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Boreal Peatland Ecosystems

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5 Peatland Fauna

André Desrochers and Gert-Jan van Duinen

5.1 Introduction

Peatlands (especially bogs) are among the last large undisturbed ecosystems in the world, and are home to substantial numbers of animals; however, bogs have almost completely disappeared from certain areas in western Europe (Joosten and Clarke 2002) and temperate North America (Poulin and Pellerin 2001) and basic information on the fauna of bogs is often lacking. The first descriptions of the invertebrate fauna of European peatlands were compiled in the first decades of the twentieth century (Dampf 1924a, b; Harnisch 1925; Goffart 1928; Peus 1932). From the point of view of vertebrate animals, peatlands remain one of the least studied terrestrial habitats. Perhaps one of the reasons for the modest interest in the vertebrate fauna of peatlands is that no vertebrate species is known to occur only in peatlands, even though certain species are found mostly on peatlands (see later). In contrast, a large number of invertebrate species have been reported almost exclusively from peatlands, at least in the southern part of the distribution area of these species (Dampf 1924a, b; Harnisch 1925; Goffart 1928; Peus 1932; Petersen 1954; Krogerus 1960; Spitzer and Jaro_ 1993). Among vertebrates, birds have been well studied in Fennoscandinavian peatlands since Hakala (1971), and more recently in eastern Canada (Calmé et al. 2002, and references therein). Peatland mammals and other vertebrates have been less well studied.

Peatlands cover vast areas of the northern regions, but they are also found to a lesser extent in populated, southern regions. Peatlands are thus an increasingly fragmented and distinct habitat as one goes from north to south and toward populated areas (Fig. 5.1). Not only do boreal peatlands change in size and isolation in north–south gradients, but they also change in character (Moore and Bellamy 1974; Pakarinen 1995) and may differ in terms of predator–prey relationships (Berg et al. 1992). For example, pools are less frequent in southern peatlands than in more northern ones, at least in eastern North America (Couillard and Grondin 1986).

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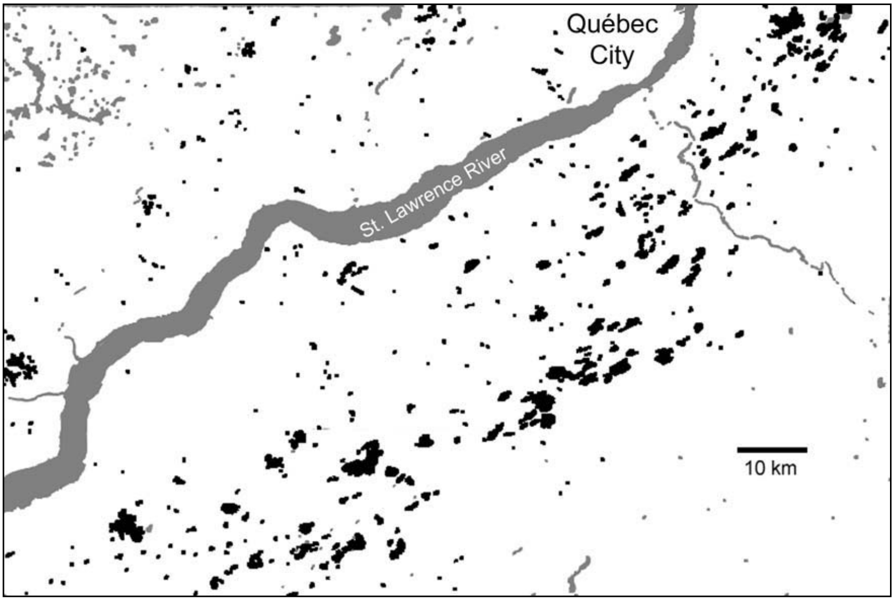

Fig. 5.1. Boreal peatlands are fragmented habitats in the southern end of their distribution. An example from southern Quebec, Canada

Besides purely latitudinal and climatic effects (Järvinen et al. 1987), the study of peatland fauna must take into account this fragmentation gradient, whereby peatlands form the main matrix of entire landscapes to a set of small, isolated pockets toward the south. Furthermore, the extent of degradation of peatlands due to human activities (drainage, agriculture, forestry, peat extraction, and atmospheric pollution) increases from north to south (Poulin and Pellerin 2001).

In this chapter, we review diversity and distribution patterns of peatland fauna, concentrating on *Sphagnum*-dominated raised bogs. Although there are reports on the wildlife of peatlands in most of the Holarctic region, the focus of this chapter will be northwestern Europe and North America, where our research on peatlands has been conducted. Our focus is birds and aquatic invertebrates – a reflection of our research interests, but partly also of the scientific literature on peatland wildlife. We review both recent and early literature on invertebrates and vertebrates, with an emphasis on conservation. More specifically, we present an overview of species diversity, followed by a more detailed discussion of distribution patterns of particular species or groups in relation to environmental key factors. We close with a presentation of conservation and restoration issues specific to peatland fauna.

5.2 Not One, but Many Wildlife Habitats

Bogs are often regarded as species-poor relative to other habitats, in regard to both vertebrates and invertebrates, either in Europe (Harnisch 1925; Peus 1932; Bölscher 1988) or in North America (Desrochers 2001; Mazerolle et al. 2001). Because of their acidity, extremely low nutrient availability, and wetness, bogs are generally regarded as hostile habitats for many species and some complete taxonomic groups. Chemical deficiencies almost entirely exclude, for example, lumbricid worms, isopods, and snails from acidic bogs (Harnisch 1925; Peus 1932; Speight and Blackith 1983), and low nutrient availability may exclude animal species that have high nutrient demands. Those claims of species poorness may be correct for several taxonomic and functional groups of animals or when these peatlands are compared with heterogeneous upland habitats such as mixed forests. However, the variation in wetness (from open water to relatively dry) and the structural diversity of bog vegetation sometimes makes them more diverse than surrounding habitats (Peus 1932; Stockwell 1994; Schikora 2002a).

While peatlands are often easy to distinguish and delimit from other landscape units, their internal diversity is great and provides a wealth of habitats for a large number of animal species. For example, different bird assemblages are found depending on the amount of forest cover (Kouki et al. 1992), and large open areas of peatlands are typically home to water birds, pipits, and some sparrows, while more generalist species are encountered along peatland edges. Furthermore, factors such as the nutrient availability and acidity – fens vs. bogs (Smits et al. 2002), presence of pools (Poulin et al. 1999), and soil drainage (Mazerolle et al. 2001) have marked effects on amphibians, reptiles, birds, and arthropods alike. On a smaller scale, arthropod communities differ considerably between dry hummocks and wet hollows in raised bogs (Göttlich 1980) or even on a smaller scale in the case of, for example,, testate amoebae (Mitchell et al. 2000a, b). This internal diversity of bogs, as well as gradients to the surrounding landscape, provides a suitable environment for species that need different sites to complete their lifecycle, such as carabid beetles inhabiting the open bog plateau, which stay in the top of dry hummocks in winter and in damp *Sphagnum* lawns in summer (Främbs 1994), and golden plover (*Pluvialis apricaria*) and black grouse (*Tetrao tetrix*) breeding in the central raised bog, but foraging in the more nutrient-rich edges of the bog landscape (Niewold 1993, 1996; Heckenroth 1994).

