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https://doi.org/10.1146/annurev-ento-011613-161958

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Freshwater Biodiversity and Aquatic Insect Diversification

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Annu. Rev. Entomol. 2014. 59:143–63

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-011613-161958

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Keywords

aquatic habitats, ecology, phylogenetics, adaptation, speciation

Abstract

Inland waters cover less than 1% of Earth's surface but harbor more than 6% of all insect species: Nearly 100,000 species from 12 orders spend one or more life stages in freshwater. Little is known about how this remarkable diversity arose, although allopatric speciation and ecological adaptation are thought to be primary mechanisms. Freshwater habitats are highly susceptible to environmental change and exhibit marked ecological gradients. Standing waters appear to harbor more dispersive species than running waters, but there is little understanding of how this fundamental ecological difference has affected diversification. In contrast to the lack of evolutionary studies, the ecology and habitat preferences of aquatic insects have been intensively studied, in part because of their widespread use as bioindicators. The combination of phylogenetics with the extensive ecological data provides a promising avenue for future research, making aquatic insects highly suitable models for the study of ecological diversification.

INTRODUCTION

Diversification: the net result of speciation and extinction; the formation of species or the increase in taxonomic diversity

Inland waters cover less than 1% of the Earth's surface yet harbor 10% of all known animal species, of which 60% is composed of aquatic insects. This diversity today numbers close to 100,000 described species (11) (**Table 1**). This is probably an underestimate, and with the taxonomic deficit skewed toward the insects, we estimate that aquatic insects may well number more than 200,000 species and thereby make up 80% of aquatic animal diversity. Aquatic insects spend one or more stages of their life cycles in the water, with the majority living in water as eggs and larvae and moving to terrestrial habitats as adults. They play important ecological roles in both aquatic and terrestrial realms as primary consumers, detritivores, predators, and pollinators. The ecology of many groups is well studied, owing to their roles as bioindicators or disease vectors, but freshwaters have been largely overlooked as a hotbed of diversification, despite their disproportionate contribution to global biodiversity. A review by Mayhew (74) explored why there are so many insect species but included very few aquatic examples. The investigation of aquatic insects is therefore timely, with freshwater habitats widely recognized as the most threatened on Earth (133).

The fossil record suggests that all aquatic insect groups are the result of the invasion of freshwaters by terrestrial groups (143). Although belonging to 12 orders, aquatic insects may represent more than 50 separate invasions (**Table 1**). Ephemeroptera, Odonata, Plecoptera, Trichoptera, and Megaloptera are almost exclusively restricted to freshwater by an aquatic larval stage and make up over 27,000 known species, of which over half belong to Trichoptera. The remaining diversity includes over 10% of the hemipteran suborder Heteroptera, approximately 30% of Diptera, approximately 3% of Coleoptera, and very small proportions of Hymenoptera, Lepidoptera, Neuroptera, and Orthoptera. The order Diptera is by far the largest group, containing nearly half of all aquatic insects. All major orders are cosmopolitan, with the notable exception of the Megaloptera, and have 50–75% of known species in the tropics, except Plecoptera, of which 65% are Holarctic species (11).

Freshwaters are highly diverse and include ponds, lakes, springs, streams, rivers, wetlands, reservoirs, and ditches (139). The transition to freshwaters demanded adaptation in mechanisms of thermo- and osmoregulation, respiration, feeding, and locomotion. Among the most notable characteristics of freshwaters are their daily and seasonal temperatures, which are more stable than air and soil temperatures. Freshwaters occupy a low position on the landscape where they accumulate nutrients and detritus. Aquatic autotrophs are smaller (often unicellular), grow faster, and have a higher nutritional quality than land plants. Aquatic habitats also exhibit marked spatiotemporal gradients of connectivity and permanence, ranging from stable to dynamic and from insular to connected: For example, seasonal precipitation makes some habitats temporarily dry, turns small streams into large rivers, or reconnects previously separated wetlands. This heterogeneity is important to freshwater biodiversity because of the variety of life histories and ecological roles it enables. Because of their shape and size, freshwater habitats have a large interface with adjacent terrestrial habitats. We estimate that over 70% of aquatic animal species, including most insects, have complex life cycles, providing great adaptability and the potential to disperse outside water. This potential to adjust and disperse, and to access opportunity and evade extinction, sets insects apart from less diverse life forms (74) and separates the freshwater majority from better-studied minorities such as fish.

