

# Chapter 7

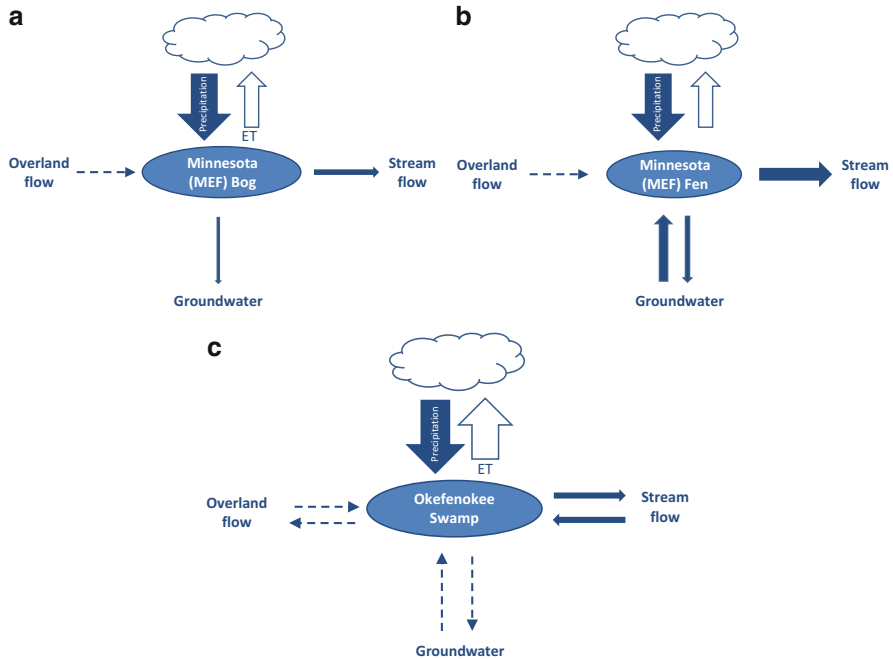
## Peatland Invertebrates

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### Introduction to Peatlands

Peat can develop in any wetland area where plant production exceeds decomposition. Peatlands are most prevalent in flat landscapes at high latitudes (tundra, boreal zones) where cool temperatures, low evaporation rates, water-logging, and low pH combine to retard plant decomposition (Vitt 1994; Rochefort et al. 2012). Although much less expansive, peatlands can also occur under other climatic conditions provided decomposition is still slow (see the below section on the Okefenokee Swamp). Peatlands are often classified as either bogs or fens, with bogs receiving nutrients almost exclusively from precipitation (i.e., ombrotrophic) and fens also receiving nutrients from surface or subsurface inputs of water (minerotrophic) (Bridgham et al. 1996; Wheeler and Proctor 2000; Rochefort et al. 2012; Fig. 7.1). However, most peatlands are not exclusively ombro- or minerotrophic, and exist along a gradient from bog to fen (e.g., poor fens). Due to the lack of mineral inputs and active acidification by *Sphagnum* mosses, bog-type peatlands tend to be highly acidic (pH < 5). Fens can range from being acidic (pH ~ 5) to circumneutral to basic (pH > 8), depending on hydrology and climate.

The study of invertebrates in peatlands has been unique from other types of wetlands (e.g., other chapters in this book) in that there has been a much stronger emphasis on the terrestrial and semiaquatic fauna (Annelida, Arachnida, Carabidae, brachyceran Diptera, Lepidoptera, Hymenoptera; e.g., Blades and Marshall 1994; Finnamore and Marshall 1994; Marshall et al. 1999; Koponen 2002; Spitzer and Danks 2006) rather than just the aquatic fauna (Odonata, Dytiscidae, nematoceran Diptera, e.g., Rosenberg and Danks 1987). This is probably because dense carpets of vegetation and peat above the waterline provide ample habitat for terrestrial invertebrates (plant and soil dwellers, and their predators), while areas of open, standing water can be limited in many peatlands. The



**Fig. 7.1** Examples of water budgets quantified from different peatlands: (a) Minnesota bog (Bay 1968, 1969; Boelter and Verry 1977); (b) Minnesota fen (Verry and Boelter 1975; Boelter and Verry 1977); (c) Okefenokee Swamp, Georgia (Rykiel 1984)

terrestrial invertebrate fauna of a peatland and the adjacent upland can overlap to some extent, but many terrestrial taxa are unique to peatland habitats (Spitzer et al. 1999).

For aquatic invertebrates, peatlands can be challenging places to live. On one hand, peatlands rarely dry completely due to close proximity of water tables, whether perched (bogs) or groundwater (fens), or to water retention by peat soils (Rocheffort et al. 2012), and thus desiccation is not a strong constraint on peatland invertebrates. On the other, peatland waters tend toward anoxia, and in the case of bogs can be highly acidic. These chemical conditions prevent certain aquatic organisms from becoming well established across peatlands habitats (Mendelsohn et al. 2014). In this chapter, we first review peatland areas across the globe where invertebrate ecology has been a major focus of research including Europe, Canada, the United States, and China. We then look for emerging themes from that body of research to generalize about how invertebrates function across varying peatland habitats.

## Focal Areas of Research for Peatland Invertebrates

### *European Peatlands*

#### **Peatland Habitats of Europe**

Most European peatlands occur across the northern and western regions (Scandinavia, Great Britain, Ireland, Netherlands) (Verhoeven 2014). As elsewhere, bog peatlands (often called mires in Europe) are dominated by *Sphagnum* mosses and ericaceous shrubs, with the most acidic and least fertile habits being fairly open. In fens, woody trees (*Betula*, *Salix*, *Alnus*) and sedges and grasses becoming more prevalent as pH and nutrient levels rise (Wheeler and Proctor 2000; Hájek et al. 2006).

In terms of invertebrates, the peatland fauna of the United Kingdom and Ireland is perhaps the best known, but excellent recent work has also been conducted in peatlands of Sweden, Finland, Germany, the Netherlands, the Czech Republic, and Spain. Emerging areas of research emphasis include investigating how hydrologic variation affects invertebrate distributions, and especially how peatland invertebrates can be used as bioindicators of human land-use and a changing global climate. Basic ecological work in Europe focuses mostly on the aquatic fauna, while impact assessment work relies more heavily on terrestrial and semiaquatic groups.

#### **Basic Invertebrate Ecology in European Peatlands**

Distinct communities of ground-dwelling invertebrates occur across different peatland sites of northern England (e.g., oligotrophic mires, blanket bogs, mixed moor; Coulson and Butterfield 1985). Similarly the compositions of these communities vary greatly seasonally. Thus, both spatial and temporal factors affect invertebrate faunistic diversity of peatlands (Coulson and Butterfield 1985). Invertebrate community composition can also vary across a single peatland, with distinct invertebrate assemblages in bog margins (i.e., laggss) versus bog centers (Bezděk et al. 2006; Mieczan et al. 2014).