As with other systems, the diversity of microhabitats in a peatland generally increases with its size. This pattern was well illustrated in eastern North America (Fig. 5.2). Because of this, larger peatlands will tend to be more species-rich, as reported in Fennoscandinavia (Hakala 1971; Nilsson

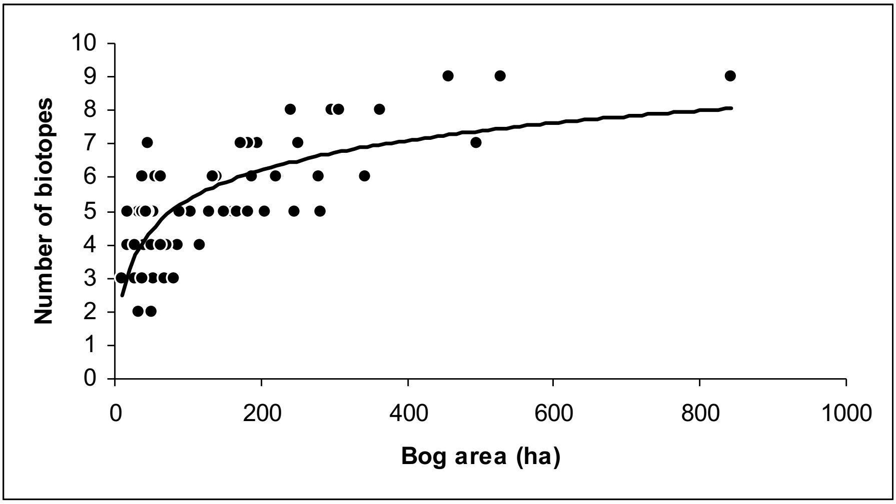

Fig. 5.2. Large eastern North American bogs have more microhabitats (number of biotopes) than smaller ones (adapted from Calmé and Desrochers 2000)

1986), Maine (Stockwell 1994), and Quebec (Calmé and Desrochers 2000). However, patterns of species diversity vary greatly among taxonomic groups, each of which responds to a particular set of environmental gradients.

5.3 Species Diversity and Distribution

As with other habitats, species diversity patterns in peatlands are shaped by or result from a combination of intrinsic and extrinsic abiotic and biotic factors. The importance of the various factors differs between taxonomic and functional groups of animals, but among the most important intrinsic factors availability of nutrients, vegetation structure, peatland size (see before), and the presence of pools can be regarded as key. However, subtler factors also influence species distributions. Among these are plant species composition (at least the part of it independent from vegetation structure), interspecific relationships like predation and competition, and, finally, intraspecific spacing or attraction.

Additionally, peatland species diversity would be impossible to understand without accounting for landscapes in which peatlands are embedded, especially in more southern regions. In this section, we describe species diversity of peatlands in light of known and likely influences of intrinsic and extrinsic ecological factors.

5.3.1 Invertebrates

5.3.1.1 Species Richness

Although raised bogs are often regarded as species-poor systems, Maavara (1955) found about 800 insect species in Estonian raised bogs and Valk (1988) gave 1,200 insect species, of which 49 are only found in bogs in Estonia. In the study of Maavara (1955) the most species rich taxonomic groups were Coleoptera (244 species found), Lepidoptera (250 species), Diptera (150 species), Rhynchota (103 species), and Hymenoptera (70 species). Continued research will have added many species to these numbers. In the Wagner Natural Area, a boreal spring fen in central Alberta, 2,181 species of arthropods were found, of which 1,410 were Hymenoptera (Finnamore 1994). From the number of parasitoid wasps this fen area is estimated to contain about 6,000 species of arthropods, of which Lepidoptera, Diptera, and Hymenoptera are the most species rich groups. Krogerus (1960) took samples from 38 Fennoscandinavian peatlands – including bogs, poor fens, rich fens, and peaty woods – and found 4,020 insect species and 296 other arthropod species. To these numbers many species from other arthropod and nonarthropod groups, like Cladocerans, Rotifers, and unicellular Rhizopods and Ciliates, can be added. The latter figures largely depend on the taxonomic focus, sampling methods used in the study, and of course on the characteristics of the areas studied, especially their heterogeneity.

According to Maavara (1955) the proportion of characteristic species in raised bogs is quite high, compared with that in other biotopes, showing the high level of specialization of bog fauna, because of the special environmental conditions in raised bogs. On the other hand, most of the species living in bogs, including a number of abundant species, can also live outside bogs (Maavara 1955) or can be characterized as generalists (Danks and Rosenberg 1987; Runtz and Peck 1994). For example, New England bogs and adjacent forests have 22 ant species in common. Two ant species were only found in bogs and 15 species were only collected from forests. In these bogs the ant community is dominated by the generalist species *Dolichoderus pustulatus*, occurring in a variety of open habitats, and the specialist *Myrmica dobifrons*, occurring in boreal bogs and other humid microsites (Gotelli and Ellison 2002). For spiders in northern and central European bogs, 80 % of the species (including the four most dominant species) can be regarded as eurytopic[1] species (Schikora 2002a).

Still, generalist or eurytopic species, even those blown into the bog from the surrounding landscape, are part of the bog community and

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[1] Eurytopic species are species occurring in various types of biotopes.

foodweb (Reynolds 1990). A number of the so called eurytopic species might depend on the combination of the bog *and* the surrounding biotopes to complete their life cycle or for persistence of the population. Valk (1988), for instance, mentions insects coming to raised bogs from outside when plants, especially heather, are flowering. Some of these insects, like the fly *Tephritis* sp., stay for a longer time in the bog, even to hibernate. Other species may depend on the specific conditions in the lagg zone that exist as a result of both the adjacent bog plateau and the adjacent minerotrophic landscape. To understand the importance of peatlands for animal species and the role of the species in the functioning of peatland ecosystems, the functions of the distinguished elements of the peatland ecosystem in the species' lifecycles and relations with (a)biotic processes should be analyzed. The lack of these analyses is mainly due to the large number of species and taxonomic groups, the different stages in the lifecycle, the use of different parts of the landscape by mobile animals, and the complex ecological relations, like foodweb relations and competition (Esselink 2002).

5.3.1.2 Latitudinal Variation and Temperature

When analyzing the effects of environmental factors on peatland fauna communities, factors operating at different scales should be taken into account, as well as the biological traits of the species. At both larger and smaller geographic scales species assemblages of peatlands change from north to south. Koponen (1994, 2002) and Koponen et al. (2001) studied spider assemblages along a geographic gradient in northern Europe and northern America from the arctic or hemiarctic to the hemiboreal or temperate zone and found that about half of the species occur along the whole gradient, few were only found in more northern peatlands, and a larger number of species were only found in more southern peatlands. Also along a shorter gradient in New England, within the relatively small range of 45–42° N, bog ant species richness declines with increasing latitude (Gotelli and Ellison 2002).

An important factor determining the occurrence of species along this north–south gradient is undoubtedly the climate. A species has to be able to grow during summer and survive in winter. Schäfer and Lundström (2001) found a clear pattern in the occurrence of mosquito species in forested wetlands from northern to southern Sweden that could be related to the lifecycles and life stage in wintertime of the respective species. Almost all mosquito species present above the Arctic circle have overwintering eggs and one generation per year (univoltine). In mid and southern Sweden species with more than one generation per year (multivoltine) and species with overwintering larvae or females were abundant. Most probably, only eggs can survive the harsh, long winters in the north and because of short summers not more than one generation can develop. The survival costs of the winter period may explain why the waterstrider *Aquarius najas* is wingless in northern Europe while frequently winged in central and southern Europe. This trend also exists between southern and central Finland (60–62° N). Overwinter survival in laboratory conditions was found to be higher in wingless individuals (Ahlroth et al. 1999).

In the southern range of raised bogs a considerable number of species only occur in raised bogs, whereas they can be regarded as generalist of eurytopic species in the northern range of their distribution area. These species are regarded as glacial relicts in the temperate zone. The temperature regime in raised bogs differs from that in surrounding landscape types by both lower-temperature and higher-temperature extremes, a higher chance of ground frost in summer nights, and a lower mean temperature (Peus 1932; Eggelsman 1980). This is due to the efficient absorption and radiation of long-wavelength radiation by the bog surface, as well as the high water content (Moore and Bellamy 1974). Furthermore, owing to the humic substances the bog water is brownish (dystrophic) and tends to warm up relatively fast, compared with clear water. Relatively high maxima are reached, especially between floating *Sphagnum* (Schmidt 1964). These characteristics make bog pools warm “islands” in a colder environment (Sternberg 1993). This could explain the aberrant habitat preference of the dragonfly species *Anax imperator* in Estonia, the northern range of its distribution area. In Estonia, *Anax imperator* is a thermophilous species, occupying smaller, dystrophic water bodies in raised bogs, presumably as these waters warm up fast (Kalkman et al. 2002).

