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Ecology of Terrestrial Arthropods in Freshwater Wetlands

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Abstract

The terrestrial arthropod fauna of wetlands has been largely ignored by scientists compared to other ecological elements, yet these organisms are among the most important influences on the ecology of these systems, with the vast majority of the biodiversity in wetlands found among the terrestrial arthropods. Wetlands present a range of habitat for terrestrial arthropods, with unique faunas being associated with soils and ground litter, living-plant substrates, and peatlands. Myriapoda, Araneae, Collembola, Carabidae, Formicidae, and assorted herbivorous Coleoptera and Lepidoptera are the terrestrial arthropod groups that most influence the ecology of wetlands. Despite their success, most terrestrial arthropods possess fairly rudimentary adaptations for life in wetlands, with most simply moving to higher ground or up vegetation during floods, although some species can tolerate immersion. Many terrestrial arthropods are environmentally sensitive and show considerable promise as bioindicators of wetland ecological conditions.

1. INTRODUCTION

Freshwater wetlands are among the most valuable, yet most threatened, habitats on the planet (39), and the invertebrate fauna holds a focal position in their functioning (15). Wetland invertebrates include not only aquatic species but also a plethora of terrestrial arthropods. Yet most studies of invertebrates from freshwater wetlands focus solely on aquatic organisms (e.g., 14, 16). However, terrestrial invertebrates are crucially important components of many wetlands (2, 21, 96, 101, 103, 120), and their importance needs broader recognition. Terrestrial invertebrates comprise most of the biodiversity in freshwater wetlands, play important roles in food webs, and are key bioindicators of wetland ecological health.

This review highlights various aspects of the ecology of terrestrial invertebrates in freshwater wetlands, focusing on arthropods. We define what constitutes a freshwater wetland, describe adaptations of terrestrial arthropods for flooding, cover the major arthropod groups existing in wetlands, discuss how different kinds of arthropods (e.g., ground-dwelling, plant-dwelling) are ecologically controlled, and finally discuss key roles that terrestrial arthropods contribute to ecosystem functioning and values of freshwater wetlands.

Wetlands have been defined in different ways depending on whether the intended purpose was scientific or legal, with definitions varying somewhat among different parts of the world (115). Most definitions focus on attributes of hydrology, plants, and soils, but a definition used in Canada (95) is perhaps particularly appropriate for this review because it also encompasses animal activity; it defines a wetland as:

> land that has the water table at, near, or above the land surface or which is saturated for a long enough period to promote wetland or aquatic processes as indicated by hydric soils, hydrophytic vegetation, and various kinds of biological activity that are adapted to the wet environment.

2. ADAPTATIONS OF TERRESTRIAL ARTHROPODS FOR LIFE IN WETLAND HABITATS

As they are typically highly mobile, terrestrial arthropods in wetlands can easily avoid flooding by running, crawling, or flying to higher ground (2, 90); climbing emergent vegetation or tree trunks (**Figure 1**) (11, 136); or using floating wood as life boats (23). Some carabid beetles simply follow rising and falling waters, residing in the moving narrow strip of dryer land along the water's edge (150). Colonies of red imported fire ants (*Solenopsis invicta*) will congeal into floating rafts during flooding (**Figure 1**), an adaptation likely developed for life in South America's Pantanal wetland, where this ant is native (91). For sedentary forms (e.g., some Diplopoda, Acarina) or for organisms that live in wetlands that flood rapidly and expansively (e.g., floodplains), adaptations to tolerate actual inundation may become necessary to survive (1). Braccia & Batzer (23) found that many terrestrial arthropods (myriapods, acarines, beetle larvae and adults) persist in wetland wood that has been submersed for long periods, presumably by accessing air pockets in the wood or being able to tolerate immersion. Under laboratory conditions (74), Carabidae beetle adults trapped on the water surface or under water with access to air pockets survived for weeks, but even beetles lacking access to air survived submersed for considerable periods of time if water temperatures were cool; experimental removal of elytra reduced survival, suggesting that carabid beetles used air trapped under their wings, similarly to aquatic beetles. A Carabidae larva (149) from the Amazon was able to live for weeks beneath anoxic water, presumably by depressing its metabolic rate. Curculionidae larvae from the Amazon (44) survived under water for months, likely by employing cutaneous respiration. Most (70%) planthoppers and leafhoppers in a European floodplain had overwintering eggs tolerant of extensive inundation (106). Terrestrial mites of the Amazon

Figure 1

Photo of imported fire ants (*Solenopsis invicta*) congealing into a floating mass, and also climbing up vegetation, to survive flooding. From *Ecology of Freshwater and Estuarine Wetlands: Second Edition*, edited by Darold P. Batzer and Rebecca R. Sharitz. © 2014 by the Regents of the University of California. Published by the University of California Press. Photographer: Jennifer Henke.

floodplain vary dramatically (10-fold) among individuals in how long they can survive under water; most could not endure a normal flood, and so long-term persistence of mites relies on relatively rare super-resistant phenotypes (100). Adis & Junk (2) reviewed the host of Amazonian terrestrial arthropods adapted to tolerate inundation, typically using dormancy. They also described a millipede (*Myrmecodesmus adisi*) that is developmentally active under water, utilizing plastron respiration and feeding on algal periphyton, only requiring terrestrial conditions to reproduce.

Using literature to assess how terrestrial arthropods deal with flooding likely gives a skewed perspective; sophisticated adaptations are more likely to be studied and published than rudimentary adaptations. Certain wetland habitats might exert more selection pressure for flood tolerance than others. For example, the Amazon floodplain is an environment conducive for the evolution of highly flood-tolerant terrestrials, likely due to its large size and the predictability and extent of flooding (2). Terrestrial arthropods in smaller and less predictable wetland habitats may exhibit more rudimentary strategies of tolerance. Plum (101) reviewed the literature on terrestrial invertebrates that exploit marshes and wet meadows (flooded grasslands) of Europe and concluded that most lacked specific adaptations for wetland habitats and simply preferred moist-soil conditions. Nonetheless, despite the likelihood that elegant adaptations to flooding by terrestrial arthropods are uncommon, these organisms are very successful in wetlands.

3. KEY TERRESTRIAL ARTHROPOD TAXA IN WETLANDS

While diverse terrestrial arthropods exist in wetlands, only a handful of taxa have received sufficient research attention to merit synthetic review. We focus on the Myriapoda, Arachnida, Collembola, Carabidae, and Formicidae, and on a collective grouping of herbivorous insects (Lepidoptera and some Coleoptera). Obviously, other terrestrial groups such as the Acarina, Hemiptera, Staphylinidae, nonant Hymenoptera, and Diptera exist in wetlands, but because of the paucity of papers on those groups, and their limited focus on ecology, we did not synthesize that literature (taxa lists for some of those groups, however, are covered below in Section 5.1). Omission does not mean that these arthropod groups are unimportant, just that they are understudied.

3.1. Myriapoda

Myriapods (millipedes, Diplopoda; centipedes, Chilopoda; garden centipedes, Symphyla) are among the best-studied terrestrial wetland arthropods, in part because they were favored research subjects of Joachim Adis, the most prolific scientist to study terrestrial arthropods in wetlands (e.g., 1, 2). Myriapods are particularly important to some of the world's most prominent wetlands, such as the Amazon floodplain (2) and Pantanal (10, 11, 51) of South America. Large, tropical wetlands appear conducive to exploitation by myriapods, possibly due to unique climatic, hydrologic, and geologic conditions; numerous taxa are specifically adapted for conditions in Amazonia or the Pantanal.

Myriapods from South America's large tropical wetlands have been reviewed by others (cited above), so we focus on their occurrence in wetlands elsewhere. Millipedes and centipedes on temperate floodplains, as in the tropics, are tolerant of flooding, although most simply avoid it (41, 122, 125). Most myriapods on temperate floodplains, however, do not invade from adjacent uplands, but are instead full-time wetland residents (26).

Besides hydrology, distributions of myriapods on floodplains can be influenced by soil conditions (nutrient levels, pH, moisture levels) (122). However, in a montane fen, Diplopoda were unresponsive to most environmental variation (123), and Diplopoda in German floodplains were unresponsive to invasion by a noxious weed (71). Many myriapods likely have generalist tendencies, and can thus cope with a wide range of conditions.

3.2. Araneae

Araneae (spiders) are generalist predators that can be very abundant (64) and diverse (114) in wetlands, especially peatlands. They are prevalent in floodplain habitat (65), where emerging aquatic insects from the river or stream channels provide an important dietary supplement (25, 32). While spiders are key predators in wetlands, we found no studies that quantified their impacts on prey populations. Spiders themselves, however, are important foods for some wetland birds (111).