As is the case for most kinds of wetland, hydrologic variation is considered a primary control on the aquatic invertebrate fauna in European peatlands. Downie et al. (1998), Standen (1999), and Hannigan and Kelly-Quinn (2012) all compared the aquatic invertebrate faunas in permanent pools and temporary pools/hollows of peatlands (Scotland and Ireland), and found taxonomically richer communities in the permanent water sites. Larger predatory invertebrates (species of Odonata, Hemiptera, Dytiscidae) were restricted to the permanent pools, and Hannigan and Kelly-Quinn (2012) surmised that their presence or absence may serve to structure overall invertebrate communities in peatland pools. Carroll et al. (2011) found that low soil moisture levels, induced by peatland drainage, decreased the abundance of soil-dwelling tipulidae crane fly larvae. Nilsson and Svensson (1995) looked at forested and open (logged) Arctic swamp pools, and found the open pools to be considerably warmer and to support a richer and more abundant dytiscidae and culicid

fauna than the forested pools. The study of Hannigan and Kelly-Quinn (2012) addressed mostly acidic bogs, but they also sampled a fen habitat; the community in that fen was dramatically different from the bog-type habitats, being much more taxonomically rich (see taxa lists in the [Appendix](#), and discussion below).

Carrera et al. (2009, 2011) focused on how enchytraeid worms in peatlands were controlled by temperature and moisture levels in the peat, and how in turn the activities of the worms controlled peat breakdown and carbon flux (see also below consideration of climate change). In one study (Carrera et al. 2011), they conducted laboratory incubations of soils from a Spanish peatland under ambient moisture and temperature conditions crossed with elevated temperature or reduced moisture conditions. They further introduced enchytraeid worms to half of the replicates from each treatment. Neither temperature nor moisture level by itself affected CO<sub>2</sub> flux from these soils. However, under moist conditions, higher temperatures induced worm populations to increase, which resulted in greater loss of dissolved organic carbon from the soils, suggesting an important role of enchytraeids in peat decomposition. A companion study focusing solely on temperature (Carrera et al. 2009) also pointed to the importance of the worms to peat breakdown, and suggested that worm activity resulted in a lower release of H<sup>+</sup> ions, possibly reducing the effects of acidity in limiting peat decomposition.

## Conservation and Invertebrates of European Peatlands

Invertebrates are being increasingly used in Europe to monitor the ecosystem health of peatlands. Groups considered useful as bioindicators include Annelida (Carrera et al. 2009, 2011), Arachnida (Scott et al. 2006; Więcek et al. 2013), Acarina (Więcek et al. 2013; Lehmitz 2014), Collembola (Krab et al. 2013, 2014), Odonata (Drinan et al. 2013), aquatic Hemiptera (Downie et al. 1998; Drinan et al. 2013), Lepidoptera (Spitzer et al. 1999), Tipulidae (Carroll et al. 2011), Formicidae (Vepsäläinen et al. 2000), and various Coleoptera (e.g., Carabidae, Dytiscidae: Nilsson and Svensson 1995; Downie et al. 1998; Spitzer et al. 1999; Drinan et al. 2013), as well as whole invertebrate assemblages (Standen 1999; van Duinen et al. 2003; Hannigan and Kelly-Quinn 2012).

Drinan et al. (2013) assessed impacts of forestry practices on macroinvertebrate assemblages in blanket bog lakes. The combination of conifer planting and clear-cut harvesting affected invertebrates most, presumably due to eutrophication. Peatland lakes affected by clear-cuts supported larger dytiscid beetle species and greater corixid water boatmen abundance than the natural, more-oligotrophic lakes. Nilsson and Svensson (1995), working in northern Sweden found a similar Dytiscidae response to tree harvest. Vepsäläinen et al. (2000) found that clear-cutting and drainage of Finnish bogs increased overall ant species richness, but these practices apparently eliminated habitat for a few bog-specialist ant species.

Peat extraction and drainage (e.g., Fig. 7.2) have significantly impacted many European bogs, and efforts to restore the habitats are being conducted, using invertebrate response as a metric of success (van Duinen et al. 2003; Hannigan et al.



**Fig. 7.2** Ditched peatland at Marcell Experimental Forest, Minnesota. Photo by Sue Eggert, USDA Forest Service, Northern Research Station

2011; Więcek et al. 2013). In some rehabilitated raised bogs in the Netherlands, van Duinen et al. (2003) found limited evidence that the restoration strategies being used were enhancing rare and bog-characteristic invertebrate species. In contrast, Hannigan et al. (2011) found that aquatic invertebrate communities were very similar between pools of a restored bog, where some limited peat extraction and ditching had been conducted, and a largely intact bog, suggesting that here significant progress towards reestablishing natural conditions had been achieved. Więcek et al. (2013) similarly found that water mites, which have very complex life cycles (parasitic larvae, predaceous nymphs and adults), making them especially useful bioindicators, had made significant reestablishment progress in some German peatlands where natural hydrology had been restored after past ditching and peat extraction. Finally, integrating microbial and aquatic invertebrate metrics may provide more insight into environmental responses to anthropogenic impacts than invertebrates alone (Whatley et al. 2014).

It is predicted that climate change may dramatically affect European peatlands through desiccation and warming. Invertebrate responses may be useful in detecting changes, and invertebrate responses may in some ways contribute to any changes in the ecological structure and function of affected peatlands. As mentioned above, Carrera et al. (2009, 2011) found that enchytraeid worms will be harmed by drying, but enhanced by warming conditions, and changes in worm populations may functionally

alter carbon cycles in some peatlands. Krab et al. (2013) found that experimental warming of a Swedish subarctic peatland reduced densities of collembolan spring-tails, another important decomposer, potentially reducing the importance of these invertebrates to peat breakdown. Similarly, drying of a Welsh peatland resulted in declines in tipulidae crane fly larvae populations (Carroll et al. 2011). Invertebrates in peatlands should respond to climate change, although the ecological consequences of invertebrate change will probably be complex.

## ***Canadian Peatlands***

### **Canadian Peatland Habitats**

Canada has more peatland habitat than any other country (Vitt 1994). Peatlands occupy 12 % of Canada's landmass and the great majority (97 %) is in the boreal and subarctic regions (Tarnocai 2006), although there are isolated temperate outliers as far south as 42° in Ontario. Most northern peatlands in Canada are fens, usually dominated by brown mosses, *Sphagnum*, and sedges (Vitt 1994). Some arctic wet tundra meadows have many characteristics of fens although they are underlain by permafrost and have shallower accumulations of peat (Vitt 1994). Bogs dominated by *Sphagnum* mosses, ericaceous shrubs, and spruce (*Picea*)/tamarack (*Larix*) forest are widespread in the mid to southern boreal, as well as temperate outliers (Vitt 1994; Rochefort et al. 2012). Because most of Canada was glaciated during the Pleistocene, most extant Canadian peatlands date from the early to mid Holocene, within the last 9000–6000 years (e.g., Vitt 1994; Lavoie et al. 1997).

### **Diversity and Ecology of Canadian Peatland Invertebrates**

Although most Canadian peatlands are boreal or subarctic, much of the research on peatland invertebrates has focused on temperate outliers in southern Canada, especially in Ontario and Quebec. This is likely partly due to accessibility, but also to the perceived higher conservation relevance of these southern sites relative to more extensive and contiguous northern peatlands. Arthropods have received considerably more attention than other invertebrate taxa.