Here we review the important contributions to our understanding of aquatic insect diversification. We emphasize phylogenetic studies that infer processes that led to species diversification. Where these are lacking, we refer to studies of population divergence within species that suggest relevant mechanisms. Our arrangement of these mechanisms into discrete sections oversimplifies the diversification process, because mechanisms are not mutually exclusive and many studies

Table 1 The major aquatic insect lineages, their character, and their value for diversification research

Radiation[a]		Species[b]	Tax[c]	Lot[d]	Diversity and ecology	Diversification research potential
Ephemeroptera (mayflies)		3,046	+	+	Rivals Plecoptera as third largest purely aquatic order (15) Differs notably from sister-group Odonata in that larvae feed mainly on algae and fine detritus and are morphologically more diverse; adults do not feed, emerge synchronously, live for a short time, disperse poorly, and are morphologically uniform	Comparatively well studied taxonomically; few species-level phylogenies available Suitable for studying the role of life history in diversification, e.g., parthenogenesis and temporal isolation through reproductive synchronicity Offers/enables interesting comparison of two ecologically different radiations in Palaeoptera (see Odonata)
Odonata (dragonflies, damselflies)		5,952	++	–	Second largest purely aquatic order; fourth largest aquatic insect radiation (61) All species are predators with highly developed sight and adult flight, and extrudable mouthparts of larva Broad range of dispersal capacities rivaled only by some Coleoptera; most visible sexual behavior among aquatic insects	Best-researched group relative to species numbers, with most work on sexual selection and conflict by sperm displacement (unique secondary genitalia), male courtship displays (often with colored wings and body), and female color forms Taxonomy and distribution best known of any aquatic group; only insects with global overview of species' threat status (26)
Heteroptera	Nepomorpha (water bugs)	2,404	++	–	Two radiations, both largely predatory, in the otherwise strictly terrestrial order Hemiptera In contrast to complex invasion history and extreme ecological diversity of Diptera and Coleoptera, all life stages bound to water Unlike most freshwater insects, ecology of larvae and adults notably similar and with high frequency of flightless forms in adults (5) Gerromorpha the main animal group to invade freshwater surface	Moderately well studied; potential to study sexual conflict in groups with sexual dimorphism remains unexploited (6) Good potential for studying historical biogeography; despite many lentic species, allopatric diversification is thought to predominate due to hololimnic life cycle and low dispersal, which also offers unique potential for radiation in old lakes (102)
	Gerromorpha (water striders)	2,021	+	–		
Plecoptera (stoneflies)		3,497	–	++	Third largest purely aquatic order, most notable coldwater radiation with distinct Northern and Southern Hemisphere radiations (42)	Very underworked Ecologically sensitive and relatively uniform, with limited dispersal; mostly allopatric speciation Suitable for studies of historical biogeography, but also for temporal isolation

(*Continued*)

Table 1 ***(Continued)***

Radiation[a]		Species[b]	Tax[c]	Lot[d]	Diversity and ecology	Diversification research potential
Diptera (flies)	Culicomorpha (mosquitoes, midges, black flies)	19,618	–	–	Only mainly terrestrial order with large freshwater proportion, including 1st, 2nd, and 5th aquatic insect radiations (but see Trichoptera) With >20 freshwater invasions possibly up to 50% of aquatic insects in Diptera and 30% of Diptera in freshwater Greatest ecological diversity and flexibility of any aquatic order; however, species' ecologies often unknown (most notably in Tipulomorpha) and vast majority possibly in moist substrates rather than in water (135) Specific preadaptation for multiple freshwater invasions and radiations unclear but likely related to exceptionally diverse functional morphology, physiological adaptability (e.g., to extreme chemical and physical environments), and numerous feeding modes	Large body of work with focus on disease vectors and medical applications, e.g., Simuliidae and Culicidae; excellent process work on *Anopheles gambiae* (see sidebar), but notable lack of studies on patterns; strong correlation of aquatic larvae with blood-sucking adults, perhaps due to preadapted mouthparts and host concentration near water Research on most families hampered by lack of taxonomic and ecological knowledge; only reasonably studied nonvectors are Chironomidae, which dominate aquatic communities in individual and species numbers with extreme ecological diversity, e.g., survive heights up to 5,600 m above sea level, depths down to 1,000 m underwater, air temperatures down to −20°C, and water temperatures up to 40°C; have 7-day to 7-year life cycles; and include marine and Antarctic species (39); ideal for geographic and diversification research, as often preserved as subfossils (103)
	Tipulomorpha (crane flies)	15,770	- -	?		
	Tabanomorpha (horse flies, deer flies, snipe flies, watersnipe flies)	5,373	?	?		
	Psychodomorpha (moth flies, net-winged midges	3,412	?	?		
	Ephydridae (shore flies)	1,994	?	?		
Trichoptera (caddisflies)		14,291	- -	+	Largest purely aquatic order, currently third most diverse taxonomically, but may be the largest aquatic insect radiation with up to 50,000 species (33) Great diversity due to microhabitat specialization, full array of feeding modes (probably second only to Diptera) facilitated by great diversity in silk-spinning strategies and case construction, and relatively low dispersal	Very underworked, especially relative to species richness, as only 25% of species may be described; few species-level phylogenies Good aquatic/terrestrial comparison possible with well-known sister-group Lepidoptera Adaptive significance of case-building and feeding behavior only poorly studied at high taxonomic resolution, though both likely to present key innovations

(Continued)

Table 1 (*Continued*)