Spiders do not appear to be restricted by flooding (7), and in some cases, species richness in wetlands may exceed that in adjacent uplands, especially if uplands are managed (53). Many spider species are wetland specialists (53). If displaced by floods, spiders can rapidly return (78).

Spiders in wetlands are typically associated with plants (herbs, grasses, shrubs, trees) (34, 64, 83, 111, 148). Variation in plant assemblage structure (64, 65), plant diversity (83), and plant density (34, 83, 111) all affect spiders, with relationships typically being positive (greater spider richness and/or density with greater plant richness and/or density). Mowing marsh or meadow vegetation can, however, harm the spider fauna (34, 111). Natural swamp forests support different spider assemblages than managed plantation forests (65). In the Pantanal, spiders associated with tree canopies vary seasonally, likely due to direct impacts of flooding on the spiders and indirect impacts of flooding on the host trees (148).

3.3. Collembola

Collembola (springtails) are small-bodied consumers (detritivores, fungivores) that can reach high densities in some wetlands. While the order is primarily associated with uplands, many Collembola species are associated with water, with wetlands being an especially favored habitat (43, 88, 151). On natural floodplains, many collembolans accumulate in upper elevation areas that flood infrequently (128). However, in managed floodplains that are partially removed from flooding, they prefer wetter areas (80). Increased wetness from elevated groundwater levels benefits collembolans in some peatlands (133) while harming them in others (139). It appears that excessive flooding and excessive drying may both serve as constraints, with moderately wet conditions perhaps being optimal. However, collembolans can tolerate a range of hydrologic conditions (77, 122). Being detritivores, wetland collembolans often congregate where plants (50) and leaf litter (82) accumulate.

In agricultural areas and managed forests, collembolans are more likely to be found in local wetlands than in disturbed uplands (88, 151). Low levels of nitrogen fertilization can increase collembolan numbers, but excessive levels cause declines (118).

3.4. Carabidae

Carabidae (ground and tiger beetles) are important predators in wetlands. Like spiders, carabids in floodplains consume aquatic insects as they emerge or wash up on river and stream shores (60, 97). As seasonal ponds dry, Carabidae move into dry basins and consume aestivating aquatic invertebrates (midge larvae, fingernail clams) (12). Wetland carabids likely prey on co-occurring terrestrial arthropods (97).

Carabidae readily avoid floods and quickly return as water levels recede (59, 78, 150), although some can survive inundation (74). In many cases, however, flooding patterns, even intense floods (59), do not affect assemblage distributions (54, 80, 109), suggesting a resilience to hydrology. In some cases, extended flooding actually increases carabid species richness (7, 48). Moist edges of seasonally flooded habitat are preferred habitats for many carabids (3, 150). Because different carabid species exhibit varying responses to hydrologic conditions, they are useful environmental indicators (49, 116). While carabids may not be constrained by seasonal flooding, we did not find reports of carabids exploiting perennially flooded wetland.

Wetland carabids segregate with vegetation, with some preferring grassy, marshy habitat; some preferring wet-forested habitat; some preferring peatland habitat (3, 81); and some preferring sparsely vegetated river banks (67). In a Rhine River floodplain, vegetation was the key environmental factor explaining most variation in carabid assemblages (110). Plant structure, however, exerts greater control on carabids than does plant taxonomy (29). Carabid assemblages in a Croatian wetland invaded by an exotic shrub changed, with some species increasing and others declining, primarily due to changing plant structure and its associated microclimate (28).

3.5. Formicidae

Formicidae (ants) make up a diverse group that can constitute a significant part of the animal biomass (47). Brigić et al. (27) recorded 16 ant species from one peatland and found that wetland–upland edges were favored habitats. Chen et al. (38) collected 21 species of ants from 11 genera in three swamps of Louisiana, with distinctly different arboreal and ground-dwelling communities. Three species of ants coexist in Northeastern China peatlands, with the density and size of their mounds differing for *Lasius flavus*, *Lasius niger*, and *Formica candida* (146).

High densities of ants in temperate wet meadows, marshes, and peatlands develop because wetlands provide desirable temperature and moisture conditions for ant colonization and ant-mound development. However, few ant species live in wetland areas with persistent flooding (6). Wetland environmental conditions and ant feeding habits affect mound distributions (63, 147). Ant species compositions in floodplains are affected by tree density and habitat structural heterogeneity (105). Within trees, the canopy and root masses support unique communities (37). Among New England bogs in the United States, patterns of ant richness were difficult to predict, being correlated only with latitude and vegetation type (52).

3.6. Herbivorous Lepidoptera, Chrysomelidae, and Curculionidae

Many terrestrial insects in wetlands are herbivores that occur on specific host plants (120). Most lepidopterans (butterflies and moths) occur in wetlands because their host plants are wetland species, and not because they have an affinity for wetland environments per se (e.g., 40, 119, 129). Rare and endangered lepidopterans are typically threatened because their wetland host plants are rare (see Section 5.1).

Host-plant specificity of herbivorous beetles (leaf beetles: Chrysomelidae; weevils: Curculionidae) makes them environmentally safer options for biological control of invasive wetland plants (e.g., 36, 66, 104, 126). The fact that herbivorous insects are viable options to control invasive plants suggests that moths (55, 140) and leaf beetles and weevils (36, 66, 94, 102, 104, 126) can be ecologically important under natural conditions.

Larvae of forest tent caterpillars (*Malacosoma disstria*) and baldcypress leafrollers (*Archips goyerana*) can defoliate large tracts of swamp tupelo and baldcypress trees, respectively, in Mississippi River Delta swamps (46). Natural insect herbivory of floating leaf macrophytes in Argentina approaches 18% of the plant biomass (87). Native larval and adult leaf beetles can consume 25% of water lily (*Nuphar*) leaf biomass, and this herbivory induces more rapid regrowth of new leaves compared to plants not subjected to herbivory (135).

Wetland environmental conditions other than plant factors also affect herbivorous wetland insects. Some diapausing lepidopteran larvae can survive for weeks under water, although more extensive flood durations cause high mortality (138). Leaf beetles may prefer moister areas because early instar larvae are vulnerable to desiccation (117, 134). Wetter conditions may indirectly benefit herbivorous butterfly larvae by reducing predator access (5). In contrast, moths associated with reeds (*Phragmites*) prefer drier areas (57). Wetland conditions and wetland plants are often interrelated; lepidopterans that are bog specialists decline if wetland vegetation changes successionally to drier, closed-canopy forest (119).

4. ECOLOGICAL CONTROLS ON COMMUNITY ASSEMBLY OF TERRESTRIAL ARTHROPODS

We divide the terrestrial arthropod fauna of wetlands into three categories based on habitat:

1. the ground-dwelling fauna of seasonally flooded river floodplains, wet meadows, and temporary ponds;
2. the plant-canopy-dwelling fauna of emergent marshes and meadows, and swamp and wetland forests; and
3. the fauna of peatlands (bogs and fens), which share some characteristics with the other categories, although the wide assortment of microhabitats in peatlands creates a unique arthropod fauna.

Each faunal group is controlled by unique ecological factors.

4.1. Ecological Controls on Ground-Dwelling Arthropods

Prominent ground-dwelling arthropods of seasonal wetlands include the myriapods, spiders and mites, collembolans, and ground beetles. Ground-dwelling arthropods are directly affected by flooding, with many organisms adapted to avoid or tolerate inundation (see above). Wetland hydrology is a key control on this fauna (139).

Wetland habitats can be classified based on hydrologic criteria (e.g., temporary ponds, floodplains, semipermanent marshes, permanent ponds, bogs, fens). For aquatic arthropods, hydrology is considered the key ecological control because aquatic organisms are directly tied to cycles of flooding and drying (14, 16). Theory explaining how hydrology controls aquatic invertebrate assemblages in wetlands might be fruitfully applied to terrestrial ground-dwelling arthropods, except in reverse. Instead of focusing on how drying constrains the aquatic fauna, we focus on how flooding constrains the terrestrial fauna.

Wissinger (142) postulated that four aspects of flooding control the aquatic fauna: (*a*) permanence and duration, (*b*) predictability and regularity, (*c*) phenology and seasonality, and (*d*) harshness. These criteria likely influence terrestrial ground-dwelling arthropods, albeit in ways different from aquatic arthropods.

4.1.1. Permanence and duration.

Wetlands occur along a gradient of flooding from permanently flooded habitat at one extreme to briefly flooded ephemeral habitat at the other (**Figure 2**). While permanently flooded wetlands (ponds, shallow lakes) support the greatest range of aquatic invertebrates (142), these habitats support few ground-dwelling terrestrial arthropods, with most restricted to shores. In contrast, ephemerally flooded wetlands (wet meadows) support few aquatic arthropods, but they support a wide diversity of ground-dwelling terrestrial arthropods (see **Figure 2**) (41, 101). Persistent flooding inhibits ant species richness, with flood-tolerant taxa being a nested subset of the ephemeral-wetland fauna (6). Distinct bee and wasp assemblages occur in the Pantanal across a hydrologic gradient from short- to long-duration inundation (4).