Most research on Canadian peatland arthropods has been species inventories. The most intensive early research was a series of natural history studies of Byron Bog, in London, Ontario by W.W. Judd, beginning in the late 1950s (Judd 1957) and continuing with a long series of papers, many of which focused on insects, over subsequent decades (e.g., Judd 1975). Judd's efforts resulted in probably the most comprehensive inventory of a Canadian peatland at that time.

To address the lack of baseline data, the Biological Survey of Canada launched an initiative in 1981 to document Canadian peatland arthropods. This effort produced two volumes on aquatic (Rosenberg and Danks 1987) and terrestrial arthropods

(Finnamore and Marshall 1994). Many of the chapters were inventories of selected taxa or sites, although there were some focused ecological studies.

Rosenberg and Danks (1987) summarized knowledge of aquatic arthropod taxa in Canadian peatlands and marshes, with species lists and ecological overviews of water mites (Smith 1987), Ephemeroptera, Trichoptera (Flannagan and Macdonald 1987), Odonata (Hilton 1987), Hemiptera (Scudder 1987), Coleoptera (Larson 1987), biting flies (Lewis 1987) and Chironomidae (Diptera) (Wrubleski 1987). Overall, the diversity of aquatic insects in peatlands was considered low, with approximately 11 % of the 4000 aquatic species recorded in Canada found in these habitats, although in many cases it was not possible to distinguish peatland-restricted from peatland-associated or generalist species. Many of the chapters emphasized the need for additional research on geographic distribution and natural history of the taxa.

A subsequent volume on terrestrial arthropods (Finnamore and Marshall 1994) included species-level inventories of selected taxa, often in more geographically limited regions. Aitchison-Benell (1994), Dondale and Redner (1994), and Koponen (1994) documented arachnids, primarily spiders, in Manitoba, Ontario, and Quebec peatlands; Cannings and Cannings (1994) reviewed Odonata of northwestern cordilleran peatlands; Finnamore (1994) provided a checklist and analysis of Hymenoptera in Wagner Fen in central Alberta. Behan-Pelletier and Bissett (1994) and Marshall (1994) provided Canada-wide overviews of peatland oribatid mites and sphaerocerid flies, respectively. Blades and Marshall (1994) summarized results of a broader taxonomic survey from isolated peatlands in southern Ontario.

In contrast to the aquatic fauna, species richness of terrestrial arthropods in peatlands is high. Finnamore (1994) recorded 1410 species of Hymenoptera from Wagner Fen, Alberta and Blades and Marshall (1994) recorded more than 2000 species of arthropods from southern Ontario peatlands. Savage et al. (2011) and Grégoire Taillefer and Wheeler (2012) identified 381 and 699 species of higher Diptera, respectively, from bogs in southern Quebec. Despite the fact that these sites are small habitat fragments, they clearly support high species diversity. One challenge to drawing conclusions about peatland biodiversity from these inventories is that comparable efforts in sampling and identification are often lacking for other habitats in the same regions. Thus it is difficult to determine which species are peatland-specialists or primarily peatland-associated, especially in taxa for which ecological knowledge at the species-level is lacking, such as Diptera (Blades and Marshall 1994; Spitzer and Danks 2006; Savage et al. 2011). Based on available knowledge, the percentage of terrestrial arthropods that are peatland-specialists (10 %) is higher than in the aquatic fauna (1 %) (Marshall and Finnamore 1994).

Several papers, cited previously, in Rosenberg and Danks (1987) and Finnamore and Marshall (1994) discussed ecological aspects of focal taxa in addition to presenting species checklists. This treatment was, in most cases, more developed in aquatic taxa, probably because of a longer history of ecological studies in aquatic entomology, but also because lower diversity, more defined habitats, and higher available taxonomic resolution make community-level analyses more tractable.

## Conservation and Invertebrates of Canadian Peatlands

Some recent ecological studies of terrestrial peatland arthropods in Canada have focused on applied questions in conservation and land-use. Peatland conservation efforts, especially in southern Canada where remaining peatlands are small remnants, focus, appropriately, on habitat-level conservation. However, some arthropods restricted to peatlands have been the focus of species-level assessments under federal species-at-risk legislation. Examples include the Bogbean Buckmoth (*Hemileuca* sp., Lepidoptera: Saturniidae) in eastern Ontario, which is listed as Endangered (COSEWIC 2009) and the Georgia Basin Bog Spider (*Gnaphosa snohomish*, Araneae: Gnaphosidae) in southern British Columbia, which is a species of Special Concern (COSEWIC 2012).

There is a need for studies of peatland biodiversity in the context of climate change, especially on boreal and subarctic peatlands, where impacts may be particularly pronounced (Tarnocai 2006). Most subarctic and arctic peatlands overlie permafrost and thawing may have major impacts on hydrology, carbon sequestration and, in turn, biodiversity. Much of the current research on northern peatlands focuses on their roles as carbon sinks and landscape elements, but research on peatland species lags behind. Ongoing research on arthropods in wet tundra (TA Wheeler, unpublished data) shows that taxonomic and ecological diversity of peatland arthropods in the arctic is much higher than documented. Given the suitability of arthropods as bioindicators (McGeoch 1998), further studies of arctic peatland arthropods may provide valuable insights into climate change impacts in the north.

Horticultural peat extraction is one of the major threats to temperate peatlands in eastern Canada. Drainage ditches (e.g., Fig. 7.2) are dug to lower the water table, herbaceous vegetation is removed, and a thin upper layer of dried peat is removed by vacuuming each year (Gorham and Rochefort 2003). Once the usable supply of peat has been exhausted the site is usually abandoned but restoration efforts have been implemented for some sites that are no longer being used for industrial extraction. The restoration process involves restoring the hydrological balance and seeding plant fragments and propagules from nearby undisturbed peatlands, along with mulching and fertilization (Gorham and Rochefort 2003). Restoration success in these sites has primarily been assessed using plants, but some recent studies have also examined the recolonization of insects.

Mazerolle et al. (2006) assessed recolonization of aquatic arthropods in bog pools created as part of restoration efforts and found that species diversity was lower than in natural pools. Assisted restoration of vegetation had a positive effect on arthropod colonization, but aquatic insect diversity was still considerably lower in newly created pools 4 years after restoration. However, most of the species that did colonize successfully were peatland-associated species that are probably adapted to dispersal between isolated bog pools.

Grégoire Taillefer and Wheeler (2012) focused on the response of terrestrial Diptera to restoration of peatland sites in the lower St. Lawrence region of Quebec. They compared higher Diptera diversity in three treatments: natural bogs, abandoned bogs that had been used for peat extraction and left to recover on their own, and bogs that had been restored 7 years earlier. Although overall community structure in



restored sites approached that of natural bogs, some functional groups of Diptera (small species, some trophic groups) had not yet recovered. These results suggested that assisted recolonization may be required for small insects in restored sites, much as for plants. Grégoire Taillefer and Wheeler (2013) subsequently found that the usual method for gathering and preparing plant material for restoration (chopping and spreading) did not introduce significant numbers of insects, so that other methods of collecting and introducing arthropods from natural donor sites may be necessary. These studies demonstrate that, despite high species diversity in peatland terrestrial insects, these assemblages may not be resilient to environmental perturbations, and that recolonization to restored and damaged sites may be difficult because of dispersal limitation of the arthropods and fragmented distribution of peatland sites.