Temperatures on the surface of hummocks in raised bogs can also reach relatively high temperatures (Norgaard 1951; Schikora 2002a). Norgaard (1951) has shown that two lycosid spider species living in *Sphagnum* bogs differ in their temperature tolerance and found a clear relation between the respective tolerance ranges and the activity of the spiders on, respectively, the *Sphagnum* capituli as well as the basking behavior. Species occupying raised bogs have to cope with, and can benefit from, both low and high temperatures, either by being in a resistant life stage or by moving to suitable parts in or outside the bog during unsuitable periods of time.

5.3.1.3 Environmental Factors

To identify the most important environmental factors in aquatic invertebrate assemblages within pristine raised bog systems, Smits et al. (2002) compared macroinvertebrate assemblages between the various types of water bodies in the Nigula raised bog system (southwestern Estonia).

Within this bog system, species assemblages were most different between the lagg, on the one hand, and the transitional mires and the more ombrotrophic central bog, on the other hand. This is not surprising, of course, as these elements of the bog system clearly differ in environmental conditions, such as pH, nutrient availability, and vegetation composition and structure. Minerotrophic primary bog lakes also generally differ from more ombrotrophic water bodies. Within the transitional mires, variation in macroinvertebrate assemblages was found, related to variation in the proportions of minerotrophic surface or subsoil water and ombrotrophic water. Water bodies that are only slightly influenced by minerotrophic water resemble the species assemblages of the pools and hollows in the central raised bog. Some species were, however, only found in the transitional mires and were absent from the central bog, like the damselfly species *Coenagrion johanssoni* and the dragonflies *Somatochlora arctica* and *Somatochlora flavomaculata*.

Within the Nigula bog, a complex pattern of water flow is present, and as a consequence so is variation in aquatic macroinvertebrate assemblages. In the bog, springs of acidic water are present, giving rise to a water flow through small brooks and a series of pools are influenced by this flow, each to a different extent. The water bodies that are, at least for some part of the year, connected to the bog brooklets or the more diffuse water flow, being a continuation of the brook, have several species in common with the most ombrotrophic sites. They are, however, also inhabited by some species mainly occurring in more minerotrophic or nutrient-rich water bodies, as in transitional mires or outside raised bog systems. Some of the central bog pools are not connected to this water flow, but still show similarity in species assemblage with the connected ones. This is probably due to the presence of subsurface water flows or the presence of fen peat at the pool bottom, resulting in a higher decomposition of the peat, a higher nutrient availability, and probably a higher microbial activity. A higher availability of nutrients in the flowing brooklet and some connected pools was apparent from the presence of filamentous algae in spring. Apart from the lagg, herbivorous water beetles in the central raised bog were only found in these water bodies with algae. The mayfly species *Leptophlebia vespertina* was observed emerging in highest numbers from the bog pools with slightly higher nutrient availability and only in these pools were the phytophagous larvae of the cranefly species *Phalacrocera replicata* (Cylindrotomidae) found (Smits et al. 2002).

Apart from availability of food in a proper quality and quantity, vegetation structure, volume of open water, and permanence are important factors in the occurrence of aquatic macroinvertebrate species (Macan 1954; Crisp and Heal 1996; Smits et al. 2002; van Duinen et al. 2004a). Several species, for example, the water beetle *Laccophilus poecilus* and the bug *Cymatia bonsdorffi*, were found only in central bog pools with open water, whereas other species, like the typical nonbiting midge *Lasiodiamesa* sp., were only found between fairly dense *Sphagnum* percolated by slightly minerotrophic water.

For most terrestrial invertebrate groups the species assemblage differs between the bog plateau and the lagg zone, as just described for aquatic invertebrates. Väisänen (1992) found the highest species richness of diurnal Lepidoptera in the lagg zone of a Finnish raised bog. For these herbivores the availability of host plants having a sufficient nutritional value is an important factor for both larvae and adults. Also for the (semi)terrestrial species in the bog system nutrient availability, acidity, and vegetation structure are important factors. According to Schikora (2002a) light situation and vegetation structure are the most important factors in the spatial distribution of spiders in bog complexes and moisture can be of general importance. For the carnivorous carabid beetles the availability of prey (e.g., springtails) and the presence of dry hummocks for overwintering are important, according to Främbs (1994). The presence of dry overwintering sites is important for all (semi)terrestrial invertebrates living in peatlands with a fluctuating water table, unless they have a resistant life stage in wintertime.

To understand causal relations behind the observed patterns in species assemblages and how species cope with the conditions in raised bogs, research has to be focussed on the "match" between, on the one hand, species traits, like locomotion, home range, growth rate, and feeding guilds, and on the other hand traits of their environment, including structures and processes, like decomposition and bioproduction. This research should also take into account the effects of competition and predation. An unknown number of the characteristic aquatic and terrestrial bog invertebrates are potentially able to live outside bogs, as well, but might be excluded from other types of landscapes, because they are poor competitors. For these species the absence, low abundance, or poor performance of competitor and predator species in bogs will be an important factor.

5.3.2 Amphibians and Reptiles

Owing to their acidity, raised bogs are not normally the first habitat to come to mind when one thinks about an amphibian habitat. Indeed, amphibians are highly vulnerable to the biogeochemistry of their habitat because of the osmotic exchanges through their skin, and acidity is often considered as harmful to their development (Pough 1976; Leuven et al. 1986). However, in recent years, there has been growing evidence of amphibians not only occurring in peatlands, but also occasionally breeding in associated pools, as evidenced by tadpoles (Mazerolle and Cormier 2003).

Species commonly found in boreal peatlands of North America include generalists such as the wood frog (*Rana sylvatica*), American toad (*Bufo americanus*), northern spring peeper (*Pseudacris crucifer*), green frog (*R. clamitans*), leopard frog (*R. pipiens*), and red-backed salamander (*Plethodon cinereus*). Less common North American species include eastern gray tree frog (*Hyla versicolor*), western chorus frog (*Pseudacris triseriata*), and mink frog (*R. septentrionalis*). Four-toed salamanders (*Hemidactylium scutatum*) are reputed to occur in peatlands, for they are closely associated with mosses, particularly *Sphagnum* (Wood 1955); however, intensive surveys done recently in bogs in their eastern North American range have resulted in no reports of the species (Mazerolle 2003), despite their regional occurrence (Bider and Matte 1994).

Amphibians have complex life cycles (Wilbur 1980), which may lead them to use peatlands as part of larger sets of habitats during their lifetime (Mazerolle 2001). It has been hypothesized that amphibians retreat to peatlands as summers advance, because other wetlands may disappear following dessication. However, one study based on capture rates across drift fences on peatland edges found no evidence of net movement toward or from peatlands (Mazerolle, personal communication). Within a peatland, pools are clearly an important asset for amphibians. Despite their low pH, peatland pools harbor a rich invertebrate life (see before) and may thus provide an important feeding habitat for frogs (e.g., mosquito and mayfly larvae) and salamanders, at least in certain periods of their life cycle. Pool size and proximity to areas cut over by the peat industry do influence the probability of occurrence of species such as the green frog (Mazerolle and Cormier 2003).

Unlike amphibians, reptiles are seldom encountered in boreal peatlands. In northern Europe, the common lizard (*Lacerta vivipara*) and common viper (*Vipera berus*) are frequently seen in peatlands, and are able to survive and reproduce, according to sightings of pregnant females and juveniles (H. Strijbosch, unpublished data). However, frogs and toads are rarely observed in Estonian raised bogs. Our surveys in eastern Canadian peatlands have on a few occasions produced garter and green snakes (Rochefort, personal communication). However, we are aware of no quantitative data on bog reptiles.

5.3.3 Birds

Detailed knowledge of peatland birds in North America is a recent phenomenon. However, Fennoscandinavia has been the stage for quantitative work on peatland birds since as early as the 1950s (reviewed in Desrochers 2001). In North America, most of the information on peatland birds comes from Minnesota, Maine, Michigan, and eastern Canada, leaving much to be learned about birds of northern peatland landscapes. The pioneering work by Erskine (1977) provides a notable exception.