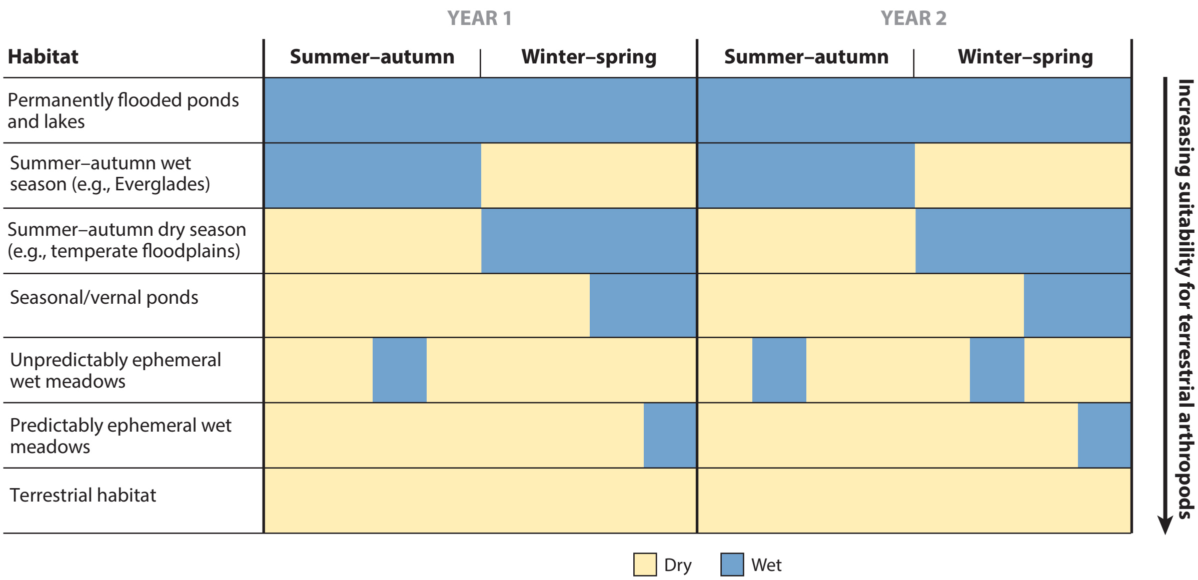

Figure 2

Dry (*yellow*) and wet (*blue*) periods in various types of wetland habitat over a hypothetical two-year span, showing how permanence/duration, predictability/regularity, and phenology/seasonality of habitat availability (*yellow periods*) for terrestrial arthropods can change. In general, the suitability of the habitats for terrestrial arthropods increases from top to bottom. Peatlands do not have distinct wet-dry cycles and are not shown. Figure inspired by a similar aquatic-focused model presented by Wissinger (142).

4.1.2. Predictability and regularity.

Flood predictability is important because organisms can adapt to exploit a resource if it occurs reliably. Vernal ponds only flood briefly (in spring) but support a diversity of aquatic organisms (14) because suitable habitat develops consistently. Similarly, while the Amazon floodplain floods extensively, flooding occurs predictably during the tropical wet season, and waters recede predictably. Adis & Junk (2) maintain that this predictability is responsible for the plethora of Amazonian terrestrial arthropods with special adaptations to tolerate flooding. In contrast, the fauna of the Pantanal is less diverse than the Amazon because the Pantanal floods unpredictability (69).

4.1.3. Phenology and seasonality.

When a wetland floods or dries will affect terrestrial arthropods (**Figure 2**). Wetlands that dry during warm seasons (e.g., temperate-zone floodplains; 59, 78), the period when terrestrials are most active, will provide more opportunities for terrestrial arthropods than those that flood in the hot summer. If dry wetland habitat becomes available only during cold seasons, it will provide few opportunities for terrestrial arthropods.

4.1.4. Harshness.

Many ground-dwelling arthropods that exploit wetlands prefer moist soils (101). In humid climates, dry wetlands retain considerable moisture after floods recede, and a rich ground-dwelling fauna exists. In harsher arid climates, dry wetlands support few ground-dwelling wetland arthropods, and drought years further constrain the resident soil fauna (41). In turn, extreme flooding conditions, such as rapidly rising and persistent waters, also constrain ground-dwelling terrestrial arthropods (59).

Another aquatic-focused ecological paradigm applicable to ground-dwelling terrestrial arthropod communities of wetlands is the flood pulse concept (68), which postulates that in floodplains, the community and ecosystem ecology in the aquatic realm is controlled by flood pulses. A key attribute of flood pulses is the development of the aquatic–terrestrial transition zone (ATTZ), which is the flood front that moves across the landscape (ebb and flow); aquatic invertebrates and fish track this zone to exploit resources from the terrestrial realm as they become inundated. Terrestrial arthropods also track the ATTZ as it moves across wetland surfaces. Prior to flooding, many terrestrial arthropods inhabit the channel–floodplain riparian zone (i.e., the ATTZ at low flows), and these organisms have important ecological impacts on the channels (103). For invertivorous riverine fishes, terrestrial arthropod prey that fall into the water from riparian areas are crucially important food resources (e.g., 92). Assorted predaceous spiders and beetles inhabiting the riparian zone rely heavily on aquatic insect prey (mayflies, caddisflies) that emerge from channels (see 25, 32, 60, 98). Some riparian grasshoppers consume algae growing along stream edges (9). As floods ebb and flow, and the ATTZ moves across the floodplain, many terrestrial arthropods track this highly productive area, especially as it ebbs and potential aquatic prey or other foods become stranded and exposed (3, 12, 78, 116, 150).

4.2. Ecological Controls on Plant-Canopy-Dwelling Arthropods

Harms & Grodowitz (58) reviewed insect herbivory of native aquatic and wetland plants of North America. Of the terrestrial insects addressed, most were either Coleoptera (50%; mostly Chrysomelidae and Curculionidae) or Lepidoptera (36%; mostly Crambidae and Noctuidae). Orthoptera (9%) and Hemiptera (5%) were less common. The lack of Orthoptera is noteworthy because in upland grasslands, Orthoptera are ubiquitous (130). The paucity of this group in wetlands is likely related to hydrology; many Orthoptera lay eggs in soils, and this reproductive strategy would be inhibited by wet, anoxic wetland soils. Wet soils likely also inhibit below-ground herbivory, a dominant form of insect herbivory in upland grasslands (130). In wetlands, only 11%

of insect herbivores feed on roots, and only 2% feed exclusively on roots; almost 90% of insect herbivores in wetlands target leaves, stems, petioles, flowers, or seeds (58).

Hydrology indirectly impacts insect herbivores on wetland plants by controlling host plant factors. Wetland plant genera with the greatest numbers of insect herbivore species include *Potamogeton* with 140, *Polygonum* with 95, *Nymphaea* with 53, *Sagittaria* with 47, *Nuphar* with 41, and *Salix* with 39 (58). Many herbivorous wetland insects are specific to single or a few host plant species (35). Hydrology largely dictates which plants dominate wetlands, and the kinds of insect herbivores vary by plant form as follows, listing from the wettest to the driest habitats (58):

- submersed species (*Potamogeton*, *Myriophyllum*) are consumed mostly by aquatic insects (76% of total; Chironomidae, Ephydridae, Trichoptera, *Paraponyx* Lepidoptera);
- floating species (*Nymphaea*, *Nuphar*) are consumed by a mix of aquatic taxa (49%) and terrestrial Coleoptera (30%);
- grasses (*Carex*, *Juncus*, *Schoenoplectus*, *Typha*) are consumed by a mix of terrestrial Coleoptera (36%), Lepidoptera (34%), and Orthoptera (15%);
- moist soil annuals (*Polygonum*) are consumed mostly by terrestrial Lepidoptera (62%) and Coleoptera (26%); and
- woody shrubs and trees (*Alnus*, *Populus*, *Salix*) are consumed mostly by terrestrial Coleoptera (92%).

As wetlands become drier, and more like terrestrial habitats, Lepidoptera and Coleoptera, both major terrestrial insect orders, become increasingly dominant.

Despite their ubiquity across wetlands, grasses (order Poales) have relatively depauperate herbivore faunas (e.g., insect species on North American grasses: *Carex*, 8 spp.; *Juncus*, 10 spp.; *Phragmites*, 2 spp.; *Schoeoplectus*, 12 spp.; *Scirpus*, 10 spp.; *Typha*, 32 spp.; see 58). In grasslands overall, insect herbivores are more diverse on grass species that are physically large, are perennial, and occur in monoculture (130). In North America, *Typha*, a large ubiquitous perennial wetland grass that often occurs in monoculture, supports the most insect herbivores, 32 species; *Carex*, an equally ubiquitous yet shorter wetland grass, supports only 8 species (58). In Europe, *Phragmites australis*, a very tall wetland grass, supports by far the most insects (approximately 100 species) of any grass, upland or wetland (130); curiously, however, North American *P. australis* appears to be virtually devoid of native insect herbivores (58).