Radiation[a]		Species[b]	Tax[c]	Lot[d]	Diversity and ecology	Diversification research potential
Megaloptera (fishflies, dobsonflies, and alderflies)		328	+	+	Very small purely aquatic order; relict distribution, mostly in Americas and Asia (28) Monophyly previously contested but recently supported (136)	Low species and ecological diversity, limited distribution, suitable for historical biogeography
Coleoptera (beetles)	Hydradephaga (diving beetles, whirligigs)	5,126	+	–	Largest group of animals on Earth, but 97% of species strictly terrestrial; >20 freshwater invasions with diverse life histories; aquatic and terrestrial behaviors often merge at shoreline Only 8% of aquatic species with typical amphibiotic life cycle (submerged larva, shorter-lived terrestrial adult); most groups aquatic in all life stages, some with terrestrial larva and aquatic adult (56) Sealed air tank under elytra as major preadaptation for frequent and flexible invasion of freshwaters; individuals could reinvade freshwater daily	Prominent in the literature, perhaps second only to Odonata, with most work on diversification of any aquatic group Much focus on habitat stability (107), providing good comparisons with strongly lotic (Gyrinidae, Elmidae), lentic and dispersive (Dytiscoidea), or specialized groups (Hydraenidae), as well as one of the best recent fossil records (1, 40) Ecology often linked to notable key innovations such as adult surface dwelling (Gyrinidae), swimming by simultaneous stroke of adult middle and hindlegs (Dytiscidae), and antimicrobial exocrine secretion (Hydraenidae)
	Hydrophyloidea (water scavenger beetles)	2,205	+	–		
	Scirticidae (marsh beetles)	1,330	–	–		
	Hydraenidae (minute moss beetles)	1,380	–	+		
	Elmidae (riffle beetles)	900	+	++		

[a] Only groups of more than 300 species resulting from single freshwater invasion are shown; Culicomorpha and Psychodomorpha probably form one lineage with more than 23,000 known species (140), as do Ephemeroptera and Odonata (Palaeoptera) with more than 9,000 species (128). Many smaller or partly aquatic groups, all of which are in mostly terrestrial orders, are excluded; thus only 17 of over 50 aquatic invasions are considered. Groups tied closely to freshwater but lacking aquatic life stages are also excluded, e.g., Leptopodomorpha (shore bugs). The list of included Diptera groups is tentative, because the number of actually aquatic species (and thus separate invasions) is unclear. Other families with hundreds and possibly thousands of aquatic species are Dolichopodidae, Muscidae, Stratiomyidae, and Syrphidae.

[b] Numbers of described species are taken from stated sources and updates (50, 94). Major (>300 species) constituents of Culicomorpha are Chironomidae (7,290), Ceratopogonidae (5,902), Culicidae (3,725), and Simuliidae (2,121). Major constituents of Tipulomorpha are Limoniidae (10,777), Tipulidae (4,415), and Pediciidae (496). Major constituents of Tabanomorpha are Tabanidae (4,434) and Rhagionidae (756). Major constituents of Psychodomorpha are Psychodidae (3,026) and Blephariceridae (331). Major constituents of Hydradephaga are Dytiscidae (3,908) and Gyrinidae (750). The major constituent of Hydrophyloidea is Hydrophylidae (1,800).

[c] State of taxonomy is inferred from estimates of species described: under 30% (- -), over 50% (–), over 70% (+), over 80% (++), or unknown (?) and likely very low.

[d] Proportion of lotic species is based on estimates from North America and Europe: almost all species strictly lotic (++), most lotic but good number lentic (+), >25% lentic (–), or knowledge deficient but many edge species and lotic/lentic distinction often unclear (?).

address multiple factors. Our synthesis suggests that a good knowledge of general patterns of diversity exists, but that few studies explicitly investigate the processes responsible.

Dispersal: the establishment by a species of a new population in a noncontiguous habitat patch

GEOGRAPHICAL DIVERSIFICATION

Habitat Stability, Dispersal, and Diversification

Freshwater habitats can be broadly grouped into running (lotic) and standing (lentic) water bodies, and the majority of aquatic species is restricted to one or the other. The relatively short geological life span of standing waters makes dispersal necessary for lentic species, whereas running water habitats are more geologically stable and therefore lotic species may be less dispersive (107). Lentic dragonflies and beetles have larger ranges than lotic species do (2, 49), and dispersal ability rather than ecological tolerance accounts for this (10, 29). The contrasting persistence of habitats is likely to have implications for lineage diversification. Low dispersal may increase speciation through allopatry in stable habitats, and lotic insects demonstrate more genetic differentiation than lentic species do (72, 93). The net result is that greater species turnover is expected in lotic than in lentic clades; however, the only explicit test of habitat stability on diversification showed no significant difference in beetle species turnover between lentic *Ilybius* and lotic *Deronectes* (108). This equivocal result may be because diversification operates at different spatial scales in the two groups, with investigation of lentic taxa requiring more widespread sampling.