Grégoire Taillefer and Wheeler (2010) assessed the role of drainage ditches originally excavated to lower water tables in Johnville Bog in southern Quebec. The presence of ditches (e.g., Fig. 7.2) significantly altered the community structure of terrestrial Diptera at the scale of a few meters from the ditch, suggesting that fine-scale heterogeneity and habitat alteration may have an impact on insect diversity in small peatlands. On a larger scale, Savage et al. (2011) examined the effect of peatland size, vegetation, and surrounding land-use on higher Diptera in six isolated bogs in southern Quebec and northern Vermont. Although peatland size (ranging from 12 to 900 ha) had no measureable impact on community structure, vegetation cover in the sites and surrounding land-use patterns exerted significant influences on the structure of insect assemblages in the peatland. The presence of a forest buffer surrounding these southern sites seemed especially important in maintaining species diversity.

## *Minnesota Peatlands*

### **Peatland Habitats of Minnesota**

Northern peatlands of North America extend into the northern tier of the United States, with Minnesota supporting the greatest area (over 3 million ha; MN DNR 1980). Most are found in the northern half of Minnesota in the lower Glacial Lake Agassiz Region, which extends up into the Great Slave/Great Bear Lake region and the Hudson Bay lowlands of Canada (Glaser 1987; Wright et al. 1992). While the hydrology, chemistry, and vegetation of Minnesota's northern peatlands have been extensively studied (e.g., Heinselman 1970; Boelter and Verry 1977; Glaser et al. 1981; Wheeler et al. 1983), faunal studies are limited to amphibians and reptiles (Karns 1992) and mammals (Berg 1920; Niemi and Hanowski 1992; Nordquist 1992). Little is known about the invertebrate communities inhabiting northern Minnesota's peatlands (Gorham 1990; Wright et al. 1992).

Marcell Experimental Forest (MEF) in north central Minnesota has been a focus of peatland research for decades (e.g., Kolka et al. 2011b). Forested bogs and fens at MEF formed from ice-block depressions that filled with peat ranging in depths of 1–8 m in bogs to 1–6 m in fens (Bay 1967; Verry and Janssens 2011). Sedge and forested peats accumulated in regions where calcium-rich groundwater seeped into

depressions forming minerotrophic fens (Boelter and Verry 1977). *Sphagnum* peat accumulated in depressions that were influenced more by low ionic precipitation yielding ombrotrophic bogs.

Bogs at MEF are perched above the aquifer and are primarily precipitation driven (e.g., Bay 1968, 1969; Boelter and Verry 1977) (Fig. 7.1a *water budget of MN bog*). Centers of MEF bogs are raised and surrounded by lagg zones (Sebestyen et al. 2011). Water from the uplands flows into the lags and drains from the bogs through short outlet streams. At the single fen monitored at MEF, the outlet stream is perennial, a result of continuous groundwater inputs and precipitation (e.g., Verry and Boelter 1975; Boelter and Verry 1977) (Fig. 7.1b *water budget of MN fen*). Bogs at MEF are ion-poor and acidic with pH from 3.7 to 4.9, while groundwater-based fens are ion-rich with water pH ranging from 6 to 7.5 (Boelter and Verry 1977).

Topography, hydrology, and water chemistry influence bog and fen vegetation. Bogs are dominated by black spruce (*Picea mariana*), eastern tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*), *Sphagnum* mosses, and ericaceous shrubs (Sebestyen et al. 2011). Speckled alder (*Alnus incana*) is common in lags. Fens contain a higher diversity of understory species including speckled alder, sedges (*Carex* spp.), marsh marigold (*Caltha palustris*), ferns, mosses, and trees (black spruce, balsam fir (*Abies balsamea*), northern white cedar, eastern tamarack, and white birch (*Betula papyrifera*)) (Bay 1967).

## Invertebrate Diversity and Ecology in Minnesota Peatlands

Current knowledge of the aquatic invertebrate community composition in northern Minnesota peatlands is limited to an inventory conducted at two bogs and one rich fen at MEF. Twenty-four family or higher-order invertebrate taxa were found in fishless MEF bogs (Appendix). Predators (e.g., Dytiscidae: *Dytiscus* spp., and Cordulidae: *Somatochlora* spp.) and collectors (Culicidae: *Culex*, *Ochlerotatus*, and *Aedes* spp., and Chironomidae: *Chironomus* spp.) were more common than other functional feeding groups, although shredder caddisflies (Limnephilidae: *Limnephilus submonifer*, and *L. indivisus*) were locally common in lagg habitats (Fig. 7.3) where speckled alder trees were abundant. Mitchell et al. (2008) described hotspots of methylmercury production in lagg zones that were related to upland runoff of solutes. Nitrogen-rich leaves from speckled alder trees in lags may also serve as a high-quality food resource for shredder caddisflies and create hotspots of invertebrate productivity in bog lags (Fig. 7.3). Multiple individuals of *Philarctus quaeris*, a caddisfly species thought to be extirpated from Minnesota (Houghton 2012) were found in the lagg of a MEF bog during the survey. Despite low pH in the bog water, fingernail clams were present in the lagg habitats and their empty shells are used as case building material by *P. quaeris*. Most bog taxa complete their life cycles in a 2–3 month period since surface water runoff usually ends by mid-June, bog water levels drop, and hollows and lagg habitats become dry.

The fen invertebrate community was somewhat more diverse (33 taxa) than in bogs (24 taxa) (Appendix). Invertebrates in the fen were similar in taxonomic and functional composition to those in bogs, with additional crustaceans (*Hyalella*),

**Fig. 7.3** Lagg habitat along upland periphery of a Minnesota peatland (Marcell Experimental Forest). Photo by Sue Eggert, USDA Forest Service, Northern Research Station



snails (*Fossaria*, *Armiger*, and *Gyraulus*), leeches, a mayfly (*Leptophlebia*), and a caddisfly (*Ptilostomis*) found in the permanent outlet stream. *Chilostigma itascae*, an endemic and endangered caddisfly species in Minnesota was not found in peatlands at MEF, although it has been found in similar habitats in the region. Phantom crane fly larvae (*Bittacomorpha*) were common in an iron seep associated with the fen. Several fish species [central mudminnow (*Umbra limi*), brook stickleback (*Culaea inconstans*), and fine-scale dace (*Phoxinus neogaeus*)] were present in the outlet stream which was linked to a downstream lake via a tributary stream. The continuous, nutrient-rich groundwater inputs likely allow for longer invertebrate life cycles, higher animal productivity, and more frequent predator interactions in the fen, although studies of invertebrate life history and trophic interactions in fen and bog food webs at MEF are lacking.