4.3. Ecological Controls on Peatland Arthropods

Spitzer & Danks (120) reviewed the literature on the insects of peatlands. Briefly, they maintain that the fauna of peatlands is controlled by (*a*) the internally heterogeneous nature of peatlands (in structure: hummocks, hollows, pools; in plants: mosses, herbs, shrubs, trees); (*b*) the relative stability of the systems over time and the fact that they are typically climax rather than successional communities; (*c*) the cooler internal temperatures of peatlands relative to their surrounding landscapes; (*d*) the tendency of peatlands to function as unique wetland islands in an upland landscape, meaning that aspects of island biogeography may apply; and (*e*) the fact that many insect species are specifically adapted for peatland habitats (termed tyrphobiont or tyrphophilic species).

Since the review of Spitzer & Danks (120), more recent literature has expanded on some of the themes that they developed, with mixed success. The unique environmental conditions and plant communities in peatlands were found to have a stronger control on dipteran assemblages than they did in marshes and swamps (124). Hummock-hollow microtopography was found to control communities of microarthropod decomposers (8). However, efforts to increase habitat heterogeneity in fen meadows via mowing (112), in peat bogs via prescribed fires (62), and in black spruce peatlands via retention logging (42) were found to only modestly affect terrestrial arthropod assemblages (spiders, Orthoptera, and Syrphidae, respectively). Successional status controls spider assemblages, with unique species for individual successional states, and with late successional states having the most specialists (30). Aspects of island biogeography, such as habitat size (108) and dispersal capabilities (86), were not found to apply to terrestrial arthropods in peatlands, likely because the insects are excellent dispersers and are able to find even isolated habitats. Unexpectedly, a specialist butterfly that exhibits dispersal plasticity was less mobile when inhabiting small peatlands than when inhabiting large peatlands (40). Scant recent literature addresses ecological controls of terrestrial arthropods in peatlands, with most newer peatland work instead focusing on issues of conservation and climate change (see below), especially arthropod impacts on greenhouse gas emissions (e.g., 143, 145, 146).

5. TERRESTRIAL ARTHROPODS AND WETLAND ECOSYSTEM FUNCTIONS AND VALUES

5.1. Contributions of Terrestrial Arthropods to Wetland Biodiversity

Within the strictly aquatic realm, Diptera is the only invertebrate group that is diverse in wetlands (e.g., 50–100 species per wetland habitat), with most being Chironomidae (midges) (15). It is often not known whether wetland Diptera species have aquatic or terrestrial larvae, but most larvae of the higher flies (Brachycera) from wetlands are terrestrial (73), and this group can be very diverse. Beaulieu & Wheeler (18) reported more than 338 species of Brachycera from three sedge meadows in Canada, and Savage et al. (108) collected 381 species of muscoid flies from six bogs in Canada (96–182 species/bog).

Besides the terrestrial Diptera, several other terrestrial arthropods are very diverse in wetlands:

- 1,410 and 584 terrestrial Hymenoptera species were collected, respectively, in Alberta and Ontario peatlands, with the majority being small parasitic wasps (84); 377 species of bees and wasps alone were collected from the Brazilian Pantanal (4);
- >400 species of Lepidoptera were collected from a Czech bog (119) and a Croatian floodplain forest (76);
- 302 spider species were reported from 11 bogs in England (114), 214 spider species were reported from 23 bogs in Germany (30), and reports of 50 to >100 spider species from other wetlands are routine (e.g., 7, 34, 53, 65, 78, 83, 112, 148);
- 50 to 100 species of carabids per wetland are commonly reported (20, 28, 78, 80, 81, 85, 110);
- 76 species of soil Acarina (70) and 52 species of Collembola (122) were collected from European floodplains; and
- 31 species of Diplopoda were reported from the Pantanal (51).

Strikingly, many of the extremely high species counts of terrestrial arthropods come from northern peatland habitats (bogs and fens), which may reflect habitat conditions (diverse plant communities, numerous microhabitats; see above) or, alternatively, reflects that entomologists from Europe and Canada have a special interest in bogs and fens (120) and target the most diverse arthropod groups (Diptera, Hymenoptera, Coleoptera, Lepidoptera, Araneae).

Besides comprising much of the overall biodiversity, terrestrial arthropods include many rare and threatened species in wetlands. Numerous wetland butterflies and moths (see 45, 76, 79, 93, 121) and wetland grasshoppers (62, 72) have become threatened because their host plants are threatened. Nonherbivorous wetland arthropods are also threatened. Carabid beetles from wetlands are more vulnerable than nonwetland species (89, 107). Scott et al. (114) listed many wetland spiders that are on the European Red List of threatened taxa. Some wetland arthropods associated with wetlands, however, are thriving, despite ongoing wetland loss. For example, butterflies with broad host plant ranges, the ability to exploit host plants that exist beyond wetland boundaries, and the ability to exploit nonwetland habitat can remain successful (152); flexible patterns of aerial dispersal enable specialist butterflies to successfully exploit a broader range of wetland habitat (40).

The overall species richness of terrestrial arthropods in wetlands clearly dwarfs the species richness of aquatic arthropods and, for that matter, the richness of all other biota combined. Yet many of the threatened species in wetlands are terrestrial arthropods. Thus, when invoking the importance of wetlands as foci of biodiversity, the terrestrial arthropod component should play a prominent role. Regrettably, the total richness of terrestrial invertebrates in wetlands is rarely known, hindering efforts to conserve biodiversity (69). While many terrestrial arthropods in wetlands are not wetland obligates (69, 119, 120), an overlap between wetland and upland faunas means that conserving wetland habitats will contribute to conservation of upland species.

5.2. Roles of Terrestrial Arthropods in Ecosystem Processes

Terrestrial arthropods play important trophic roles in wetlands, although direct empirical evidence is scant. The simple fact that wetlands support a plethora of predaceous beetles and spiders and parasitic wasps suggests that top-down effects on herbivorous arthropods are important. The "world is green" hypothesis (56) may have application for wetlands; i.e., wetlands are green, suggesting that plants are thriving and herbivory is not a strong force, likely because natural enemies effectively control herbivores (e.g., 5, 134). Interactions among wetland plants, herbivores, and predators may be stable naturally. However, the fact that wetlands are frequently invaded by exotic plants indicates that natural herbivory is an important force; newly introduced plants explode in new environments because they are not kept in check by herbivory. Similarly, range extensions of invasive, exotic herbivores into new wetlands can have profound impacts on native wetland plants and wetland ecosystems (e.g., 75).

Attempts to quantify impacts of arthropod herbivores on wetland plants point toward moderate effects. In Minnesota *Typha* stands, insect herbivores only attacked 20% of the plants and consumed only a small proportion of those plants (99). As mentioned above, most wetland grasses support few herbivores. However, insect herbivory can be a stronger force on nongrass wetlands such as floating water lily beds (135) and wet forests (46, 75).

Impacts of terrestrial arthropods on the breakdown of wetland detritus (dead leaves, wood) are poorly understood. For wetland wood, most breakdown related to invertebrates likely results from the terrestrial, rather than the aquatic, fauna. Breakdown rates of dead wood, and patterns of invertebrate colonization of wood, in floodplains are more similar to wood in uplands than to wood in rivers (24). Exclusion studies indicate that terrestrial insects have similar impacts on wood breakdown in both upland and wetland settings (13.7–20.5% loss over three years); however, below-ground breakdown of wood in wetlands is slower because termites are lacking (131). Terrestrial arthropod feeding rates on leaf litter can be higher in wetlands than in uplands (88). Moisture levels, wetland type, and litter type can all affect how terrestrial arthropods influence leaf-litter breakdown (133, 144). However, the direct impact of terrestrial arthropods on the breakdown of leaf litter in some wetlands appears negligible (8, 33).