5.3.3.1 Avian Diversity Patterns

No bird species are found exclusively in peatlands, either North American or Eurasian ones. Peatlands are home to well over 100 bird species and several families of birds in western Europe and North America. Yet, only mallard and northern harrier (for scientific names not mentioned in the main text, see Table 5.1) are commonly found both in North American and Fennoscandinavian peatlands (Table 5.1). Surveys of breeding birds by Desrochers and colleagues in 120 eastern Canadian bogs from 1993 to 2002 yielded 10,575 birds in point counts, the majority of which belonged to four species. Those species are (in decreasing order) common yellowthroat, white-throated sparrow, Lincoln's sparrow, and savannah sparrow.

As in other habitats, some bird species are very abundant, while most species are only found there occasionally. Certain peatlands in the south can harbor a large avian diversity, for example, 81 species reported by Stockwell (1994) in Maine. It would be tempting to explain the increase of avian diversity in peatlands from north to south (Boström and Nilsson 1983; Desrochers 2001) by the location of the northern limit of species ranges in latitudes where peatlands are found. However, this applies only to a few species and therefore the latitudinal gradient begs another explanation. Besides diversity, species composition varies greatly among regions, with land birds predominant in North American peatlands, and water birds predominant in Eurasian peatlands (Fig. 5.3). The most likely explanations for such contrast are the presence of a latitudinal gradient in the abundance of pools (larger in the north), as well as the greater inputs from surrounding habitats in the south, where peatlands tend to be smaller and more isolated. Despite the north–south gradient of bird diversity, enough species are retained in this latitudinal gradient to confer a contrasting, boreal fauna relative to that found in surrounding landscapes (Calmé et al. 2002). As a result, peatlands are often the most southern locations for certain species, such as palm warbler (Stockwell 1994).

Outside the breeding season, however, avian diversity patterns change drastically. In both North America and Europe (and undoubtedly Asia), peatlands often represent important staging areas for migrants, mostly shorebirds such as snipes and pectoral sandpipers (*Calidris melanotos*), but also ducks and geese that use the pools as staging stops. In winter, a very small number of birds can be found in peatlands, with grouse, for example, sharp-tailed grouse (*Tympanuchus phasianellus*) in North America, red grouse (*Lagopus scoticus*) in the UK, and black grouse in

Table 5.1. Bird species commonly found in North American peatlands have little in common with those found Fennoscandinavian peatlands

Species	Quebec	Michigan	Finland	Sweden	Germany	Western Russia
Horned grebe (*Podiceps auritus*)						x
Red-throated loon (*Gavia stellata*)				x		x
Bean goose (*Anser fabalis*)						x
Eurasian wigeon (*Anas penelope*)						x
Common teal (*Anas crecca*)				x	x	x
Mallard (*Anas platyrhynchos*)		x	x	x	x	x
Black duck (*Anas rubripes*)	x					x
Pintail (*Anas acuta*)						x
Northern shoveler (*Anas clypeata*)						x
Tufted duck (*Aythya fuligula*)					x	x
Common goldeneye (*Bucephala clangula*)				x		x
Osprey (*Pandion haliaeetus*)				x		
Northern harrier (*Circus cyaneus*)	x	x	x			
Peregrine falcon (*Falco peregrinus*)			x			x
Willow ptarmigan (*Lagopus lagopus*)			x			
Common crane (*Grus grus*)			x	x		x
Common snipe (*Gallinago gallinago*)				x	x	
Wilson's snipe (*Gallinago delicata*)			x			
European jacksnipe (*Lymnocryptes minimus*)			x			
Black-tailed godwit (*Limosa limosa*)					x	
Whimbrel (*Numenius phaeopus*)			x	x		x
Eurasian curlew (*N. arquata*)			x	x	x	x
Common redshank (*Tringa totanus*)				x	x	
Common greenshank (*Tringa nebularia*)			x			x
Green sandpiper (*Tringa ochropus*)				x		
Wood sandpiper (*Tringa glareola*)			x	x		x
Broad-billed sandpiper (*Limicola falcinellus*)			x			
Eurasian golden plover (*Pluvialis apricaria*)			x	x	x	x
Northern lapwing (*Vanellus vanellus*)			x	x	x	x

Common gull (*Larus canus*)			x	x	x	
Herring gull (*Larus argentatus*)			x			x
Lesser black-backed gull (*Larus fuscus*)						x
Black-headed gull (*Larus ridibundus*)			x	x		x
Common tern (*Sterna hirundo*)						x
Mourning dove (*Zenaida macroura*)		x				
Common cuckoo (*Cuculus canorus*)				x	x	
Short-eared owl (*Asio flammeus*)			x			
Whip-poor-will (*Caprimulgus vociferus*)		x				
Ruby-throated hummingbird (*Archilochus colubris*)		x				
Northern flicker (*Colaptes auratus*)		x				
Alder flycatcher (*Empidonax alnorum*)[a]	x	x				
Eastern kingbird (*Tyrannus tyrannus*)	x					
Red-backed shrike (*Lanius collurio*)				x		
Northern shrike (*Lanius excubitor*)			x	x		
Blue jay (*Cyanocitta cristata*)	x					
American crow (*Corvus brachyrhynchos*)	x					
Cedar waxwing (*Bombycilla cedrorum*)	x	x				
Eastern bluebird (*Sialia sialis*)		x				
Veery (*Catharus fuscescens*)		x				
Hermit thrush (*Catharus guttatus*)	x					
American robin (*Turdus migratorius*)	x	x				
Whinchat (*Saxicola rubetra*)			x	x	x	
Stonechat (*Saxicola torquata*)					x	
Gray catbird (*Dumetella carolinensis*)		x				
Brown thrasher (*Toxostoma rufum*)		x				
Black-capped chickadee (*Poecile atricapillus*)		x				
Tree swallow (*Tachycineta bicolor*)		x				
Ruby-crowned kinglet (*Regulus calendula*)[a]	x					
Grasshopper warbler (*Locustella naevia*)					x	
Yellow warbler (*Dendroica petechia*)		x				
Skylark (*Alauda arvensis*)			x	x	x	x

Table 5.1. (*Continued*)

Species	Quebec	Michigan	Finland	Sweden	Germany	Western Russia
Pied wagtail (*Motacilla alba*)			x	x		
Yellow wagtail (*Motacilla flava*)			x	x	x	
Tree pipit (*Anthus trivialis*)			x		x	
Meadow pipit (*Anthus pratensis*)			x	x	x	
American goldfinch (*Carduelis tristis*)	x	x				
Linnet (*Carduelis cannabina*)					x	
Purple finch (*Carpodacus purpureus*)[a]						
Yellowhammer (*Emberiza citrinella*)			x			
Reed bunting (*Emberiza schoeniclus*)			x	x	x	
Song sparrow (*Melospiza melodia*)	x	x				
Lincoln's sparrow (*Melospiza lincolnii*)[a]	x					
Swamp sparrow (*Melospiza georgiana*)	x					
White-throated sparrow (*Zonotrichia albicollis*)[a]	x					
Savannah sparrow (*Passerculus sandwichensis*)[a]	x					
Field sparrow (*Spizella pusilla*)		x				
Eastern towhee (*Pipilo erythrophthalmus*)		x				
Tennessee warbler (*Vermivora peregrina*)	x					
Nashville warbler (*Vermivora ruficapilla*)	x	x				
Magnolia warbler (*Dendroica magnolia*)[a]	x					
Yellow-rumped warbler (*Dendroica coronata*)[a]	x					
Palm warbler (*Dendroica palmarum*)[a]	x					
Common yellowthroat (*Geothlypis trichas*)	x	x				
Northern cardinal (*Cardinalis cardinalis*)		x				
Common grackle (*Quiscalus quiscula*)	x					
Brown-headed cowbird (*Molothrus ater*)	x	x				

Data for Quebec from Calmé et al. (2002), for Michigan from Brewer (1967), for Finland from Hakala (1971) and Järvinen and Sammalisto (1976), for Sweden from Boström and Nilsson (1983), for Germany from Bölscher (1995), and for western Russia from Häyrinen (1986). Species sorted according to Monroe and Sibley (1993)

Crosses denote species found in the majority of years or field sites.