Homogenizing gene flow under widespread dispersal should suppress allopatric divergence, as supported by morphological stasis in the fossil record during periods of instability (119). Dispersal can also reduce extinction because of large population sizes and an ability to track environmental changes. Indeed, most African Odonata threatened with extinction are lotic (25). Dispersal also allows occupation of new habitat: Lentic *Labiobaetis*, *Dabulamanzia*, and *Cloeodes* mayflies diverged after dispersal between Africa and Madagascar (83) and *Megalagrion* damselflies diverged by colonizing new islands in Hawaii (59). Similar isolation will occur in continental habitat refuges caused by changing climates and associated range shifts. Quaternary fossil records of 20% of 259 European water beetle species, especially lentic ones, fall outside their current range (1).

The observations imply that freshwater species diverged and survived under very different impacts, timing, and scales and at very different rates of turnover, depending on their habitat and thus dispersal capacity (**Figure 1**). Nonetheless, net diversification may be similar: We estimate that about 40% of Holarctic species occur mainly in standing water, including over half of the Odonata, Heteroptera, Coleoptera, and probably the Diptera. The strictly lotic proportion is higher in the tropics, although 37% of African Odonata are not bound to running water (25). Currently, we lack quantitative data at appropriate scales to test these hypotheses. Habitat stability and dispersal ability are also not truly dichotomous but vary gradually, as suggested by complex relationships between wing morphology and ecology in caddisflies (87). Moreover, aside from (but often as a result of) their stability, lotic and lentic systems differ in many other ways (e.g., structure, distribution, connectivity, chemistry, microclimate, seasonality, biotic interactions), with great potential for ecological diversification.

Environment and Allopatry

The extensive population genetics literature on stream insects finds repeated evidence for intraspecific differentiation, demonstrating the potential for allopatric speciation. Differentiation is typically associated with restricted overland dispersal between mountain regions (51). Finer-scale differentiation between (sub)catchments within mountain ranges is less prominent but also

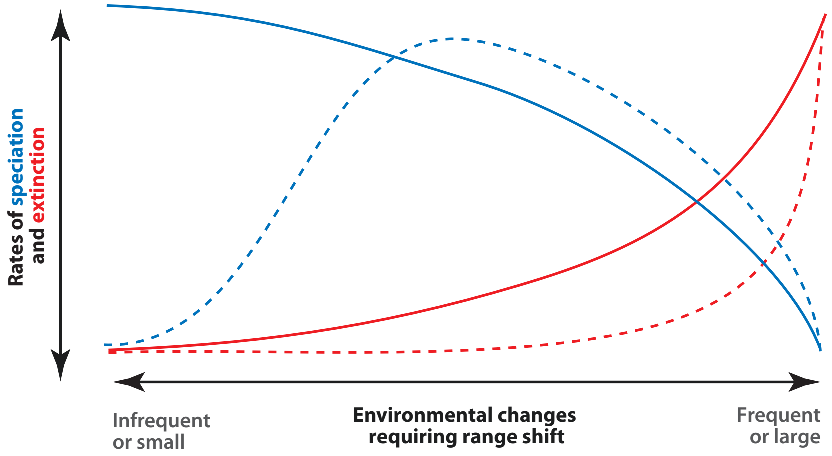

Figure 1

The habitat stability hypothesis of freshwater diversification. The plot indicates speciation (*blue*) and extinction (*red*) rates under environmental change for immobile (*solid lines*) and highly mobile (*dashed lines*) groups. Note that because of the lower extinction rate, diversification is not necessarily highest when speciation is maximal in the mobile groups. See Synthesis for further discussion.

important (41). For example, surrounding forest probably impaired dispersal in the mayfly *Ephemerella invaria* (3) but facilitated it in the caddisfly *Orthopsyche fimbriata* (120). The mayfly *Andesiops torrens* and caddisfly *Smicridea annulicornis* differentiated within catchments, as they are adapted to avoid drift in torrential streams (114), and the mayfly *Baetis alpinus* diverged across lakes in valleys that have been ice-free since the Holocene (84).

Allopatric diversification under these conditions predicts parallel radiations of (largely) nonoverlapping species that are ecologically similar. Examples are six simultaneous splits of New Zealand stoneflies by glaciations (75), the retreat into aquifers of Australian aquatic beetles with desertification (66), and intra- and interspecific diversification of European headwater caddisflies following Pleistocene range regression and expansion (97, 105). The Australian midge *Echinocladius martini* and European stonefly *Arcynopteryx dichroa* underwent strong allopatric processes in upland refuges, in response to drying and cooling climates, respectively (62, 127). Other examples are parallel radiations of *Hydropsyche* caddisflies in upper, middle, and lower stream reaches (88) and *Hydraena* beetle diversification following expansion and geographic fragmentation (109), both in the western Mediterranean. Ecological divergence in allopatry allows new species to remain segregated once barriers disappear: Three geographically separated lineages in the beetle *Ochthebius glaber* inhabit distinct climatic envelopes, suggesting this is in progress (116).