Of all terrestrial wetland arthropods, ants are perhaps the most important in terms of ecosystem impacts, sometimes acting as ecosystem engineers (143, 146). Wetland ants can affect soil physical structure, nutrient dynamics, and biological properties of the soil environment by building mounds or nests (17). In Northeastern China peatlands, the mounds of *L. flavus*, *L. niger*, and *F. candida* ants had greater concentrations of total organic C, dissolved organic C, total N, NO_3^-, and NH_4^+ than the surrounding soils (147). Importantly, ant mounds increased the spatial heterogeneity of these nutrient pools by altering soil C and N concentrations among soil layers and soil bulk density. Formation of ant mounds can change overall soil C and N storage, contributing measurable amounts (5.3–7.6%) to the total nutrient pools of peatland soils (143), and influence soil nutrient processes such as respiration, decomposition, mineralization and denitrification. Ant mounds can be hot spots for CO_2 emissions, change soils from being CH_4 sources to CH_4 sinks, alter seasonal fluctuations for N_2O emissions in wetland soils, and thus alter the spatial and temporal heterogeneity of soil gas emissions in wetlands (145, 146). Thus, ant mounds are important to the complete understanding of wetland ecosystem C and N cycles and balances, important issues in a changing global climate.

5.3. Terrestrial Arthropods as Bioindicators of Wetland Health

Bioassessment uses living organisms to indicate the ecological health or condition of habitats. Although aquatic invertebrates are widely used bioindicators in streams and rivers (22), the use of aquatic invertebrates to assess wetland ecological health has had mixed success, likely because highly tolerant, generalist species prevail (13). However, efforts to use terrestrial arthropods for wetland bioassessment show more promise. While bioassessment in aquatic habitats focuses on whole communities, workers using terrestrial wetland arthropods tend to focus on specific groups, with Carabidae being the most widely used (e.g., 20, 28, 31, 49, 54, 67, 85, 86, 127, 141). Spiders (112, 114, 132) and lepidopterans (19, 79, 93, 113, 137) are used occasionally. The enormous taxonomic richness of terrestrial arthropods in wetlands likely makes whole-community approaches impractical.

Terrestrial arthropods from wetlands have been successfully used to assess a range of environmental factors, including habitat conservation values (85, 96, 114, 141), the success of wetland restorations (5, 54, 67, 137), the ecological impacts of invasive plants (28, 82, 113, 127), the hydrologic status of wetlands (49, 96, 123), and the negative impacts of pollutants (61) and acidification (31). Terrestrial arthropods are used to assess impacts of various plant management techniques, such as mowing, disking, burning, and flooding of herbaceous vegetation (19, 96, 111, 112, 132) and logging (42).

6. CONCLUSIONS

For arthropods, wetlands have often been considered a subset of aquatic ecosystems. Our review suggests, however, that if wetlands are a subset of anything, then they are more likely a subset of terrestrial ecosystems. Terrestrial arthropods in wetlands are much more diverse than aquatic arthropods, and perhaps more important ecologically. While wetland conditions provide major constraints to aquatic organisms (16), they provide few constraints to terrestrial arthropods.

However, instead of viewing wetlands in terms of aquatic or terrestrial environments, it is perhaps most appropriate to view wetlands as making up an ecosystem class unto themselves. While wetlands share attributes of both aquatic and terrestrial ecosystems, they support aquatic organisms not found in streams, rivers, or lakes (142) and support terrestrial organisms not found in grasslands or upland forests (120). For terrestrial arthropods, wetlands provide ample food and water for sustenance, and numerous and heterogeneous subhabitats to exploit. In terms of ecosystem services, wetlands have values disproportionate to their spatial prevalence across the globe (39); this is likely also the case for values associated with the arthropods of wetlands.

DISCLOSURE STATEMENT

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LITERATURE CITED

1. Adis J. 1992. How to survive 6 months in a flooded soil—strategies in Chilopoda and Symphyla. *Stud. Neotrop. Fauna Environ.* 27(2–3):117–29
2. Adis J, Junk WJ. 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. *Freshw. Biol.* 47:711–31
3. Antvogel H, Bonn A. 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography* 24:470–82
4. Aranda R, Aoki C. 2018. Diversity and effect of historical inundation on bee and wasp (Hymenoptera: Apoidea, Vespoidea) communities in the Brazilian Pantanal. *J. Insect Conserv.* 22:581–91
5. Aschehoug ET, Sivakoff FS, Cayton HL, Morris WF, Haddad NM. 2015. Habitat restoration affects immature stages of a wetland butterfly through indirect effects on predation. *Ecology* 96:1761–67
6. Ballinger A, Lake PS, Mac Nally R. 2007. Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. *Oecologia* 152:227–38
7. Ballinger A, Mac Nally R, Lake PS. 2005. Immediate and longer-term effects of managed flooding on floodplain invertebrate assemblages in south-eastern Australia: generation and maintenance of a mosaic landscape. *Freshw. Biol.* 50:1190–205
8. Barreto C, Lindo Z. 2018. Drivers of decomposition and the detrital invertebrate community differ across hummock-hollow microtopography in Boreal peatlands. *EcoScience* 25:39–48
9. Bastow JL, Sabo JL, Finlay JC, Power ME. 2002. A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore dwelling grasshoppers. *Oecologia* 131:261–68
10. Battirola LD, Golovatch SI, Pinheiro TG, Batistella DA, Rosado-Neto GH, et al. 2018. Myriapod (Arthropoda, Myriapoda) diversity and distribution in a floodplain forest of the Brazilian Pantanal. *Stud. Neotrop. Fauna Environ.* 53:62–74
11. Battirola LD, Marques MI, Rosado-Neto GH, Pinheiro TG, Pinho NGC. 2009. Vertical and time distribution of Diplopoda (Arthropoda: Myriapoda) in a monodominant forest in Pantanal of Mato Grosso, Brazil. *Zoologia* 26:479–87
12. Batzer DP. 2004. Movements of upland invertebrates into drying seasonal woodland ponds in northern Minnesota, USA. *Wetlands* 24:904–7
13. Batzer DP. 2013. The seemingly intractable ecological responses of invertebrates in wetlands: a review. *Wetlands* 33:1–15
14. Batzer DP, Boix D, eds. 2016. *Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology*. Berlin: Springer
15. Batzer DP, Cooper R, Wissinger SA. 2014. Wetland animal ecology. In *Ecology of Freshwater and Estuarine Wetlands*, ed. DP Batzer, RR Sharitz, pp. 151–83. Berkeley, CA: Univ. Calif. Press. 2nd ed.
16. Batzer DP, Wissinger SA. 1996. Ecology of insect communities in nontidal wetlands. *Annu. Rev. Entomol.* 41:75–100

17. Batzer DP, Wu HT, Wheeler T, Eggert S. 2016. Peatland invertebrates. In *Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology*, ed. DP Batzer, D Boix, pp. 219–50. Berlin: Springer
18. Beaulieu F, Wheeler TA. 2005. Diptera diversity in a homogeneous habitats: Brachycera associated with sedge meadows (Cyperaceae: *Carex*) in Quebec, Canada. *Proc. Entomol. Soc. Wash.* 107:176–89
19. Benson TJ, Dinsmore JJ, Hohman WL. 2007. Response of plants and arthropods to burning and disking of riparian habitats. *J. Wildl. Manag.* 71:1949–57
20. Bettacchioli G, Taormina M, Bernini F, Migliorini M. 2012. Disturbance regimes in a wetland remnant: implications for trait-displacements and shifts in the assemblage structure of carabid beetles (Coleoptera: Carabidae). *J. Insect Conserv.* 16:249–61
21. Boix D, Batzer D. 2016. Invertebrate assemblages and their ecological controls across the world's freshwater wetlands. In *Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology*, ed. DP Batzer, D Boix, pp. 601–42. Berlin: Springer
22. Bonada N, Prat N, Resh VH, Statzner B. 2006. Development in aquatic insect monitoring: a comparative analysis of different approaches. *Annu. Rev. Entomol.* 51:495–523
23. Braccia A, Batzer DP. 2001. Invertebrates associated with woody debris in a southeastern forested floodplain wetland. *Wetlands* 21:18–31
24. Braccia A, Batzer DP. 2008. Breakdown and invertebrate colonization of dead wood in wetland, upland, and river habitats. *Can. J. For. Res.* 38:2697–704
25. Briers RA, Cariss HM, Geoghegan R, Gee JH. 2005. The lateral extent of the subsidy from an upland stream to riparian lycosid spiders. *Ecography* 28:165–70
26. Bright EG, Batzer DP, Garnett JA. 2010. Variation in invertebrate and fish communities across floodplain ecotones of the Altamaha and Savannah Rivers. *Wetlands* 30:1117–28
27. Brigić A, Bujan J, Alegro A, Šegota V, Ternjej I. 2017. Spatial distribution of insect indicator taxa as a basis for peat bog conservation planning. *Ecol. Indic.* 80:344–53
28. Brigić A, Vujčić S, Kepčija RM, Stančić Z, Alegro A, Ternjej I. 2014. Taxon specific response of carabids (Coleoptera, Carabidae) and other soil invertebrate taxa on invasive plant *Amorpha fruticosa* in wetlands. *Biol. Invasions* 16:1497–514
29. Brose U. 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia* 135:407–13
30. Buchholz S. 2016. Natural peat bog remnants promote distinct spider assemblages and habitat specific traits. *Ecol. Indic.* 60:774–80
31. Buckton ST, Ormerod SJ. 1996. Effects of liming on the Coleoptera, Hemiptera, Araneae and Opiliones of catchment wetlands in Wales. *Biol. Conserv.* 79:43–57
32. Burdon FJ, Harding JS. 2008. The linkage between riparian predators and aquatic insects across a stream-resource spectrum. *Freshw. Biol.* 53:330–46
33. Bush BM, Hutchens JJ Jr., Gulis V, Godwin KS. 2017. Impact of macroconsumers on leaf breakdown and detritivores in wetlands on a Southeastern US Coastal Plain floodplain during drought. *Wetlands* 37:1169–79
34. Cattin MF, Blandenier G, Banašek-Richter Bersier LF. 2003. The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. *Biol. Conserv.* 113:179–88
35. Center TD, Dray FA Jr., Jubinsky GP, Grodowitz MJ. 1999. *Insects and other arthropods that feed on aquatic and wetland plants*. Tech. Bull. 1870, Agric. Res. Serv., US Dep. Agric., Washington, DC
36. Center TD, Purcell MF, Pratt PD, Rayamajhi MB, Tipping PW, et al. 2012. Biological control of *Melaleuca quinquenervia*: an Everglades invader. *Biocontrol* 57:151–65
37. Chen X, Adams B, Layne M, Swarzenski C, Norris D, Hooper-Bùi L. 2017. Effects of isolation on ant assemblages depend on microhabitat. *Ecosphere* 8(12):e02049
38. Chen X, Adams B, Sabo A, Crupi T, Hooper-Bùi L. 2016. Ant assemblages and co-occurrence patterns in cypress-tupelo swamp. *Wetlands* 36:1–13
39. Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, et al. 2014. Changes in the global value of ecosystem services. *Glob. Environ. Change Hum. Policy Dimens.* 26:152–58