[a] Species marked with an *asterisk* are of high conservation concern in Canada (Dunn et al. 1999).

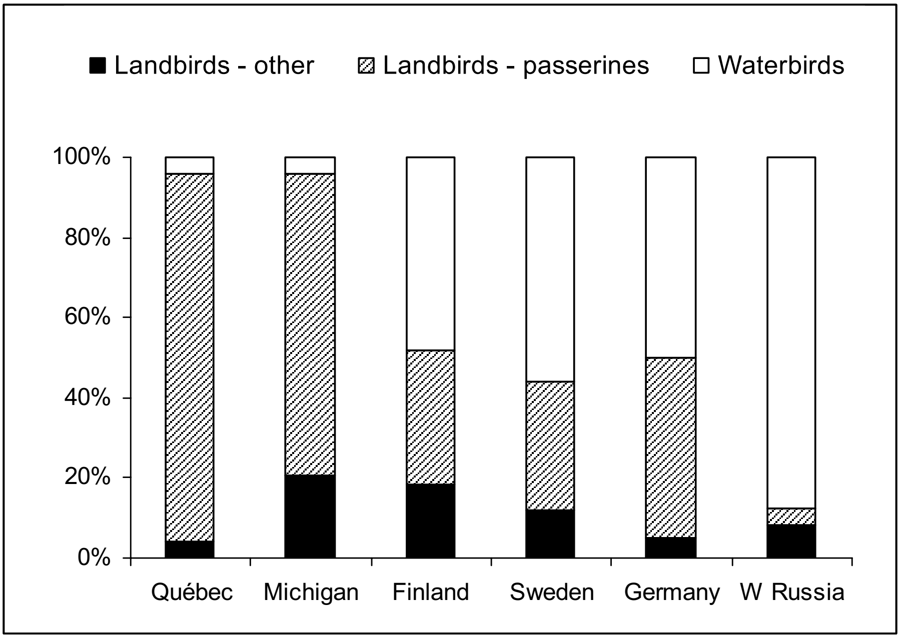


Fig. 5.3. Avian species groups in peatlands of six geographic regions (see Table 5.1 for data sources)

Fennoscandinavia, being among the most notable species. Snow buntings can also be seen in most northern peatlands in winter. In regions under milder winter conditions, such as the UK, geese also widely use peatland pools.

Avian diversity is somewhat greater in North American peatlands than in Fennoscandinavian ones. On the basis of the published literature, the main contrast between Eurasian and North American peatlands in regard to birds would appear to be the preeminence of shorebirds in Eurasian peatlands (Hakala 1971; Väisänen and Järvinen 1977), as opposed to North American peatlands, in which songbirds usually dominate (Calmé et al. 2002). While most species of shorebirds of western Europe are commonly found in peatlands, the only shorebirds to be found regularly in southern peatlands of North America are Wilson's snipe (*Gallinago delicata*) and upland sandpiper (*Bartramia longicauda*). However, peatlands of northern North America do have a more complete assemblage of shorebirds (Morneau 1995), and it is likely that most differences in peatland bird communities between western Europe and North America come about from a purely latitudinal effect, with water birds dominant north of 60° N and songbirds to the south.

5.3.3.2 The Role of Vegetation Structure

While vegetation structure in open peatlands of both continents is somewhat similar, i.e., large expanses of ericaceous shrubs with clumps of conifers, important differences exist, particularly in composition of tree species. In North America, black spruce and tamarack are the main tree species, as opposed to pine *Pinus sylvestris* in Fennoscandinavian peatlands (Chap. 2).

As with other wildlife groups, birds are highly responsive to vegetation structure. From large open areas found deep inside large peatlands to forested areas in their periphery, bird assemblages change almost completely, and it is the wetter and more open areas of peatlands that harbor most peatland specialists. Interestingly, Niemi (1985) found evidence for evolutionary convergence between North American (Minnesota) and Finnish granivorous and insectivorous birds of peatlands. For example, birds found in shrubby habitats are relatively small, with long legs and small flight muscles, compared with species more typically found in forested peatlands.

Vegetation patterns may explain why distributions of bird species in peatlands are nested subsets, i.e., most of the time, all species in a species-poor peatland will be found in peatlands with a larger number of species. In their southern Quebec study area, Calmé and Desrochers (1999) showed that in 67 peatlands whose bird assemblages were measured intensively five bird species were found exclusively in peatlands in the upper 30th percentile range of sizes. Those species were Wilson's snipe, upland sandpiper, American bittern (*Botaurus lentiginosus*), clay-colored sparrow (*Spizella pallida*), and field sparrow. Those species were not typical of peatlands, but rather of large open or biologically-productive areas, such as fen laggs that appear more frequent in Quebec's larger peatlands (Calmé and Desrochers 1999). Nested subsets are not unique to peatlands, but pertain to a wide variety of systems (Glenn and Nudds 1989; Blake 1991; Cutler 1991; Patterson and Brown 1991; McCoy and Mushinsky 1994; Bert 2001; Fernández-Juricic 2002).

5.3.3.3 Landscape and Spatial Issues

While small-scale differences in vegetation patterns may explain distribution patterns of peatland species, larger-scale (landscape) factors also play an important role. In southern Quebec, Calmé and others (Calmé and Haddad 1996; Calmé and Desrochers 2000) demonstrated the importance of peatland area and isolation in explaining species occurrence patterns. Isolation per se may appear as an unlikely cause for bird distribution patterns, given the high vagility of these organisms. However, despite their ability to migrate over large distances, birds are apparently inhibited in their movements during the dispersal periods by small intervening gaps between their habitat patches (Desrochers and Hannon 1997).

Landscape and spatial issues are further complicated by the fact that bird territory sizes can easily vary by 1 or 2 orders of magnitude (0.1–10.0 ha), with obvious consequences for their space needs. Furthermore, recent work on conspecific attraction (Etterson 2003; Green and Ostling 2003; Wagner and Danchin 2003) suggests that species "real-estate" needs may be much larger than expected solely from the size of individual territories. Work by Hokkanen (2004) in the Siikaneva peatland, Finland, supports the conspecific attraction hypothesis (Fig. 5.4).

Vegetation structure generally follows predictable trends from the edge toward the center, especially in large peatlands (Poulin et al. 1999). Thus, because of their association with vegetation structure (see before), bird assemblages are expected to change predictably along the same gradient. The latter prediction has been supported with Finnish peatlands, with yellow wagtails and whinchats associated with peatland edges, in contrast to meadow pipits and wood sandpipers (Sammalisto 1957; Hakala 1971). In eastern Canada, savannah and Lincoln's sparrows are associated with the interior of large peatlands, whereas palm warblers and common yel-

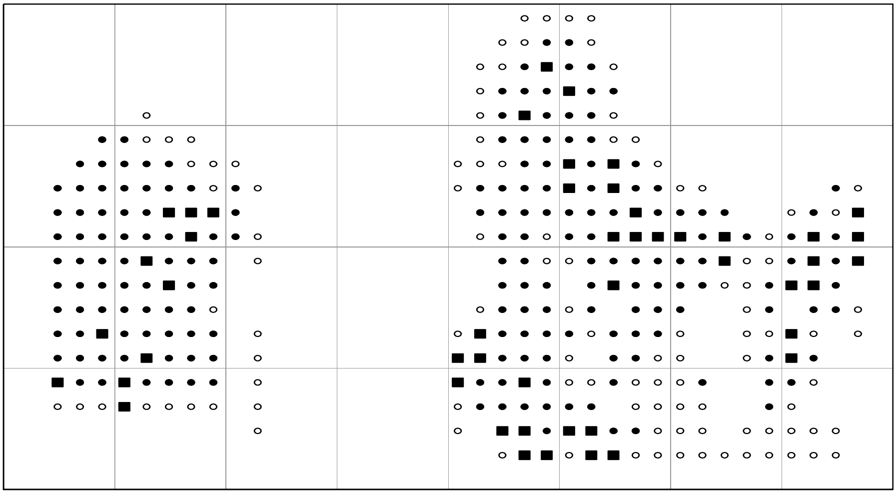


Fig. 5.4. Clumped distribution of meadow pipits and their habitat in Siikaneva Peatland, Finland. *Open circles* peatland outside vegetation parameters suitable for pipits, *closed circles* peatland with suitable vegetation for pipits, *squares* areas used by pipits. Spatial autocorrelation of occurrence within habitat, measured by Moran's I, was significantly positive with distance lags less than 200 m. (Data courtesy of Reijo Hokkanen, University of Helsinki)

