draped over summits and fed only by rainfall; spring mires may be associated with geological contact zones on hillsides where the rainfall supply is augmented by spring water; and floodplain mires occur where, as the name suggests, rainfall and seepage are periodically supplemented by floodwater. Hydrogenetic mire classifications (Succow 1988, Steiner 1992, Succow & Joosten 2001) are based on these similarities. It follows that, in the absence of human influence, the extent of peatland and the massif types represented in a particular landscape will express its signature combination of geomorphology, water sources and climatic wetness. In semi-arid zones, depressions with groundwater influence or floodplains may host the only peatlands to be found; whereas the perennial rainfall surplus of oceanic climates enables blanket mire to spread onto all but the steepest slopes of temperate-zone mountains, and in the low-lying terrains of the wet tropics supports the formation of vast domed peat swamp forest systems as described by J.A.R. Anderson (1983) and Dommain *et al.* (2010).

A legacy of human activities in highly populated

areas is that peatlands have disappeared from many locations that would be suitable on physical grounds alone, so their potential extent is now accessible only through modelling. An example based on some simple assumptions about the geomorphological limits for peatland development is provided by a recent exploration of the maximum potential expansion of peatland in Sweden during a hypothetical human-free interglacial, which uses gridded altitude (digital elevation model, DEM) data to identify all land with slope $\leq 1^\circ$, $\leq 2^\circ$ and $\leq 3^\circ$ as the basis of three peatland extent scenarios (Franzén *et al.* 2012). Further insights are provided by correlation analyses of the relationship between peatland extent and slope based on an extensive dataset for the whole of Karelia (Kolomytsev 1993). A more comprehensive modelling approach using a combination of DEM and national environmental datasets (e.g. water bodies, flood risk) to identify locations for six geomorphic settings (river marginal, basin, estuarine, coastal, extensive and slope) capable of accommodating wetland types with different relative dependencies on water from meteoric, telluric, flood and underground sources is provided by McInnes *et al.* (2007). Modelling of this kind may be required for the task of (re)placing 'missing' nodes within the habitat-patch network, which might be forgotten archaic peatlands under other uses or locations that currently have no peat but could support the establishment of mire vegetation, perhaps for commercial paludiculture (e.g. Sphagnum farming) or even with a long-term aspiration that a peat layer will develop. Finally, where a peatland habitat patch is required and no hydromorphologically suitable location is available, it may be necessary to adjust geomorphology. Some relevant techniques have already been developed; for example, in creating a new catchment for fen restoration in the Alberta oil sands area (Price *et al.* 2010) and in forming artificial catchments to support the re-establishment of peat swamp systems in the Niger Delta (Whisenant 1999 referring to Thomas L. Thurrow pers. com.).

Regardless of whether peatland is widespread or rare within a particular landscape, its natural distribution expresses the pattern of water movement from the highest to the lowest points; whether as surface runoff, as seepage through the soil or a peat layer, or through underground aquifers. Thus, the maintenance of natural peatland biodiversity at its highest spatial scale depends ultimately upon the hydrological integrity of the landscape, which man's activities can all too readily disrupt. To see obvious examples, we must travel to sparsely populated parts of the world. At the Rancho Hambro mire complex in

Tierra del Fuego (Argentina), where surface water draining from the valley side is intercepted by a road constructed in the upslope margin of the mire, Grootjans *et al.* (2010) report drowning of tree stands at the discharge points of culverts; and in the extensive patterned mirelands of Western Siberia, road and railway embankments constructed as access routes for the oil and gas industry cause water to pond upslope and cut off the water supply to the peatland downslope (Novikov 2009). In more heavily populated regions, more than a century of river engineering and other activities have often long ago obliterated the natural flow patterns of runoff water. Even in the ‘wilderness’ of the Scottish Highlands, many catchments have been modified by flow diversions installed in the mid-19th century to feed hydro-electricity reservoirs (Payne 1988). Under such circumstances, the first challenge of restoring a mire massif that has become degraded due to disruption of a water source, or blanket peatland that has been dissected by ditches or trackways, or an ecological network to support the top level of peatland biodiversity, may be to reinstate the hydrological integrity of the landscape.

On the one hand, landscape-level manipulations offer a holistic approach to biodiversity restoration, primarily by (re)creating suitable preconditions for development of a complete spectrum of ecosystem, species and genetic diversity. On the other hand, unless they are supported by perfect models and complete control of any prejudicial activities of other land users, single-intervention restoration projects based on this strategy might in practice be confounded by departures from the expected successional trends due to unpredicted changes in regional or global conditions driven by a combination of direct human pressure and climate change. In such cases, ongoing management may be required to establish and/or maintain the optimal habitat network, approaching the so-called ‘novel ecosystems’ scenario of Hobbs *et al.* (2009), which offers the opportunity for humankind to live in artificial ecosystems at the cost of assuming permanent responsibility for their maintenance.

In Europe, the ability of peatlands to support well-preserved habitats and contribute to ecological networks has not been sufficiently exploited in environmental conservation, despite the fact that peatlands can be included in regional Natura 2000 Special Protection Area (SPA) systems (Minayeva *et al.* 2008). In the future, yet another layer of landscape manipulation may be needed to safeguard the full biodiversity value of peatlands, given their potential role in supporting species adjusting to climate change. In this context we may expect, for example,

a northward advance of steppe conditions and related species in some regions of the world. Then, to achieve their maximum functionality as refugia and in providing habitat connectivity to enable the adaptive migration of species, the spatial distribution of individual mire massifs within the wider landscape will become increasingly important. Even without human influence, this might itself undergo adjustments in response to climate change, in that peatlands located in geomorphological settings with more resilient water supplies (e.g. including a groundwater component) may better survive a transition to drier climate than those that receive only rainfall and surface water. Thus, optimal planning for peatland restoration may ultimately require an exercise in landscape architecture based on a combined hydrogeomorphic and ecological network model capable of simulating climate-change scenarios and delivering solutions in the form of species migration routings.

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