40. Crawford LA, Keyghobadi N. 2018. Flight morphology corresponds to both surrounding landscape structure and local patch conditions in a highly specialized peatland butterfly (*Lycaena epixanthe*). *Ecol. Entomol.* 43:629–39
41. Davis CA, Austin JE, Buhl DA. 2006. Factors influencing soil invertebrate communities in riparian grasslands of the Central Platte River floodplain. *Wetlands* 26:438–54
42. Deans AM, Smith SM, Malcolm JR, Crins WJ, Bellocq MI. 2007. Hoverfly (Syrphidae) communities respond to varying structural retention after harvesting in Canadian peatland black spruce forests. *Environ. Entomol.* 36:308–18
43. Deharveng L, D'Haese CA, Bedos A. 2008. Global diversity of springtails (Collembola; Hexapoda) in freshwater. *Hydrobiologia* 595:329–38
44. Delgado C, Couturier G, Fine PVA. 2014. Survival of seasonal flooding in the Amazon by the terrestrial insect *Conotrachelus dubiae* O'Brien & Couturier (Coleoptera: Curculionidae), a pest of the camu-camu plant, *Myrciaria dubia* (Myrtacae). *Neotrop. Entomol.* 43:380–84
45. Drahovzal SA, Loftin CS, Rhymer J. 2015. Environmental predictors of shrubby cinquefoil (*Dasiphora fruticosa*) habitat and quality as host for Maine's endangered Clayton's copper butterfly (*Lycaena dorcas claytoni*). *Wetl. Ecol. Manag.* 23:891–908
46. Effler R, Goyer RA, Lenhard GJ. 2006. Baldcypress and water tupelo responses to insect defoliation and nutrient augmentation in Maurepas Swamp, Louisiana, USA. *Forest Ecol. Manag.* 236:295–304
47. Folgarait PJ. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers. Conserv.* 7:1221–44
48. Gerisch M, Agostinelli V, Henle K, Dziock F. 2012. More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos* 121:508–15
49. Gerisch M, Schanowski A, Figura W, Gerken B, Dziock F, Henle K. 2006. Carabid beetles (Coleoptera, Carabidae) as indicators of hydrological site conditions in floodplain grasslands. *Int. Rev. Hydrobiol.* 91:326–40
50. Giordano R, Weber E, Darby BJ, Soto-Adames FN, Murray RE, Drizo A. 2014. Invertebrates associated with a horizontal-flow, subsurface constructed wetland in a northern climate. *Environ. Entomol.* 43:283–90
51. Golovatch SI, Hoffman RL, Adis J, Marques MI, Raizer J, et al. 2005. Millipedes (Diplopoda) of the Brazilian Pantanal. *Amazoniana* 18(3/4):273–88
52. Gotelli NJ, Ellison AM. 2002. Biogeography at a regional scale: determinants of ant species density in New England bogs and forests. *Ecology* 83:1604–9
53. Greenwood MT, Bickerton MA, Petts GE. 1995. Spatial distribution of spiders on the floodplain of the River Trent, UK: the role of hydrologic setting. *Regul. Rivers Res. Manag.* 10:303–13
54. Günther J, Assmann T. 2005. Restoration ecology meets carabidology: effects of floodplain restitution on ground beetles (Coleoptera, Carabidae). *Biodivers. Conserv.* 14:1583–606
55. Haefliger P, Schwarzlaender M, Blossey B. 2006. Impact of *Archanara geminipuncta* (Lepidoptera: Noctuidae) on aboveground biomass production of *Phragmites australis*. *Biol. Control* 38:413–21
56. Hairston NG, Smith FE, Slobodkin LB. 1960. Community structure, population control and competition. *Am. Nat.* 44:421–25
57. Hardman CJ, Harris DB, Sears J, Droy N. 2012. Habitat associations of invertebrates in reedbeds, with implications for management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 22:813–26
58. Harms NE, Grodowitz MJ. 2009. Insect herbivores of aquatic and wetland plants in the United States: a checklist from literature. *J. Aquat. Plant Manag.* 47:73–96
59. Hering D, Gerhard M, Manderbach R, Reich M. 2004. Impact of a 100-year flood on vegetation, benthic invertebrates, riparian fauna and large woody debris standing stock in an alpine floodplain. *River Res. Appl.* 20:445–57
60. Hering D, Platcher H. 1997. Riparian ground beetles (Coleoptera, Carabidae) preying on aquatic invertebrates; a feeding strategy in alpine floodplains. *Oecologia* 111:261–70
61. Hobbelen PHF, van den Brink PJ, Hobbelen JF, van Gestel CAM. 2006. Effects of heavy metals on the structure and functioning of detritivore communities in a contaminated floodplain area. *Soil Biol. Biochem.* 38:1596–607