### Conservation Biology and Invertebrates of Minnesota Peatlands

For invertebrates, the main thrust of conservation research in Minnesota peatlands has focused on impacts of mercury toxicity. Peatlands are sources of mercury to downstream lakes and rivers via export from outlet streams (Grigal et al. 2000; Kolka et al. 2011a). Methylmercury (MeHg) is produced by microbial processes that respond to the availability of sulfate. To determine the effects of increased atmospheric sulfate deposition on rates of methylation of mercury in MEF

peatlands, sulfate was added through a network of PVC pipelines and sprinklers encompassing the downstream half of a bog for 5 years and compared to an upstream control section (Jeremiason et al. 2006). Percent MeHg increased in the treatment section of the bog and in stream water (Jeremiason et al. 2006; Coleman-Wasik et al. 2012). After sulfate addition ended, %MeHg declined in the recovery section relative to the treatment section, but remained higher than the control section. Concentrations of total mercury in mosquito larvae collected in each experimental treatment paralleled MeHg levels in bog water of treatment sections. Study results suggest that reductions in sulfate emissions could result in reductions of MeHg contamination in aquatic food webs in the Upper Midwest United States (Coleman-Wasik et al. 2012).

## *Northeastern China Peatlands*

### **Peatland Habitats of Northeastern China**

Northeastern China (from 38° to 53°N, and 115° to 135°E) is one of the most important areas of peatland wetlands distribution, including Heilongjiang, Jilin and Liaoning Provinces, and the northeast portion of the Inner Mongolia Autonomous Region. This high latitude area, located at the southern margin of the permafrost region of Asia, is conducive to peatland formation due to cold temperatures (mean annual air temperature <1 °C), ample precipitation (400–630 mm, mostly falling from July to September), relatively low evaporation rates, and seasonally frozen soils (Jin et al. 2007). Water and soils in the active permafrost layer (from 45 to 50 cm depths) freeze from October to April.

Peatlands in Northeastern China include both bogs and fens. Bogs are mainly distributed in mountainous areas (e.g., Da Hinggan Mountain with 485 km<sup>2</sup>, Xiao Hinggan Mountain with 727 km<sup>2</sup>, and Changbai Mountain with 463 km<sup>2</sup> of peatland) (Ma 2013). Fens are most widespread across the Sanjiang Plain, with 350 km<sup>2</sup> of remaining peatland (Ma 2013). Many peatlands of Northeastern China are ombrotrophic, being fed primarily by direct precipitation (Fig. 7.1). Permafrost peatlands typically occur in broad valleys, where frozen soils and flat topographies retain rainwater and surface flow, and prevent water from percolating into the substratum underground (Sun et al. 2011). The peat thickness of both bogs and fens typically ranges from 50 to 60 cm above the permafrost layer (Wang et al. 2010), but can be 1–3 m thick in some places.

Mountain peatlands of northeastern China are vegetatively diverse (700 plant species), with larch (*Larix gmelinii*) being the major tree species (Sun et al. 2011) and the understories being dominated by various shrubs (*Betula fruticosa*, *Chamaedaphne calyculata*, *Ledum palustre*, *Vaccinium* spp.), grasses and sedges (*Calamagrostis angustifolia*, *Carex* spp., *Eriophorum vaginatum*), and mosses (*Sphagnum* spp., *Polytrichum*). Peatland surfaces are a mosaic of microforms, including *Sphagnum* hummocks with woody shrubs (see above), mossy hollows (*Polytrichum juniperinum*), and sedge tussocks (*Eriophorum vaginatum*) (Miao

et al. 2012). Marsh develops across some peatlands in Sanjiang Plain, where open water is interspersed with sedges (*Carex schmidtii*, *C. meyeriana*, *C. appendiculata*, *C. lasiocarpa*, *C. appendiculata*), grasses (*Calamagrostis angustifolia*), and other emergent and submersed plants (*Equisetum heleocharis*, *Menyanthes trifoliata*, *Potentilla chinensis*, *Iris laevigata*, *Utricularia minor*) (Zhao 1999; Wang et al. 2013). Almost 10 % of the total area of fen peatland on the Sanjiang Plain is classified as marsh (Liu and Ma 2000), and given the presence of ample open water, these marshes are likely important habitats for aquatic invertebrates (Fig. 7.4).

### Invertebrate Diversity and Ecology in Northeastern China Peatlands

The vast majority of work on invertebrates in Chinese peatlands has focused on the terrestrial and soil faunas, rather than the aquatic fauna. To some extent, this is logical because bogs and fens of the region lack extensive open water, and the dense vegetative cover and often non-saturated surface soils provide ample habitats for a terrestrial and semiaquatic fauna to develop. In fact, the list of taxa (49 families) in the [Appendix](#) of this chapter represents the only known community inventory of aquatic invertebrates from Chinese peatlands (collected from nine fen peatlands in the Sanjiang Plain). Obviously, if basic descriptions of the aquatic fauna are lacking, essentially nothing is known about the ecological dynamics of aquatic invertebrates in Chinese peatlands.

Yin et al. (2003), Zhang et al. (2006, 2008), Wu et al. (2008, 2009), and Bao et al. (2009) each provide descriptions of the terrestrial and semiaquatic invertebrate fau-



**Fig. 7.4** Marsh-type habitat in a fen peatland of Northeast China (Honghe National Preserve). Photo by Haitao Wu

nas of Chinese peatlands. The soil invertebrates of peatlands are mainly distributed in the surficial layers (Yin et al. 2003; Zhang et al. 2006; Wu et al. 2008), much as they are in terrestrial forests and grasslands. In many cases, this terrestrial fauna is both taxonomically rich and highly abundant. For example, Zhang et al. (2006) found that soil invertebrates in bogs of Da Hinggan Mountain reached densities of 170,000 individuals/m<sup>2</sup>. This fauna was comprised of 4 phyla, 7 classes, 23 orders, and 54 families, with Enchytraeidae worms and Formicidae ants being the numerically dominant families (Huang and Zhang 2008a). From a fen wetland of Sanjiang Plain, Wu et al. (2008) collected 5 phyla, 12 classes, 27 orders and 46 families of soil invertebrates, with mites (Acarina), beetles (Coleoptera), and worms (Enchytraeidae) dominating. In the peatlands of the Xiao Hinggan Mountains, Yin et al. (2003) and Wang et al. (2014) also found that worms (Enchytraeidae) and mites (Acarina), plus springtails (Collembola), were numerically dominant. In terms of biomass, Lumbricidae and Enchytraeidae worms contribute the most (Huang and Zhang 2008b; Zhang et al. 2008). In fens of Sanjiang Plain, Wu et al. (2009) found that soil invertebrate densities peaked in spring. Bao et al. (2009) sampled insects living on fen plants (using sweep nets and yellow-pan traps), and found that Diptera and Hemiptera were numerically dominant, followed by Hymenoptera, Thysanoptera, Collembola, Coleoptera, and Orthoptera.

At local scales, the main environmental factors impacting soil invertebrates in peatlands include temperature, water conditions, soil quality, and vegetation (Zhang et al. 2001). Zhang et al. (2014) found that soil temperature was the main factor affecting the distribution of soil invertebrates across different types of tundra peatlands, and further found a relationship between litter biomass, soil organic matter content, and nutrient content and the distribution of soil macrofauna. In the Changbai Mountains, peatland soil invertebrate densities and community complexities decreased with increasing altitude, mirroring vegetative patterns (Wang et al. 2014). Xin et al. (2009) found that densities of the soil mesofauna were higher in forested bogs than wetland meadows. Zhang and Zhang (2006, 2013) showed that the diversity of the soil macrofauna significantly decreased from continuous to patchy tundra, while the mesofauna and microfauna exhibited the opposite pattern. Water conductivity, pH, soil organic matter content, and water depth all significantly influence water beetle communities (Wei et al. 2002; Dong et al. 2008).