Whereas geographic isolation under low dispersal is easily demonstrated, ongoing dispersal obscures allopatric patterns in mobile groups. Dispersal to new habitat, divergence in isolation, and survival of sister species after re-expansion predict that recent sister taxa are allopatric and often ecologically similar. The radiation of *Trithemis* dragonflies into 40 African species probably began in open temporary pools, with peak diversification occurring when forest expansion separated these populations (30). As open landscapes coalesced thereafter, species of those habitats expanded into huge, largely overlapping ranges. These lineages thus barely radiated further, but three ecologically more constrained lineages (in cool, flowing, and swampy habitats, respectively) produced over half of the species, possibly in allopatry. More evolutionary shifts occurred to forest and running waters than to open and standing waters, confirming Ribera's (107) predictions that lentic species would be older and lotic species would have a greater tendency to specialize and be less likely to revert to lentic habitats. In this scenario, overlapping sister species should show evidence of recent expansion and/or ecological segregation. Genetic differentiation is also expected within species across current ecological barriers. Unfortunately, the few phylogeographic studies on lentic taxa at appropriate scales focus on migratory species (43). Despite strong differentiation of *Anopheles scanloni* mosquitoes in habitat islands, crossing experiments demonstrated that speciation had not yet occurred (90).

ECOLOGICAL DIVERSIFICATION

Ecotones and Habitat Gradients

The linearity of stream systems provides a downstream succession of environmental conditions and communities, which could promote parapatric diversification (122). Illies (53) suggested that warm-adapted lineages of aquatic insects arose from cold-adapted ones, with evolution within river systems progressing downstream. This was called into question by inferences that caddisflies arose in depositional habitats (137) and, for mayflies, by the observation that some Malagasy species appear to have diversified from lowland ancestors to colder and faster-flowing upstream sections (134). This is similar to the upstream invasion and ecological diversification suggested for mollusks and fish (53). In net-spinning caddisflies, strong links exist between downstream changes in flow conditions, feeding behavior, and species distribution (4). Mey (79) described an endemic radiation of *Hydropsyche* on a mountain in Luzon (Philippines) with 10 related species in a succession from headwaters to lower reaches. Statzner & Dolédec (122) examined the distribution of ecological traits and phylogenetic relationships among *Hydropsyche* species in the Loire River in France. Their data indicate ecological specialization along the gradients (e.g., net-building behavior, net mesh size, respiration range) and provide some support for a headwater ancestor with primarily downstream evolution and progressive environmental adaptation, supporting the idea of environmentally driven parapatric speciation in streams. Habitat segregation between sister species of *Epeorus* mayflies, one occurring directly upstream from the other, was proposed to be the result of adaptation to colder water in the upstream species (89). In black flies, stream velocity and altitude differ among closely related species in Thailand (104), and river ancestors gave rise to distinct cascade populations and species on Pacific islands, with increased allopatric isolation in cascade habitats subsequently furthering diversification (60).

Thermal clines are an integral characteristic of freshwater habitats, where the mean and variance of temperatures change from source to mouth in streams and with depth in lakes. Extreme temperatures have invoked many adaptations (31, 106), and one of the most diverse groups of aquatic insects, the Chironomidae, exhibit some of the most extreme tolerances (39). Few studies have related thermal adaptation to diversification. Funk et al. (45) linked it to phenology shifts and ecological diversification of three closely related mayfly species. Other studies have linked thermal tolerance, rather inconclusively, to distribution. Water temperature was a poor predictor for species occurrence in Iberian *Hydropsyche* caddisflies, despite their strong longitudinal succession (88). Whereas Calosi et al. (21) found that thermal tolerance of *Deronectes* beetles is a better predictor of range size than wing size, suggesting that ranges are determined by tolerance rather than dispersal, Arribas et al. (10) showed that thermal plasticity in *Enochrus* beetles is greater in lotic than in lentic species, and that wing size is the better predictor.

Shifts into distinct habitats may also invoke diversification. Hawaii's endemic *Megalagrion* damselflies radiated into all habitats available within islands, from ponds to streams, tree holes, and seeps, and even exhibit fully terrestrial development (59). The chironomid genus *Sergentia* comprises five species endemic to Lake Baikal (Russian Siberia) that originated in the rivers feeding into the lake. More recent species inhabit increasingly deeper regions of the lake. The small size of this radiation is linked to the terrestrial adult, which may limit the larvae from invading deeper habitats (95). Many water bugs have strictly aquatic life cycles and are thus not bound to shallow or shore habitats. For example, two poorly known endemic naucorid genera in Lake Tanganyika (Central Africa) might represent lake radiations (102). Indeed, although this and other lakes are well known for their fish radiations, examples of insect diversification in lakes are rare. Shifts into phytotelmata (small pockets of water held by plants) have received reasonable attention, for example, *Aedes* mosquitoes on Pacific islands (121) and diving beetles and giant damselflies in the Neotropics (12, 54), but apparently induced relatively minor diversification. The transition between water and land is relevant mainly in those freshwater groups with strongly terrestrial roots, such as Diptera. Although the initial aquatic invasions may have induced diversification, as occurred in Coleoptera (52), reinvasion of land and proceeding secondary invasions of water appear to have resulted in a relatively small number of new species, as seen, for example, in hydrophiloid beetles (40), *Tetanocera* flies (24), and *Nothopsyche* caddisflies (47). Truly amphibious (versus amphibiotic) larvae that can complete development both above and below water are only known from the *Hyposmocoma* moths of Hawaii. This habit evolved in parallel at least three times and led to speciation in one of these amphibious clades (112).