62. Hochkirch A, Adorf F. 2007. Effects of prescribed burning and wildfires on Orthoptera in central European peat bogs. *Environ. Conserv.* 34:225–35
63. Holec M, Frouz J. 2006. The effect of two ant species *Lasius niger* and *Lasius flavus* on soil properties in two contrasting habitats. *Eur. J. Soil Biol.* 42:213–17
64. Holmquist JG, Jones JR, Schmidt-Gengenback J, Pierotti LF, Love JP. 2011. Terrestrial and aquatic macroinvertebrate assemblages as a function of wetland type across a mountain landscape. *Arct. Antarct. Alp. Res.* 43:568–84
65. Hore U, Uniyal VP. 2008. Diversity and composition of spider assemblages in five vegetation types of the Terai Conservation Area, India. *J. Arachnol.* 36:251–58
66. Hunt-Joshi TR, Blossey B, Root RB. 2004. Root and leaf herbivory on *Lythrum salicaria*: implications for plant performance and communities. *Ecol. Appl.* 14:1574–89
67. Januschke K, Verdonschot RCM. 2016. Effects of river restoration on riparian ground beetles (Coleoptera: Carabidae) in Europe. *Hydrobiologia* 769:93–104
68. Junk WJ, Bailey PB, Sparks RE. 1989. The flood-pulse concept in river-floodplain systems. *Spec. Publ. Can. J. Fish. Aquat. Sci.* 106:110–27
69. Junk WJ, da Cunha CN, Wantzen KM, Petermann P, Strüssmann C, et al. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquat. Sci.* 68:278–309
70. Kaluz S. 1994. Contribution to the knowledge of soil mites (Acarina) in Morava River floodplain and Borska-Nizina (lowland). *Ekol. Bratislava* 13(Suppl. 1):135–44
71. Kappes H, Lay R, Topp W. 2007. Changes in different trophic levels of litter-dwelling macrofauna associated with Giant Knotweed invasion. *Ecosystems* 10:734–44
72. Kati V, Zografou K, Tzirkalli E, Chitos T, Willemse L. 2012. Butterfly and grasshopper diversity patterns in humid Mediterranean grasslands: the roles of disturbance and environmental factors. *J. Insect Conserv.* 16:807–18
73. Keiper JB, Walton WE, Foote BA. 2002. Biology and ecology of higher Diptera from freshwater wetlands. *Annu. Rev. Entomol.* 47:207–32
74. Kolesnikov FN, Karamyan AN, Hoback WW. 2012. Survival of ground beetles (Coleoptera: Carabidae) submerged during floods: field and laboratory studies. *Eur. J. Entomol.* 109:71–76
75. Kolka RK, D'Amato AW, Wagenbrenner JW, Slesak RA, Pypker TG, et al. 2018. Review of ecosystem level impacts of emerald ash borer on black ash wetlands: What does the future hold? *Forests* 9:179
76. Koren T, Vukotic K, Crne M. 2015. Diversity of the moth fauna (Lepidoptera: Heterocera) of a wetland forest: a case study from Motovun forest, Istria, Croatia. *Period. Biol.* 117:399–414
77. Krab EJ, Aerts R, Berg MP, van Hal J, Keuper F. 2014. Northern peatland Collembola communities unaffected by three summers of simulated extreme precipitation. *Appl. Soil Ecol.* 79:70–76
78. Lafage D, Sibelle C, Secondi J, Canard A, Pétillon J. 2015. Short-term resilience of arthropod assemblages after spring flood, with focus on spiders (Arachnida: Araneae) and carabids (Coleoptera: Carabidae). *Ecohydrology* 8:1584–99
79. Landis DA, Fiedler AK, Hamm CA, Cuthrell DL, Schools EH, et al. 2012. Insect conservation in Michigan prairie fen: addressing the challenge of global change. *J. Insect Conserv.* 16:131–42
80. Lessel T, Marx MT, Eisenbeis G. 2011. Effects of ecological flooding on the temporal and spatial dynamics of carabid beetles (Coleoptera, Carabidae) and springtails (Collembola) in a polder habitat. *ZooKeys* 100:421–46
81. Liebherr JK, Song H. 2002. Distinct ground beetle (Coleoptera: Carabidae) assemblages within a New York State wetland complex. *J. N. Y. Entomol. Soc.* 110:127–41
82. Maceda-Veiga A, Basas H, Lanzaco G, Sala M, de Sostoa A, Serra A. 2016. Impacts of the invader giant reed (*Arundo donax*) on riparian habitats and ground arthropod communities. *Biol. Invas.* 18:731–49
83. Malumbres-Olarte J, Vink CJ, Ross JG, Cruickshank RH, Paterson AM. 2013. The role of habitat complexity on spider communities in native alpine grasslands of New Zealand. *Insect Conserv. Divers.* 6:124–34
84. Marshall SA, Finnamore AT, Blades DCA. 1999. Canadian peatlands: diversity and habitat specialization of the arthropod fauna. In *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*, ed. DP Batzer, RB Rader, SA Wissinger, pp. 383–400. New York: Wiley

85. Martay B, Hughes F, Doberski J. 2012. A comparison of created and ancient fenland using ground beetles as a measure of conservation value. *Insect Conserv. Divers.* 5:251–63
86. Martay B, Robertshaw T, Doberski J, Thomas A. 2014. Does dispersal limit beetle re-colonization of restored fenland? A case study using direct measurements of dispersal and genetic analysis. *Restor. Ecol.* 22:590–97
87. Martínez FS, Franceschini C. 2018. Invertebrate herbivory on floating-leaf macrophytes at the northeast of Argentina: Should the damage be taken into account in estimations of plant biomass? *Ann. Brazil. Acad. Sci.* 90:155–67
88. Marx MT, Yan X, Wang X, Song L, Wang K, et al. 2016. Soil fauna abundance, feeding and decomposition in different reclaimed and natural sites in the Sanjiang Plain wetland, Northeast China. *Wetlands* 36:445–55
89. Matern A, Drees C, Meyer H, Assman T. 2008. Population ecology of the rare carabid beetle *Carabus variolosus* (Coleoptera: Carabidae) in north-west Germany. *J. Insect Conserv.* 12:591–601
90. Mendelssohn IA, Batzer DP, Holt CR, Graham SA. 2014. Abiotic constraints for wetland plants and animals. In *Ecology of Freshwater and Estuarine Wetlands*, ed. DP Batzer, RR Sharitz, pp. 61–86. Berkeley, CA: Univ. Calif. Press. 2nd ed.
91. Mescher MC, Ross KG, Shoemaker DD, Keller L, Krieger MJB. 2003. Distribution of the two social forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the native South American range. *Ann. Entomol. Soc. Am.* 96:810–17
92. Nakano S, Murakami M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *PNAS* 98:166–70
93. Noreika N, Kotze DJ, Loukola OJ, Sormunen N, Vuori A, et al. 2016. Specialist butterflies benefit most from the ecological restoration of mires. *Biol. Conserv.* 196:103–14
94. Notzold R, Blossey B, Newton E. 1998. The influence of below ground herbivory and plant competition on growth and biomass allocation of purple loosestrife. *Oecologia* 113:82–93
95. NWWG (Natl. Wetlands Work. Group). 1988. *Wetlands of Canada*. Ecol. Land Classif. Ser. 24. Ottawa, Ontario/Montreal, Quebec: Sustain. Dev. Branch, Env. Can./Polysci. Publ.
96. O'Malley RE. 1999. Agricultural wetland management for conservation goals: invertebrates in California ricelands. In *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*, ed. DP Batzer, RB Rader, SA Wissinger, pp. 857–85. New York: Wiley
97. Paetzold A, Bernet JF, Tockner K. 2006. Consumer-specific responses to riverine subsidy pulses in a riparian arthropod assemblage. *Freshw. Biol.* 51:1103–15
98. Paetzold A, Schubert CJ, Tockner K. 2005. Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. *Ecosystems* 8:748–59
99. Penko JM, Pratt DC. 1987. Insect herbivory in Minnesota *Typha* stands. *J. Freshw. Ecol.* 4:235–44
100. Pequeno PACL, Franklin E. 2014. What drives the dynamics of a soil mite population under seasonal flooding? A null model analysis. *Exp. Appl. Acarol.* 62:215–24
101. Plum H. 2005. Terrestrial invertebrates in flooded grassland: a literature review. *Wetlands* 25:721–37
102. Pratt PD, Rayamajhi MB, Van TK, Center TD, Tipping PW. 2005. Herbivory alters resource allocation and compensation in the invasive tree *Melaleuca quiquenervia*. *Ecol. Entomol.* 30:316–26
103. Ramey TL, Richardson JS. 2017. Terrestrial invertebrates in the riparian zone: mechanisms underlying their unique diversity. *BioScience* 67:808–19
104. Reeder RH, Bacon ETG, Caiden MJ, Bullock RJ, Gonzalez-Moreno P. 2018. Effect of population density of the Azolla weevil (*Stenopelmus rufiasus*) on the surface cover of the water fern (*Azolla filiculoides*) in the UK. *Biocontrol* 63:185–92
105. Ribas CR, Schoereder JH. 2007. Ant communities, environmental characteristics and their implications for conservation in the Brazilian Pantanal. *Biodivers. Conserv.* 16:1511–20
106. Rothenbücher J, Schaefer M. 2006. Submersion tolerance in floodplain arthropod communities. *Basic Appl. Ecol.* 7:398–408
107. Sasakawa K. 2016. Notes on the reproductive ecology and description of the preimaginal morphology of *Elaphrus sugai* Nakane, the most endangered species of *Elaphrus* Fabricius (Coleoptera: Carabidae) ground beetle worldwide. *PLOS ONE* 11(7):e0159164