Table 5.2. Population densities of breeding songbirds in eastern Canadian bogs (adapted from Delage et al. 2000)

	Interior		Edge	
Song sparrow	0.45	(0.45)	0.76	(0.55)
White-throated sparrow	0.74	(0.42)	2.39	(1.21)
Lincoln's sparrow	3.99[a]	(1.27)	2.94	(0.93)
Savannah sparrow	3.66[a]	(1.4)	1.30	(0.65)
Hermit thrush	1.26	(1.07)	0.99	(0.68)
Yellow-rumped warbler	0.00	–	0.45	(0.45)
Palm warbler	2.27	(0.88)	4.32[a]	(1.40)
Nashville warbler	0.00	–	0.86	(0.59)
Common yellowthroat	3.88	(1.42)	12.44[a]	(2.69)
Magnolia warbler	0.00	–	0.39	(0.28)

The numbers are pairs per 10 ha, followed by standard errors of the mean (n=20 peatlands).

[a] Associations

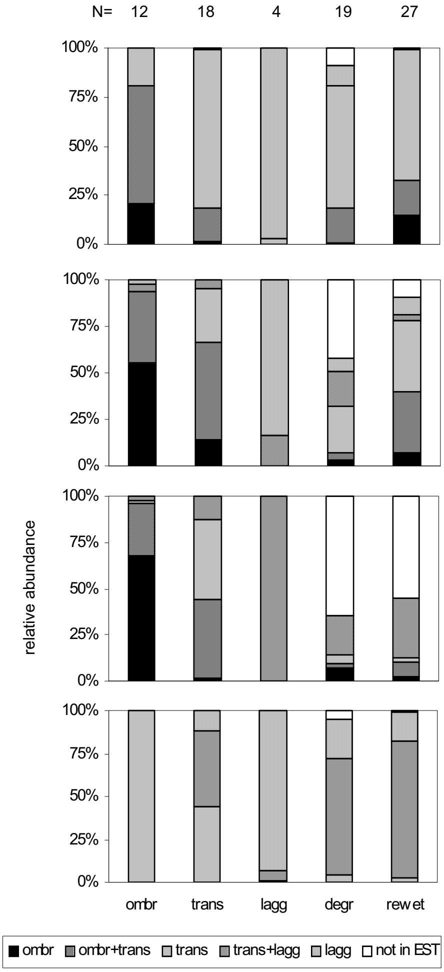
lowthroats are found disproportionately along peatland–forest edges (Table 5.2). Hakala (1971) noted that the degree to which species were associated with edges was itself associated with species' propensity to use pools or isolated trees. Besides vegetation structure, potentially lower exposure to upland predators may lead some species of birds to breed in wet and open, central parts of bogs (Berg et al. 1992).

5.3.4 Mammals

North American boreal peatlands are home to a variety of rodents, such as lemmings (*Synaptomys* sp.), shrews (*Sorex* sp.), and voles (*Clethrionomys* sp., *Microtus* sp.), as well as moose (*Alces alces*), lynx (*Lynx* sp.), black bear (*Ursus americanus*), and (in winter) deer (*Odocoileus virginianus*). In Europe, peatlands are used frequently by elk (*Cervus elaphus*), wolf (*Canis lupus*), fox (*Vulpes vulpes*), beaver (*Castor fiber*), river otter (*Lutra lutra*), muskrat (*Ondatra zibethica*), raccoon dog (*Nyctereutes procyonoides*), badger (*Meles meles*), pine marten (*Martes martes*), polecat (*Mustela putorius*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). Most of the latter species are absent from central ombrotrophic parts of peatlands. In fact, beaver, otter, muskrat, raccoon dog, badger, marten, and wild boar likely occur only on the edges of bogs.

While large mammals are sometimes found in peatlands, the bulk of species and populations are composed of small species. Mazerolle et al. (2001) found that five species accounted for 91 % of all captures of small

Fig. 5.5. Relative abundance of six groups of (from *top* to *bottom*) Chironomidae, Coleoptera, Hemiptera, and Oligochaeta species. The species are attributed to these groups based on their preference for the ombrotrophic bog, transitional mire, and lagg in the pristine Estonian bogs. Sampling sites are grouped into ombrotrophic water bodies, water bodies in transitional mires, and laggs in pristine raised bogs and water bodies in degraded and rewetted bogs. (From van Duinen et al. 2004b)



mammals made in eastern Canadian bogs: masked shrew (*Sorex cinereus*), meadow jumping mouse (*Sorex cinereus*), meadow vole (*Microtus pennsylvanicus*), pygmy shrew (*Sorex minutus*), and Arctic shrew (*Sorex arcticus*). Remarkably, the latter set of species include only one species known as bog specialists (Arctic shrew). Other bog specialists such as northern bog lemming (*Synaptomys borealis*) and southern bog lemming (*Synaptomys cooper*; Banfield 1977; Nordquist 1992) were not found in the surveys made by Mazerolle et al. (2001), despite the large sampling effort. The use of peatlands by small mammals appears highly dependent on soil moisture (Mazerolle et al. 2001). Drier sites seem to host more species than wet sites, and mostly generalists are also abundant in surrounding areas. Thus, peatland edges are expected to have a richer mammalian fauna than areas located well inside peatlands. However, the interior of peatlands may be of greater relative importance to peatland specialists such as the masked shrew, but that remains unsupported by data. Of 15 small-mammal species encountered in eastern Canadian bogs, only two are known to exhibit a preference for bogs: the Arctic shrew and the southern bog lemming (Mazerolle et al. 2001)

5.4 Conservation Issues

Our knowledge of population trends of most faunal taxa, let alone their demographic dependency on peatlands, is little. Birds are arguably the best monitored faunal taxon in that respect. From the North American Breeding Bird Survey (Sauer et al. 2003), we know that among the 20 most common bird species found in eastern North American peatlands, none have experienced severe declines since the early 1960s. However, nine common peatland birds have their geographic range primarily in peatland-rich Canada (Dunn et al. 1999; flagged species in Table 5.1). Peatlands in northern Canada may be essential to maintain large numbers of the latter nine species. Further south, peatlands may help maintain regionally uncommon species such as upland sandpiper and palm warbler in North America, or golden plover, common crane, black grouse and several dragonfly and butterfly species in parts of western Europe. For many of these species the conservation of only the central ombrotrophic parts of peatlands will not suffice to maintain or restore their populations, as they need gradients to the more minerotrophic parts of the bog landscape as well at least in part of their lifecycle (Heckenroth 1994).

The conservation of peatland fauna is probably not a pressing issue yet as far as global populations are concerned. However, peatland fauna is under pressure at the regional and local levels, particularly in populated areas, and there is associated pressure on land for urban sprawl, agriculture, forestry, or peat-extraction purposes. In fact, the majority of peatlands have disappeared in most of Europe as a result of these activities, while sizeable portions of this habitat remain untouched in North America (Joosten and Clarke 2002). Nutrient enrichment of originally nutrient-poor peatlands, owing to increased atmospheric nitrogen deposition, has affected plant and animal communities (Limpens et al. 2003, Chap. 10; Tomassen et al. 2004; van Duinen et al. 2004b).