Decomposition is a key process in nutrient recycling and energy flow in peatlands, and studies from Northeastern China on the ecosystem functions of peatland soil faunas have focused on their impacts on leaf litter decomposition. Wu et al. (2009) examined the impacts of soil invertebrates on leaf litter decomposition rates and nutrient fluxes at three successional stages of fen wetland using litterbags with different mesh sizes to include or exclude organisms. Overall, litter breakdown by soil invertebrates was 35.4 % of the total. In coarse mesh bags (4 mm) where most invertebrates had access, litter breakdown was 0.3–4.1 times higher than in fine mesh bags (0.06 mm) where most invertebrates were excluded. Breakdown rates varied among litter from different plants, ranging from 32.9 % for *Carex meyeriana* to 38.2 % for *Calamagrostis angustifolia*; prevalence of these plants in regional peatlands changes with successional status. Litter quality as reflected by carbon (C), nitrogen (N), and phosphorus (P) contents, and C:N and C:P ratios also influence

breakdown rates by invertebrates. Variation in invertebrate community compositions and season further influenced litter breakdown.

Ants are very prevalent in fens of the Sanjiang Plain (Wu et al. 2010b, 2013b), and their impacts on soil nutrient pools and cycling are excellent examples of how wetland invertebrates can affect ecosystem function. Wu et al. (2010a, 2013a) found that mounds of *Lasius flavus*, *Lasius niger*, and *Formica candida* ants had greater concentrations of organic C, dissolved organic C, total N,  $\text{NO}_3^-$ , and  $\text{NH}_4^+$  than the surrounding peatland soils. Nutrient pools in ant mounds comprised from 5.3 to 7.6 % of the total in peatland soils overall. Importantly, ant mounds increased the spatial heterogeneity of these nutrient pools.

### **Conservation and Invertebrates in Northeastern China Peatlands**

The major focus of conservation-related research on invertebrates in Chinese peatlands has focused on issues of climate change. Ant mounds also alter the spatial and temporal patterns of gas emissions from peatland soils. Wu et al. (2013b) showed that ant mounds in a Sanjiang Plain fen serve as hot spots for  $\text{CO}_2$  emissions, convert soils from being  $\text{CH}_4$  sources to  $\text{CH}_4$  sinks, and amplify seasonal fluctuations for  $\text{N}_2\text{O}$  emissions. Overall, ant mounds contributed measurable amounts to soil gas emissions from the wetland, averaging 7.0 %, -4.3 %, and 3.4 % of total soil  $\text{CO}_2$ ,  $\text{CH}_4$ , and  $\text{N}_2\text{O}$  emission, respectively. Laboratory studies suggest that altered gas emissions from ant mounds occur both from changed soil conditions and from ant respiration (Wu et al. 2015). Thus, for a complete understanding of peatland C and N cycles and balances, ant mounds should be considered.

Forest fires happen frequently in the mountains of Northeastern China, and in May 1987 a large fire (known as the Black Dragon Fire) swept across Da Hinggan Mountain forests destroying almost 10,000  $\text{km}^2$  of timber. After the fire, the number of Enchytraeidae in peatlands gradually increased until becoming stable after about five years. The meso- and microfauna was restored after about seven years, while Protura populations did not reappear in burned areas for 16 years (Zhang et al. 2006; Zhang and Zhang 2009).

### ***Subtropical Peatlands of the Southeastern United States***

#### **Southeastern US Peatlands**

Although most prevalent in cold climates, peatlands also exist in tropical and subtropical climates, despite warm temperatures and high evaporation. In the Southeastern United States, peatlands mostly occur on the Coastal Plain, such as pocosins, a handful of Carolina bays, the Okefenokee Swamp, and the Everglades (see chapters in Batzer and Baldwin 2012). Why these particular wetlands retain peat is not clear, as formative processes, hydrology, pH, and plant communities can all vary widely. Of these Southeastern peatlands, the invertebrates have only been

investigated in detail in the Okefenokee Swamp and the Everglades (and the Everglades is the subject of its own chapter in this book, and so not covered here).

The 200,000 ha Okefenokee Swamp in southeastern Georgia and northeastern Florida is among the largest freshwater wetlands in North America (Batzer et al. 2012). The name is aboriginal meaning “land of trembling earth,” presumably due to the presence of peat. Deposits of peat up to 4.5 m thick occur across much of the Okefenokee (Cohen et al. 1984a), derived mostly from remnant water lily or cypress debris, and to a lesser extent from *Sphagnum* mosses and sedge.

Hydrology in the Okefenokee is typical for an ombrotrophic peatland (Fig. 7.1c). Water input is dominated by direct rainfall (70–90 %), with some minor inflows from small tributary creeks and off uplands (Rykiel 1984; Brook and Hyatt 1985). Water output is dominated by evapotranspiration (~85 %), with most remaining water losses from stream flow-out of the Suwannee and St. Mary’s Rivers to the south. Connection to groundwater, either via discharge or recharge, is considered negligible (<3 %). Early efforts to drain the Okefenokee failed (Izlar 1984), and thus water levels and hydrologic variation remain largely natural. Water pH is acidic (3.5–4.5) (Blood 1980). Mineral concentrations (Ca, Mg, Na, K, Cl) are low, even more so than in many northern bogs (Rykiel 1984). Levels of dissolved carbon are high (46–58 mg C L<sup>-1</sup>) (Bano et al. 1997), due to organic acids from plant decomposition, which gives the water a characteristic “tea” colored appearance.

Major plant communities of the Okefenokee include forested swamp, scrub-shrub thickets, emergent (grasses, sedges) marsh, and water lily (*Nymphaea*, *Nuphar*) beds (McCaffrey and Hamilton 1984; Fig. 7.5). In peatland forests, bald cypress (*Taxodium distichum*), and pond cypress (*T. ascendens*) are dominant overstory trees (Fig. 7.5). Herbaceous wetland (grass, sedge, and water lily marsh) is locally called “prairie.” For more detailed overviews of the Okefenokee see Cohen et al. (1984b) and Batzer et al. (2012).

### **Invertebrate Community Composition and Ecology in the Okefenokee**

Kratzer and Batzer (2007) identified 103 aquatic macroinvertebrate taxa across the Okefenokee (see list of 52 families in the Appendix). Chironomid midge larvae by themselves comprised 66 % of abundance. Mollusks were very rare. Most taxa lack seasonality (Kratzer and Batzer 2007), although microcrustaceans decline in winter from cool temperatures, and in summer from fish predation (Schoenberg 1988). Ecological research on invertebrates of the Okefenokee has focused primarily on natural variation across the mosaic of plant communities and trophic relations.