Amphibiotic: having aquatic larvae and terrestrial adults

Chemical Gradients

Water is an effective medium of dissolved chemicals and thus generates many different gradients in freshwater habitats, e.g., oxygen concentration from headwaters to river mouths (see above) or salinity degrees from freshwater to marine. Water striders, for example, invaded marine environments multiple times and diversified in these habitats through behavioral and physiological adaptations (7). Water chemistry is directly influenced by atmospheric conditions, bedrock geology, and biotic interactions and has thus changed over evolutionary time, potentially affecting aquatic insect diversification. For example, Ivanov & Sukatsheva (55) hypothesized that an increase of foliage debris in freshwaters following the proliferation of angiosperms during the Cretaceous led to eutrophication and oxygen depletion, inducing extinction and large-scale range expansion in Trichoptera.

Two recent studies (20, 22) mapped tolerance to pollution on phylogenies in an attempt to identify the best taxonomic level for bioindication. In most cases, cadmium uptake and elimination differed consistently among examined families but also among two congeneric mayfly species (20) and within families of Australian midges (22). Differences in pollution tolerance among closely related taxa may indicate ecological differentiation along chemical gradients. Unfortunately, the presence of locally resistant ecotypes may complicate patterns in nature, raising questions concerning the degree to which tolerance is conserved over time (85).

A series of studies examined caddisfly diversification in relation to ultramafic geology on New Caledonia (37, 38). Ultramafic rocks lead to high pH values and mineral loads, including heavy metals. Several groups diversified upon adapting to these harsh conditions after arrival on the island. In all three groups examined, diversification started on ultramafic rocks, associated with environmentally diverse and fragmented habitats. Subsequent diversification is associated with shifts to nonultramafic rocks, as these geological layers were exposed. Such shifts are more frequent than the reverse and may reflect high fitness costs associated with persistence in inhospitable conditions. The studies show that diversification of New Caledonian caddisflies is associated with the underlying geology and that taxa retained their potential to persist in both chemical environments. Distinct lineages within the South African mayfly complex *Baetis harrisoni* probably originated in allopatry, but their continued separation is linked to catchment geology through different pH tolerance (99).

BEHAVIORAL FACTORS

Life History

Surprisingly few studies have related insect life-history traits to their diversification (74). The concept of diversification by temporal isolation seems particularly suitable for scrutiny in freshwater insects with synchronized adult emergence, particularly Ephemeroptera and Plecoptera. Although considered important in some herbivorous insects (73), there is little evidence that it is a common mechanism for speciation. Schultheis et al. (117) tested the concept on the semivoltine stonefly *Peltoperla tarteri* but found that gene flow occurred between cohorts, probably the result of some individuals increasing or decreasing their development rate to switch cohorts. In contrast, a small genetic difference was found between two populations of the damselfly *Lestes virens* that emerge in spring but mate in summer and autumn (115). Three sympatric clades of the mayfly *Baetis rhodani* complex exhibit strong genetic divergence and striking differences in phenology, but temporal isolation probably only acts to restrict gene flow among previously differentiated lineages (68). Other observations suggesting the importance of temporal isolation include offspring of experimentally hybridized caddisflies that had different development rates and emergence periods (69) and two co-occurring *Haliplus* beetle species that exhibit growth and emergence expected under an avoidance strategy (23).

Some species of mayflies are occasionally parthenogenetic in some populations, whereas in other species only females are known. Funk et al. (44) studied two sister species in which one exhibits both sexual and asexual populations and the other is purely asexual. The two are sympatric and morphologically indistinguishable, but genetic analysis and experimental hybridization show they are clearly distinct. Speciation probably preceded development of obligate parthenogenesis, but the study shows that such shifts can reinforce isolation and thus promote diversification. The only known parthenogenetic populations of Odonata (*Ischnura hastata* on the Azores) arose from one recent long-distance dispersal event from North America (67). Although it is not clear where parthenogenesis evolved and whether it forced the extinction of sexual island populations, the parthenogenetic lineage has begun accumulating unique mutations.