5.4.1 Urban Sprawl

Urbanization generally has an irreversible impact on peatlands, bringing profound and lasting changes in wildlife communities. From the standpoints of habitat and species conservation, the conversion of peatlands by urban sprawl is clearly a net loss and does not require much ecological analysis, apart from the fact that those losses are particularly important for southern temperate areas, because of their proximity to towns. The loss of peatlands through urban sprawl therefore adds to the vulnerability of species dependent on wetlands which reach their northern range limit in the southernmost peatland regions. If we take into account the high species diversity of vertebrates and, especially, invertebrates in peatlands (see previous sections), there is clearly a case for conservation of peatlands near populated areas, as part of larger wetland conservation strategies. Additionally, most states of North America and western Europe do have plans for conserving regional biodiversity and wetlands in particular (e.g., Ramsar convention).

5.4.2 Agriculture and Forestry

Peatland losses through agriculture and forestry, especially in western Europe, have clearly contributed to endangering peatland species (Chap. 16). It can be argued that replacement habitats such as pastures and crops in Europe have been hosting wildlife communities for decades, if not centuries. However, today, the role of agricultural land as viable replacement habitats is increasingly questionable because of recent changes in agricultural practices, fueled by subsidies that have simplified those ecosystems and led to the decline of flagship bird species such as skylark and barn swallow (*Hirundo rustica*; Gregory et al. 2003).

Converting peatlands into agricultural land generally has irreversible effects on the land, its vegetation, and its associated fauna (Poulin and Pellerin 2001). In continental Europe, and to some extent in the UK, agriculture has been responsible for large peatland losses (Joosten and Clarke 2002; Gregory et al. 2003). Forestry practices also have implications for peatland fauna. The most important of those is drainage of forested peatlands, which owes its existence to the fact that water-logged soils of forests on peat are improper for tree growth (Päivänen 1999). To what extent forest drainage per se affects birds and medium-to-large mammals is unclear, and remains little studied to date. Clearly, vegetation changes through drainage will affect the nesting habitat for birds, especially those nesting on the ground, such as most game species. Drainage may also change food (browse) availability for large mammals. Unlike most birds and medium-to-large mammals, small mammals and amphibians should be significantly affected by forest drainage (Mazerolle 2001). Unlike agricultural practices, changes to peatlands brought by forestry drainage may have the potential to be reversed in part, by restoring a high water table if drainage channels are blocked, although we know of no studies demonstrating such a reversal.

One major northern forestry practice, clear cutting, has an additional, intriguing impact on wildlife. Clear cutting is obviously not designed to a create wildlife habitat, but ironically, by raising the water table and opening the vegetation cover, it has the potential to attract animal species typical of peatlands. For example, in eastern North America, birds such as Lincoln's sparrow and palm warbler will often invade clear-cuts during the period in which vegetation structure is open. But, whether clear-cuts constitute high-quality or suboptimal habitats remain unknown, because of the lack of data on reproduction.

5.4.3 Nutrient Enrichment

Owing to agriculture and industry, the atmospheric deposition of nitrogen, sulfur, and phosphorus has increased in the southern range of originally extremely nutrient poor bogs. In northwestern European raised bogs the increased nutrient deposition has resulted in the invasion of birch (*Betula* spp.) and purple moor grass (*Molinia caerulea*). These effects have been reported from several European countries (Risager 1998; Limpens et al. 2003; Tomassen et al. 2004). These changes in the vegetation composition and its structure may affect the faunal species assemblages, for example, ground-breeding birds, because of their frequent reliance on ground vegetation for nest-site selection (Larison et al. 2001). The increased nutrient availability has resulted in an increase of the nutrient content of plant material. This will have consequences for the herbivorous and detritivorous invertebrates that eat this material, but also species at higher trophic levels, such as carnivorous aquatic beetles (Dytiscidae), are affected (van Duinen et al. 2004b).

A comparative study on aquatic oligochaetes, dragonflies, chironomids, bugs, and beetles between pristine raised bogs in Estonia (low deposition level) and degraded and rewetted raised bog remnants in the Netherlands (high deposition level) showed clear differences in the species assemblages. Compared with pristine ombrotrophic sites (central raised bog), the relative abundance of species preferring ombrotrophic conditions is generally low in both the degraded and the rewetted bog sites in the Netherlands. The species assemblages in Dutch bogs are dominated by species that in Estonian bogs prefer the transitional mire or lagg that naturally have higher nutrient availability (van Duinen et al. 2004b).

Regarding the oligochaetes, in the Estonian ombrotrophic water bodies only the enchytraeid *Cognettia sphagnetorum* was found. In both degraded and rewetted sites in the Netherlands *Cognettia sphagnetorum* is always accompanied by *Nais variabilis*, whose occurrence in Estonian bogs is limited to the lagg and transitional mire. For dragonflies the same type of changes in species assemblage was found. In Estonian bogs, *Leucorrhinia dubia* is the most abundant dragonfly larva in spring in the ombrotrophic sites, whereas larvae of *Leucorrhinia rubicunda* are only found in transitional mires. In the Netherlands, however, *Leucorrhinia rubicunda* is the most abundant species found in spring in both degraded and rewetted sites, whereas *Leucorrhinia dubia* is fairly rare. These shifts in species dominance were found for bugs, beetles, and chironomids as well (van Duinen et al. 2004b). To understand the mechanisms behind these shifts, differences in species traits and demands have to be elucidated. Structural aspects of the biotopes might be involved, but many of these shifts are likely related to nutritional requirements of the species involved. Species ability to build up biomass using decomposing organic matter, bacteria, fungi, algae, or microinvertebrates with a low nutrient content (Elser et al. 2000) will play an important role in the species composition of the macroinvertebrate assemblage.

5.4.4 Peat Harvest

The effects of peat harvesting on peatland fauna depend on the manner in which the peat is extracted. In western Europe, the first peat harvesting activities were small scale and started in small peatlands and on the edges of larger peatlands. Large-scale industrial peat harvesting leaves hardly any room for animals. As a consequence of the disappearance of the various habitats of pristine peatlands (first laggs and edges of bogs, later more central bog ecotopes) a number of characteristic faunal species have declined or disappeared. In degraded bogs, characteristic species can still be present, but the species dominant in natural bogs have declined and other species have increased, as has been shown for spiders (Koponen 1979), carabid beetles (Främbs 1990), and aquatic macroinvertebrates (van Duinen et al. 2003a, 2004b), for example. Human activities have also resulted in new habitats within the mire landscape. Dehydration and mineralization of peat and the inlet of minerotrophic or nutrient-rich water have changed water and soil qualities (Lamers 2001), water tables, and vegetation composition and structure. As a result, species that do not occur under ombrotrophic (i.e., acidic, nutrient-poor) conditions were able to establish themselves in bog remnants (Göttlich 1980; Wheeler and Shaw 1995; Irmler et al. 1998). For some of these species, the original habitats have been degraded or have disappeared as a result of cultivation, making remaining peatland areas nowadays a refugium for species that were originally not dependent on peatlands (Akkermann 1982). Changes within peatlands may also translate into intraspecific patterns. Mazerolle (2001) found that near drainage for peat mining, leopard frogs were larger than individuals occurring in undisturbed peatlands. He suggested that this size difference resulted from the higher resistance of larger animals to dessication, although he could not rule out the possibility that growth near drained areas was promoted by a greater abundance of food.

Certain bird species seem particularly affected by peat harvesting. Palm warblers have never been observed in sites previously harvested, either by block cutting or vacuum, even after 15 years. By contrast, generalist bird species do invade postharvest peatlands, such as mourning dove, American goldfinch and killdeer (*Charadrius vociferus*), in North America. However, a study by Haddad et al. (2000) suggested that nest predation is much greater in remaining natural parts of five harvested peatlands, compared with nine unharvested peatlands of Quebec (63 vs. 8% of nests). However, nest predation risk was not associated with actual proximity of harvest operations, nor with distance to peatland edge. The results by Haddad et al. (2000) are in accordance with those of Berg et al. (1992) in Swedish peatlands. The latter two studies were based on artificial nests with quail (*Coturnix* sp.) eggs and may only provide a coarse assessment of true nest predation (Faaborg 2004).