Kratzer and Batzer (2007) also assessed spatial and temporal variation in macroinvertebrate communities across the Okefenokee Swamp, examining communities in forested, scrub-shrub, prairie, and deepwater (lakes and canals) habitats across different sub-watersheds and in different seasons (29 total locations). They, however, discovered remarkably few invertebrate community patterns across the different plant communities, sub-watersheds, or seasons. A handful of individual taxa exhibited some specialization for particular plant types or seasons, although responses were largely unique for each taxon. Kratzer and Batzer (2007) concluded





**Fig. 7.5** Marsh prairie, scrub-shrub thickets, and cypress forest of the Okefenokee Swamp, Georgia. Photo by Mark Galatowitsch, Univ Georgia

that the macroinvertebrate communities in the Okefenokee were dominated by generalist taxa able to exploit the full range of habitat available.

Taylor and Batzer (2010) used stable isotope analyses (C, N) to assess diets of midge larvae in forested and prairie habitat of the Okefenokee. These larvae appeared to be generalist feeders, simply focusing on foods as they were available. Cypress wood was important in forested habitats, and algae and herbaceous plants in marsh prairies; sediment was an important midge food in both habitat types.

Aside from midges, the aquatic invertebrate community of the Okefenokee is dominated by a plethora of large predators (odonates, hemipterans, coleopterans) (Kratzer and Batzer 2007). The presence of so many predatory invertebrates seems at odds with the fact that fish productivity in the Okefenokee Swamp is high (Freeman and Freeman 1985); fish typically exclude predatory invertebrates (Wellborn et al. 1996). However, most fish production is from small-bodied species such as killifish (*Fundulus* spp.), pygmy sunfish (*Elassoma* spp.), and mosquitofish (*Gambusia* spp.). These small fishes feed primarily on microcrustaceans and midge larvae (Freeman and Freeman 1985; Oliver 1991), and probably cannot tackle the larger invertebrate taxa. In much of the Okefenokee (deepwater habitats with large fishes excepted), invertebrates may actually hold a higher position in the food web than fishes. For example, dragonfly nymphs in the Okefenokee frequently have small fish in their guts (B. Freeman, unpublished data).



**Fig. 7.6** Wildfire in the Okefenokee Swamp (2007). Photo from US Fish Wildl Serv, Okefenokee National Refuge

### Conservation Biology and Okefenokee Invertebrates

Fire, integrated with drought, is considered the most important factor controlling the structure of Okefenokee plant communities (Schlesinger 1978). Fire is believed to maintain open prairie habitat, which otherwise would convert into woody vegetation. Deeper “lakes” scattered across the Okefenokee may have developed where fire burned deep into the peat deposits. Large fires occur every few decades (Yin 1993). A particularly large fire occurred in 2007, and burned >75 % of the Okefenokee (Fig. 7.6). Beganyi and Batzer (2011) assessed invertebrate response to that fire, contrasting burned and non-burned prairie, scrub-shrub, and cypress-forest habitats. Only in cypress forest was significant invertebrate response detected, with populations of leptocerid caddisfly larvae (*Oecetis* sp.) and coenagrionidae damselfly nymphs (*Ishnura* sp.) declining, and populations of corixid water boatmen (*Sigara* sp.) increasing in burned cypress. The rest of the invertebrate community in cypress forest did not appear to numerically respond to fire. In prairie and scrub-shrub thickets, no invertebrate responses to fire were detected. In prairies, fire burned quickly through the habitats; flooded and moist sediments did not burn and herbaceous plants grew back rapidly, likely precluding any invertebrate response. While fire may be a crucial control for plant communities in the Okefenokee, it appears to have a much lesser role in controlling invertebrate community structure (mirroring the lack of plant control on invertebrate communities previously described).

Problems with heavy metals are also a concern in the Okefenokee, and human consumption advisories due to mercury exist for some fish. Anoxic, high temperature conditions in sediments are conducive to mercury methylation, the form of the metal that is most toxic and most likely to bioaccumulate. Mercury levels in Okefenokee macroinvertebrates are unusually high, especially in *Crangonyx* amphipods (George and Batzer 2008; Beganyi and Batzer 2011) (levels in alligators, however, are typical for the Southeast; Jagoe et al. 1998). Levels of mercury in invertebrates are similar across the range of available habitats (plant types, sub-watersheds) in the Okefenokee, suggesting that mercury is being introduced via aerial deposition (Jackson et al. 2004; George and Batzer 2008). Beganyi and Batzer (2011) assessed whether the 2007 wildfire magnified mercury levels in macroinvertebrates, but did not find this to be the case.

## Synthesis

Perhaps the most telling finding of our review was the dearth of detailed information about the ecology of invertebrates and about invertebrate functional roles in peatlands, despite these habitats being the most expansive and potentially most important wetlands on earth. Many of the published studies simply inventory the fauna or describe basic life histories. However, those studies may suggest why so little is known about the ecology of peatland invertebrates. First, unlike many other wetland types, the terrestrial fauna is especially well developed in peatlands. As noted above, Finnamore (1994) reported 1410 species of the single-order Hymenoptera, in a single Canadian peatland (studies of Hymenoptera are essentially nonexistent in any wetland type, except peatlands). If the goal is to establish the overall importance of invertebrates in peatlands, the terrestrial fauna clearly must be considered, a daunting task. Comparatively, the aquatic invertebrate fauna in peatlands is depauperate, although likely still very important. Despite being easier to work with, studies of aquatic invertebrates in peatlands are few; remarkably this chapter provides the first inventories of aquatic invertebrate from peatlands of Minnesota and China, otherwise fairly well-known habitats.

Although our knowledge remains limited, this review provided some valuable preliminary evidence on the primary ecological controls for peatland invertebrate and the major ecological roles invertebrates play in peatlands, and how invertebrates can be useful in assessing emerging environment threats to peatlands.

## *Invertebrate Community Ecology in Peatlands*

In the [Appendix](#), we report 79 aquatic invertebrate groups from peatland habitats across the globe. These aquatic faunas are moderately diverse compared to other types of wetlands (Batzer and Ruhí 2013), with from 24 to 52 families recorded per location. Some of these variations may simply reflect sampling effort, as the most

taxonomically rich peatland habitat, the Okefenokee Swamp, was also the most intensively sampled. Faunas are highly variable from place to place, with only six groups being ubiquitous across all habitats: Branchiopoda (specifically cladocerans) and Copepoda microcrustaceans; Dytiscidae and Hydrophilidae/Helophoridae beetles; and Ceratopogonidae and Chironomidae fly larvae. These same aquatic organisms also tend to dominate other kinds of wetland habitat (Batzer and Ruhí 2013). Overall aquatic invertebrate faunas of peatlands seem to be comprised mostly of generalist organisms, i.e., ubiquitous families.

We saw no obvious gradient in the total taxon richness between bogs ( $\text{pH} < 5$ ) or fens ( $\text{pH} > 6$ ). However, mollusks (Gastropoda, Bivalvia) and leeches (Erpobdellidae, Glossophoniidae) were rarely encountered in low pH habitats (see also Wheeler and Proctor 2000; Hájek et al. 2006), while these groups were widely distributed across fen habitats with more circumneutral pH (Appendix). At least for the mollusks, a lack of calcium carbonate for shell development may exclude many taxa from acidic habitats. However, most aquatic insects and crustaceans appeared to be tolerant of low pH conditions in peatlands, at least as reflected by family-level distributions. Perhaps more sensitivity might become evident in these groups if generic or species-level analyses were possible.