Feeding Ecology

Dietary specialization in herbivorous terrestrial insects is a strong correlate of diversification, though other ecological and geographical factors may play an important role (82). Coevolution with angiosperms has not been scrutinized in aquatic insects but probably plays a minor role in most groups because most larvae feed on algae or detritus and adults do not feed (Ephemeroptera, Trichoptera, Megaloptera), or both adults and larvae are largely predatory (Odonata, many Coleoptera). Carnivorous parasitism is also linked to terrestrial insect diversity, especially in the Hymenoptera, but its importance is contentious (32) and it is apparently a rare habit in freshwaters. Feeding ecology more generally, however, seems important, although empirical evidence is rare. Both Trichoptera and Diptera, which include the largest radiations (**Table 1**), exhibit exceptional diversity of larval feeding types. In caddisflies, this is linked to great diversity in silk-spinning and case-building behavior (70, 137). Case building has also been associated with respiration, prey avoidance, and desiccation protection (141, 144) and may generally have promoted ecological diversification (70). The diversification of a species-rich clade of the subfamily Drusinae (Limnephilidae) was linked to the shift from shredding detritus to grazing phytobenthic algae (96), and that of diving beetles was linked to the specialized mandibular sucking channels, which hinder dilution of feeding fluids in aqueous environments (13). Numerous dipteran invasions into freshwater are associated with hematophagy (140), but why blood-feeding adults seem correlated with aquatic larvae and whether blood feeding has promoted diversification are unclear. Bataille et al. (16) show both habitat and host shifts associated with the colonization of the Galapagos Islands by *Aedes taeniorhynchus*, but population differentiation was detected among habitats and not hosts. Diversification in the African *Simulium damnosum* black fly complex did not reveal clear patterns relating feeding, vector prevalence, or habitat preference (63).

Species Interactions

Predation and parasitism can influence diversification by divergent selection, especially in lentic habitats, as important predators such as fish cope poorly with seasonal instability (131). For example, parasitic mite loads and thus potential fitness in the North American damselfly *Ischnura verticalis* differed by habitat (57). Selection by predation under different visibility (plant densities, transparency) is influenced by water beetles' size and color (142). Two forms considered incipient species within the mosquito *Anopheles gambiae* (see sidebar, Diversification in Action: *Anopheles gambiae*) outcompete one another in their preferred habitat without predation, but in the presence of a predator the permanent water form has an advantage over the temporary water form in both habitats (46). In a contrasting case, three congeneric dragonfly pairs in Namibia, each with one species in temporary water and one in perennial water, had growth rates correlated with habitat but conserved antipredator behavior, i.e., in accordance with ancestral habitat (124). Stoks & McPeek (123) described two North American damselfly diversifications, both of which were shaped by changes in antipredator behavior and growth rates but fill ecological space by habitat shifts from opposite ends of the pond permanence gradient: *Lestes* began in temporary ponds with only dragonfly predators, and *Enallagma* started in lakes with fish. The phylogeny of *Chaoborus* midges showed multiple shifts between habitats with and without fish, with evasive behavior adjusting each time (17). Plasticity in defensive strategies possibly enabled the Holarctic dragonfly genus *Leucorrhinia* to diversify in habitats with different types of predators (101).

DIVERSIFICATION IN ACTION: *ANOPHELES GAMBIAE*

Research on incipient speciation in the malaria mosquito *Anopheles gambiae* exemplifies the use of an integrative approach in the study of diversification and "provides us with an exceptional opportunity to observe evolution in action" (34). Studies have revealed two molecular forms, M and S, with strong but incomplete barriers to gene flow between them (35). The forms are maintained by asymmetric introgression where hybrids exhibit low fitness outside zones of intensive hybridization, leading to geographic mosaics of reproductive isolation. Prezygotic isolation between forms has been linked to mate recognition and choice of wing-beat frequency and flight tone (98), as well as timing of swarming behavior (113). The diversification likely began in western Africa in response to human land use over the past few thousand years (35). M is associated with permanent and anthropogenic conditions, particularly irrigation, and is better adapted to predation (46). Although S developed insecticide resistance first, introgression presumably transferred this to M (35). Another form, Bamako, is also differentiating in laterite rock pools in Mali (71).

Variable habitat stability and dispersal will affect the intensity of interspecific competition locally too. For example, two genetically close and ecologically identical *Enallagma* damselfly species can coexist in the mosaic distribution of lentic habitats, thus helping maintain diversity (19), whereas competitive exclusion among congeners may be structuring populations of montane caddisflies (97).

Sexual Selection and Conflict

Sexual selection probably had a major impact on insect diversification (74). Among aquatic insects, this has been studied best in the Odonata, particularly *Calopteryx* damselflies, which use their colorful wings in territorial displays. Strong genetic divergence between Swedish *C. splendens* populations was linked to selection for male wing markings (126). Moreover, aggression of sympatric *C. virgo* males, which have darker wings, resulted in selection for smaller wing markings in *C. splendens* (130). Similarly, *C. aequabilis* has smaller spots in sympatry with the dark-winged *C. maculata*; although this was considered an example of speciation by reinforcement, there was no support for this (86). Despite the general focus on selection for male characters, Wellenreuther et al. (138) showed that gene flow between ecologically dissimilar populations of *C. splendens* is restricted by male preference for immigrant females from populations with similar predation and competition pressures as their own. Also, mating success in *C. splendens* was lower for immigrant males than for local males (125), and it is linked to male behavior (perching versus hovering) in different habitats (shaded versus sunny) in the Neotropical damselfly *Protoneura amatoria* (64). Furthermore, local variation in genital morphology within *Calopteryx* species suggests that post-mating sexual selection and sperm competition can reinforce speciation in allopatry (27). Strong phylogenetic variation of complex sperm traits in diving water beetles may have a similar impact (48). Genetic divergence across an altitude gradient in European *Agabus* beetles was attributed partly to sexual selection on elytral reticulation (36), and a similar potential case of reinforcement was suggested for two parapatric *Euphaea* damselfly species (65).