5.4.5 Peatland Restoration

The effects of peat extraction may be reversed at least in part through ecological restoration. Peatland restoration has proven successful at reestablishing a cover of *Sphagnum* mosses in several cases in Canada (Lavoie and Rochefort 1996) and Europe (Smolders et al. 2003; Chap. 17). The return of associated fauna remains uncertain, both for invertebrates (Mossakowski and Främbs 2003; van Duinen et al. 2003a) and for birds (Bölscher 1995; Desrochers et al. 1998). As opposed to vacuum-harvested sites, peatlands exploited through labor-intensive cutting of peat blocks tend to be recolonized rapidly (less than 20 years) by plant (Smart et al. 1989) and bird (Desrochers et al. 1998) species typical of untouched peatlands. However, for aquatic macroinvertebrates, like midges, beetles, and caddisflies, large-scale rewetting projects in bog remnants with either abandoned hand peat cuttings or industrial harvested peat fields all resulted in a fairly similar species assemblage (van Duinen et al. 2003a), including only a part of the species spectrum of a pristine raised bog (van Duinen et al. 2002). Compared with rewetted bog remnants, water bodies in bog remnants that had not been rewetted, like water-filled hand peat cuttings and trenches, have a relatively high cumulative species richness,

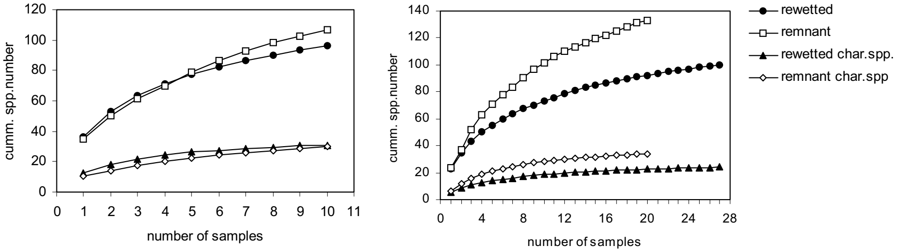


Fig. 5.6. Cumulative species richness curves for all species and for characteristic species of microinvertebrates (*left*) and macroinvertebrates (*right*) in rewetted and not rewetted remnant sites in Dutch bog reserves. The *curves* are composed of averages of 250 random sorts of the sampling sites. (From van Duinen et al. 2003a and unpublished data)

including a considerable number of characteristic macroinvertebrate species, that are not found in rewetted sites (Fig. 5.6). No relation was found between the success of restoration in terms of vegetation development and the number of characteristic macroinvertebrate species. So far, rewetting measures in Dutch raised bog remnants have resulted in a habitat for a limited number of faunal species, including only part of the characteristic raised bog species. Currently, a considerable number of characteristic and rare species are still dependent on bog remnants that have not been rewetted and that have been degraded by small-scale block peat cutting for their survival in raised bog areas, and in the Netherlands as a whole (van Duinen et al. 2003b).

It is unclear whether the return of animal species in restored areas will be complete in the long term. A prerequisite for the establishment of a more complete species spectrum is the conservation and restoration of the heterogeneity in environmental conditions, because different animal species have different demands and many species need a combination of conditions, as described in previous paragraphs. Furthermore, species should be able to reach the restored sites. Dispersal ability of the species as well as the proximity of source populations (in remaining, unharvested, peatlands) play important roles in recolonization. On the time scale of 30 years, the total number of characteristic aquatic macroinvertebrate species per site tend to increase with the time elapsed after rewetting, but this increase is slow (van Duinen et al. 2003b). Wheeler and Shaw (1995) assumed that a conservationally worthwhile, more or less balanced invertebrate community could reassemble in rewetted peat works within 50–70 years, depending on the proximity of potentially recolonizing species. Biggs et al. (2001) found that the restoration of the river Cole (UK) was successful because its upper reaches and stagnant water bodies along the river harbored many species that were able to recolonize the river after restoration. Likewise, Schikora (2002b) explained the rapid colonization by hygrophilous spider species of a rewetted bog by the vicinity of a vital population, next to the ability of dispersal by "ballooning." This stresses the importance of the conservation of current refugia in both relatively untouched and degraded bog remnants until rewetted sites have been recolonized by the species in question. Measures to conserve the current refugia, including rewetting, have to be taken with great care, including monitoring, in order to prevent decline of relict populations of rare and characteristic species (Verberk et al. 2001; van Duinen et al. 2003a).

Aquatic microinvertebrates (Rotifera, Copepoda, and Cladocera) however, seem to recover quickly after rewetting (van Duinen et al. 2003a). The difference in cumulative species richness and the number of characteristic species between rewetted and remnant sites found for aquatic macroinvertebrates was not found for microinvertebrates (Fig. 5.6). Likewise, Buttler et al. (1996) showed that the testate amoebae fauna of raised bogs can recover rapidly and fully, regardless of the initial condition of the cutover surface. As microinvertebrates like Rotifera and Cladocera are easily spread by wind or animal vectors (Cáceres and Soluk 2002; Cohen and Shurin 2003), have a short life cycle, and have parthenogenetic reproduction (Nogrady et al. 1993) they can colonize water bodies quickly after rewetting measures are taken. Probably, the first microinvertebrate species colonizing the newly created water bodies have a higher chance to successfully establish a population, as local biotic interactions (like competition and predation) may play a dominant role in structuring the plankton species assemblage by preventing invasion of new species once the community is saturated (Cohen and Shurin 2003). The local or regional species pool probably has an important influence on the final composition of the aquatic microinvertebrate community of rewetted bog remnants (Zhuge and van Duinen, unpublished data). Thus, the effects of restoration measures on microinvertebrates might be different from that on macroinvertebrates, which disperse less easily or might even be unable to fly, have a more complex life cycle, and make higher demands on their environment.

To set targets for conservation and restoration of raised bogs and to provide knowledge about how to reach those targets, reference data on intact bogs are necessary. Most of the reports on the intact raised bog fauna (compiled in the first decades of the twentieth century; Harnisch 1925; Peus 1932) do not give detailed information about the environmental conditions under which species and species assemblages were found. Moreover, at that time, many bogs were already to some extent degraded. However, knowledge about the environmental factors structuring faunal species assemblages is necessary to understand why species can or cannot establish themselves and survive in raised bogs under restoration and to give useful recommendations for restoration management. In this respect, palaeoecological research can provide useful information (Lavoie et al. 1997; Whitehouse 2004), although research on the actual occurrence and habitat demands of species is necessary, as well.

5.5 Conclusions

Like this chapter, most peatland wildlife studies to date have focused on species occurrence patterns, with little to say about the productivity, let alone the viability, of populations and only limited, correlative information about the environmental factors that limit or facilitate the occurrence of species. Besides this, the function of animal species in peatland systems is hardly known. The impact of beavers' activities on peatland hydrology, the effects of selective grazing by large herbivores, and the indispensability of insects in the survival of carnivorous plants can be easily imagined. However, also, for example, microscopic rotifers in *Sphagnum* mats seem to be important in bog ecosystems, as components in the phosphorus and nitrogen cycles (Bledzki and Ellison 1998, 2002). We would like to end by reiterating a message that is increasingly voiced in reviews such as this one, i.e., the need to move forward by favoring long-term and process studies over short-term and pattern studies. Of course, pattern studies exploring the distribution of species are an essential first step in our understanding of the role of peatlands for their associated fauna. However, they are of little use when it comes to teasing out minor roles that peatlands may play, such as staging areas, movement corridors, and complementary feeding grounds, from major roles such as population refugia and reproductive habitat. There will always be room for further ecological studies of fauna, and the study of peatlands is no exception. But better knowledge of the "functional ecology" of peatland fauna is needed here, particularly reproductive activity, dispersal, and nutritional ecology – three key factors for invertebrates and vertebrates alike. With such information, not only will we be more effective with "decision makers" and practitioners in conservation and restoration management, but, perhaps more importantly, we may help the greater public appreciate how fascinating peatlands are.

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