For aquatic invertebrate communities in peatlands, as for most wetlands, water permanence influences compositions, with longer hydroperiods promoting greater taxon richness, especially large predators. Although hydrology likely affects plant community compositions, similar aquatic invertebrate assemblages may occur across a diversity of plant communities, further suggesting that habitat generalists prevail. In northern bogs, however, peripheral lagg habitats appear to be hot spots for aquatic invertebrates, perhaps due to influences of upland water runoff, more open water, or the growth of nitrogen-rich plant foods (e.g., alder leaves). For terrestrial invertebrates, damper soils enhance terrestrial diversity and abundance. Variation of invertebrates related to plant community change is more pronounced for terrestrials, probably because the plants themselves serve as food (herbivores) or habitat.

Fire appears a pervasive influence on peatlands. However, the aquatic invertebrate community was minimally affected by a large wildfire in the Okefenokee Swamp, further evidence of a generalist tendency for that fauna. The terrestrial invertebrate fauna appears more dramatically influenced by fire, likely because the ecological influence of fire is more pronounced above the water line.

Decomposition is likely the most important ecosystem process affected by peatland invertebrates. Invertebrates tend to track the quantity and quality of organic matter in peatlands. In northern peatlands, aquatic limnephilid caddisfly larvae are likely important shredders of organic material (leaves). However, the terrestrial invertebrate fauna probably plays the most important role in decomposition, with ants and annelid worms being key. The fact that these organisms can affect emissions of greenhouse gases from peatlands make them perhaps among the most important wetland invertebrates known.

Predaceous invertebrates, both aquatic and terrestrial, are widespread in peatlands. Most of the 1410 species of Hymenoptera reported by Finnmore were parasitic wasps. The prevalence of predators/parasitoids suggests ecological importance, but we found no studies quantifying their impacts.

## ***Conservation Issues and Peatland Invertebrates***

Multiple threatened invertebrate species occur in peatlands, suggesting these habitats are at risk. Researchers frequently mentioned climate change as a major threat, given that northern peatlands primarily exist due to regionally cold temperatures. As mentioned, peatland invertebrates may play key roles in enhancing peat decomposition and gas flux, and as ectotherms their activities are controlled by temperature. This combination could lead to them exacerbating the impacts of climate change.

Drainage, logging, and peat mining are pervasive threats to peatlands. Invertebrates, both aquatic and terrestrial, have proven to be useful indicators of environmental impacts and of the success of restoration efforts, especially by workers in Europe. However, the terrestrial fauna might prove to be superior indicators, given that terrestrials tend to be more specialized than aquatics (e.g., associated with particular plants) and the terrestrial fauna appears to affect crucial ecosystem functions (decomposition, gas flux). Peatland habitats are foci of mercury methylation, and bioaccumulation of mercury in aquatic invertebrates may transfer this heavy metal up food chains.

## **Conclusion**

This review establishes that invertebrates are very diverse and ecologically important components of peatland habitats. However, our review also exposes some real inadequacies in our knowledge. The terrestrial invertebrate fauna has been shown to be especially diverse, and numerous taxa appear to be valuable environmental indicators. However, the ecological and functional roles of terrestrial invertebrates remain poorly known; and this kind of knowledge is sorely needed to understand how these organisms affect peatland ecosystems and why this fauna has tangible value for peatland bioassessment. Even less is known about the aquatic fauna. Basic inventories are lacking, the functional importance of the aquatic fauna to ecosystem processes remains essentially unknown, and their value, if any, to bioassessment is still largely undeveloped. The situation in Europe appears somewhat better than for other parts of the world, and the knowledge about arthropods is somewhat better developed than for the non-arthropod fauna. Because of the extent and importance in climate change scenarios, the virtual dearth of knowledge about invertebrates in Arctic peatlands is of special concern.

## **Appendix**

Aquatic invertebrate taxa recorded from peatlands across the globe, arranged from bogs (lower pH) to fens (higher pH). Dark shading of cells indicates ubiquitous taxa, medium shading indicates sporadic occurrence of taxa, and light shading indicates taxa reported from only a single location. Different sampling techniques and sampling intensities were utilized at each location; hence the absence of a taxon from a particular site may be a sampling artifact. (Genus level classifications are available from the applicable references or from S. Eggert or H. Wu for their previously unpublished data.)

	Okefenokee Swamp (Kratzer and Batzer 2007)	Minnesota bogs (Eggert, unpublished)	Irish bogs (Hannigan and Kelly-Quinn 2012; Hannigan et al. 2011)	Japanese poor-fen (Kato et al. 2009)	Chinese fens (Wu, unpublished)	Minnesota rich fen (Eggert, unpublished)	Irish rich fen (Hannigan and Kelly-Quinn 2012)
<b>pH</b>	3.8–4.7	3.7–4.9	4.3–4.9	4.7–6.3	5.8–6.9	6.5–7.0	6.9–8.3
<b>NEMATODA</b>							
<b>MOLLUSCA</b>							
<b>Gastropoda</b>							
Ancylidae							
Bithyniidae							
Lymnaeidae							
Planorbidae							
Succineidae							
Valvatidae							
<b>Bivalvia</b>							
Sphaeriidae							
<b>ANNELIDA</b>							
<b>Oligochaeta</b>							
Lumbriculidae							
Tubificidae							
<b>Hirudinea</b>							
Erpobdellidae							
Glossophomidae							
<b>CRUSTACEA</b>							
<b>Branchiopoda (Cladocera)</b>							
<b>Branchiura</b>							
Arguliidae							

<b>Copepoda</b>										
<b>Ostracoda</b>										
<b>Amphipoda</b>										
Crangonyctidae										
Gammaridae										
<b>Isoopoda</b>										
Asellidae										
<b>Decapoda</b>										
Atyidae										
Cambaridae										
Palaemonidae										
<b>ACARINA</b>										
<b>Hydrachnidia</b>										
<b>INSECTA</b>										
<b>Collembola</b>										
Entomobryidae										
Isotomidae										
Poduridae										
Sminthuridae										
<b>Ephemeroptera</b>										
Baetidae										
Caenidae										
Leptophlebiidae										
<b>Odonata</b>										
Coenagrionidae										
Lestidae										
Aeshnidae										
Corduliidae										

(continued)

(continued)

	Okfenokee Swamp (Kratzer and Batzer 2007)	Minnesota bogs (Eggert, unpublished)	Irish bogs (Hannigan and Kelly-Quinn 2012; Hannigan et al. 2011)	Japanese poor-fen (Kato et al. 2009)	Chinese fens (Wu, unpublished)	Minnesota rich fen (Eggert, unpublished)	Irish rich fen (Hannigan and Kelly-Quinn 2012)
Libellulidae							
<b>Hemiptera</b>							
Belostomatidae							
Corixidae							
Gerridae							
Hydrometridae							
Mesovelidae							
Naucoridae							
Nepidae							
Notonectidae							
Pleidae							
Velidae							
<b>Coleoptera</b>							
Dytiscidae							
Gyrinidae							
Halplidae							
Hydraenidae							
Hydrophilidae/ Helophoridae							
Noteridae							
Scirtidae							
<b>Neuroptera</b>							
Corydalidae							





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