108. Savage J, Wheeler TA, Moores AMA, Taillefer AG. 2011. Effects of habitat size, vegetation cover, and surrounding land use on Diptera diversity in temperate Nearctic bogs. *Wetlands* 31:125–34
109. Schipper AM, Hendriks AJ, Ragas AMJ, Leuven RSEW. 2014. Disentangling and ranking the influences of multiple environmental factors on plant and soil-dwelling arthropod assemblages in a river Rhine floodplain area. *Hydrobiologia* 729:133–42
110. Schipper AM, Lottermanh K, Geertsma M, Leuven RSEW, Hendriks AJ. 2010. Using datasets of different taxonomic detail to assess the influence of floodplain characteristics on terrestrial arthropod assemblages. *Biodivers. Conserv.* 19:2087–110
111. Schmidt MH, Lefebvre G, Poulin B, Tscharntke T. 2005. Reed cutting affects arthropod communities, potentially reducing food for passerine birds. *Biol. Conserv.* 121:157–66
112. Schmidt MH, Rocker S, Hanafi J, Gigon A. 2008. Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows. *Biodivers. Conserv.* 17:3003–12
113. Schooler SS, McEvoy PB, Hammond P, Coombs EM. 2009. Negative *per capita* effects of two invasive plants, *Lythrum salicaria* and *Phalaris arundinacea*, on the moth diversity of wetland communities. *Bull. Entomol. Res.* 99:229–43
114. Scott AG, Oxford GS, Selden PA. 2006. Epigeic spiders as ecological indicators of conservation value for peat bogs. *Biol. Conserv.* 127:420–28
115. Sharitz RR, Batzer DP, Pennings SC. 2014. Ecology of freshwater and estuarine wetlands: an introduction. In *Ecology of Freshwater and Estuarine Wetlands*, ed. DP Batzer, RR Sharitz, pp. 1–22. Berkeley, CA: Univ. Calif. Press. 2nd ed.
116. Sienkiewicz P, Żmihorski M. 2012. The effect of disturbance caused by rivers flooding on ground beetles (Coleoptera, Carabidae). *Eur. J. Entomol.* 109:535–41
117. Sipura M, Ikonen A, Tahvanainen J, Roininen H. 2002. Why does the leaf beetle *Galerucella lineola* F. attack wetland willows? *Ecology* 83:3393–407
118. Song L, Liu J, Yan X, Chang L, Wu D. 2016. Euedaphic and hemiedaphic Collembola suffer larger damages than edaphic species to nitrogen input. *Environ. Pollut.* 208:413–15
119. Spitzer K, Bezděk A, Jaroš J. 1999. Ecological succession of a relict Central European peat bog and variability of its insect biodiversity. *J. Insect Conserv.* 3:97–106
120. Spitzer K, Danks HV. 2006. Insect biodiversity of boreal peat bogs. *Annu. Rev. Entomol.* 51:137–61
121. Stephens JD, Santos SR, Folkerts DR. 2011. Genetic differentiation, structure, and a transition zone among populations of the pitcher plant moth *Exyra semicrocea*: implications for conservation. *PLOS ONE* 6(7):e22658
122. Sterzyńska M, Pižl V, Tajovský K, Stelmaszczyk M, Okruszho T. 2015a. Soil fauna of peat-forming wetlands in a natural river floodplain. *Wetlands* 35:815–29
123. Sterzyńska M, Tajovský K, Nicia P. 2015b. Contrasting responses of millipedes and terrestrial isopods to hydrologic regime changed in forested montane wetlands. *Eur. J. Soil Biol.* 68:33–41
124. Taillefer AG, Wheeler TA. 2018. Tracking wetland community evolution using Diptera taxonomic, functional and phylogenetic structure. *Insect Conserv. Divers.* 11:276–93
125. Tajovský K. 1999. Impact of inundations on terrestrial arthropod assemblages in Southern Moravian floodplain forests, the Czech Republic. *Ekol. Bratislava* 18(Suppl. 1):177–85
126. Tipping PW, Martin MR, Rayamajhi MB, Pratt PD, Gettys LA. 2018. Combining biological and mechanical tactics to suppress *Melaleuca quinquenervia*. *Biol. Control.* 121:229–33
127. Topp W, Kappes H, Rogers F. 2008. Response of ground-dwelling beetle (Coleoptera) assemblages to giant knotweed (*Reynoutria* spp.) invasion. *Biol. Invas.* 10:381–90
128. Tronstad LM, Tronstad BP, Benke AC. 2005. Invertebrate seedbanks: rehydration of soil from an unregulated river floodplain in the south-eastern U.S. *Freshw. Biol.* 50:646–55
129. Truxa C, Fiedler K. 2012. Down in the flood? How moth communities are shaped in temperate floodplain forests. *Insect Conserv. Divers.* 5:389–97
130. Tscharntke T, Greiler H. 1995. Insect communities, grasses, and grasslands. *Annu. Rev. Entomol.* 40:535–58
131. Ulyshen MD. 2014. Interacting effects of insects and flooding on wood decomposition. *PLOS ONE* 9(7):e101867

132. Valkama E, Lyytinen S, Koricheva J. 2008. The impact of reed management on wildlife: a meta-analytical review of European studies. *Biol. Conserv.* 141:364–74
133. van Dijk J, Didden WAM, Kuenen F, van Bodegom PM, Verhoef HA, Aerts R. 2009. Can differences in soil community composition after peat meadow restoration lead to different decomposition and mineralization rates? *Soil Biol. Biochem.* 41:1717–25
134. Verschut TA, Hamback PA. 2018. A random survival forest illustrates the importance of natural enemies compared to host plant quality on leaf beetle survival rates. *BMC Ecol*. 18:33
135. Wallace JB, O'Hop J. 1985. Life on a fast pad: waterlily leaf beetle impact on water lilies. *Ecology* 66:1534–44
136. Wantzen KM, Marchese MR, Marques MI, Battirola LD. 2016. Invertebrates in neotropical floodplains. In *Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology*, ed. DP Batzer, D Boix, pp. 493–524. Berlin: Springer
137. Watts CH, Didham RK. 2006. Rapid recovery of an insect-plant interaction following habitat loss and experimental wetland restoration. *Oecologia* 148:61–69
138. Webb MR, Pullin AS. 1998. Effects of submergence by winter floods on diapausing caterpillars of a wetland butterfly, *Lycaena dispar batavus*. *Ecol. Entomol*. 23:96–99
139. Wei X, Cao R, Wu X, Eisenhauer N, Sun S. 2018. Effect of water table decline on the abundances of soil mites, springtails, and nematodes in the Zoige peatland of eastern Tibetan Plateau. *Appl. Soil Ecol.* 129:77–83
140. Wheeler GS, Hight SD, Wright SA. 2017. Impact of field densities of the naturalized defoliator *Caloptilia triadicae* (Lepidoptera: Gracillariidae) on the invasive weed Chinese tallowtree. *Environ. Entomol.* 46:1304–12
141. Williams CD, Hayes M, McDonnell RJ, Anderson R, Bleasdale A, Gormally MJ. 2014. Factors affecting wetland ground beetle (Carabidae) assemblages: How important are habitats, conservation designations and management? *Insect Conserv. Divers.* 7:206–22
142. Wissinger SA. 1999. Ecology of wetland invertebrates: synthesis and applications for conservation and management. In *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*, ed. DP Batzer, RD Rader, SA Wissinger, pp. 1043–86. New York: Wiley
143. Wu HT, Batzer DP, Yan XM, Lu XG, Wu DH. 2013a. Contributions of ant mounds to soil carbon and nitrogen pools in a marsh wetland of Northeastern China. *Appl. Soil Ecol.* 70:9–15
144. Wu HT, Lu XG, Jiang M, Bao X. 2009. Impacts of soil fauna on litter decomposition at different succession stages of wetland in Sanjiang Plain, China. *Chin. Geogr. Sci.* 19:258–64
145. Wu HT, Lu XG, Tong SZ, Batzer DP. 2015. Soil engineering ants increase CO_2 and N_2O emissions by affecting mound soil physicochemical characteristics from a marsh soil: a laboratory study. *Appl. Soil Ecol.* 87:19–26
146. Wu HT, Lu XG, Wu DH, Song LH, Yan XM, Liu J. 2013b. Ant mounds alter spatial and temporal patterns of CO_2, CH_4 and N_2O emissions from a marsh soil. *Soil Biol. Biochem.* 57:884–91
147. Wu HT, Lu XG, Wu DH, Yin XM. 2010. Biogenic structures of two ant species *sanguinea* and *Lasius flavus* altered soil C, N and P distribution in a meadow wetland of the Sanjiang Plain, China. *Appl. Soil Ecol.* 46:321–28
148. Yamazaki L, Vindica VF, Brescovit AD, Marques MI, Battirola LD. 2017. Temporal variation in the spider assemblage (Arachnida, Araneae) in canopies of *Callisthene fasciculata* (Vochysiaceae) in the Brazilian Pantanal biome. *Iheringia Ser. Zool.* 107:e2017019
149. Zerm M, Adis J. 2003a. Exceptional anoxia resistance in larval tiger beetle, *Phaeoxantha klugii* (Coleoptera: Cicindelidae). *Physiol. Entomol.* 28:150–53
150. Zerm M, Adis J. 2003b. Survival strategy of the bombardier beetle, *Pheropsophus rivieri* (Col.: Carabidae) in a Central Amazonian blackwater floodplain (Brazil). *Amazoniana* 17:503–8
151. Zhang B, Chang L, Ni Z, Callaham MA Jr. 2014. Effects of land use changes on winter-active Collembola in Sanjiang Plain of China. *Appl. Soil Biol.* 83:51–58
152. Zimmerman K, Fric A, Filipova L, Konvicka M. 2005. Adult demography, dispersal and behavior of *Brenthis ino* (Lepidoptera: Nymphalidae): how to be a successful wetland butterfly. *Eur. J. Entomol.* 1–2:699–706