Sexual conflict may also induce diversification in insects (8), as can coevolution of male and female traits (18). Miller (80) reported a single origin of male suckers in diving beetles and five subsequent appearances of antisucker sculpturing in females. Similar sexual arms races occur in water striders, e.g., in species of the genera *Aquarius* (29) and *Rheumatobates* (111) and even within populations of *Gerris incognitus* (100). Arnqvist et al. (9) suggested that two female forms of *Phoreticovelia* bugs may lead to evolutionary divergence: Wingless females carry and nourish diminutive males on their backs, whereas winged females do not. McPeek et al. (77, 78) inferred that male claspers and corresponding female structures evolved synchronously in *Enallagma* damselflies and are important for species recognition but not for sexual selection. However, McPeek & Gavrilets (76) proposed that speciation is promoted by female mating preference and the reduced risk of mating unsuccessfully with closely related species. This applies especially to radiations where many recently derived species coexist, such as *Enallagma* (129).

These examples highlight the potential importance of sexual selection and conflict and show their complex interaction with environmental factors, but whether they really increase diversification has not been tested sufficiently. Misof (81) found some support that two possible proxies of sexual selection (sexual dimorphism and large body size) induced higher speciation rates in the odonate suborder Anisoptera: Proportionately larger males in larger species (Rensch's rule) are linked to territoriality, at least in damselflies (118). Wing shape is also related to dispersal and the behavior of guarding ovipositing mates in Anisoptera (58), and the shape of *Calopteryx* hindwings, which have a greater role in displays, evolved faster than forewing shape (91). Thus, wing morphology can be applied as a proxy of sexual behavior, as well as dispersal, in diversification studies, although the interplay of natural and sexual selection appears complex (92). Similarly, the evolution of female color forms in damselflies, which is linked to sexual conflict, requires rigorous phylogenetic testing (132).

SYNTHESIS

With their gradients and contrasts, freshwaters provide an extraordinary environment for the evolution of biodiversity on a global scale. By evaporating and precipitating, buffering and absorbing, and eroding and depositing, water has created perhaps the most chemically, physically, climatologically, and geologically variable of biomes. Inland waters are simultaneously stable and dynamic, and isolated and connected. They form ubiquitous veins, archipelagoes, and pulses of life, with an almost endless interface with land, sea, and air that insects perpetually straddle. This diversity and dynamic make freshwaters and their insects excellent models for understanding why life is rich: how stability and mobility, gradients and barriers, and adaptations and interactions influence evolution and shape biodiversity. Although water is known as the source of life, it is also life's most endangered home, with freshwater habitats being the most threatened on Earth.

There is tremendous potential for studying diversification rates and adaptation by reconstructing species-level phylogenies and integrating these with the considerable amount of existing ecological information (**Table 1**). To explore this potential, researchers must first gain a better understanding of the impact of habitat stability and dispersal ability on diversification (**Figure 1**). During periods of environmental (e.g., climatic) stasis, speciation across physical barriers is maximal in immobile groups and negligible in mobile ones. Speciation in mobile groups increases when environmental change induces range reconfigurations and isolation, but crashes when changes become too great or rapid. Extinction increases more rapidly with environmental change in less mobile groups. Consequently, allopatric diversification must occur at different scales and periods for the two ecological extremes: Lotic diversification peaks under greatest environmental stasis, whereas lentic diversification requires substantial change. The model requires further refinement, incorporating the ecological differences correlated with stability and the impact of dispersal on competition. Ribera (107) noted that whereas species from unstable habitats must be good dispersers, those from stable habitats can be sedentary but do not have to be. Thus, a widespread species may arise, seeding diversification pulses when its offspring revert to specialization in stable habitats: An extremely widespread Eurasian diving beetle that arose in the New Guinean highlands may represent the onset of such an event (14).

Second, researchers must quantify the relative importance of the identified mechanisms and key innovations, as each group diversified differently (**Table 1**). The habitat stability model predicts higher species turnover in predominantly lotic groups (e.g., Ephemeroptera, Plecoptera, Trichoptera, Hydraenidae) than in groups with more good dispersers (Odonata, Hydradephaga, Hydrophiloidea). The occupation of diverse microhabitats accommodates more parapatric lineages, increasing diversification in groups that easily invade small and peripheral environments, notably Diptera. By contrast, ecological constraints may have limited diversification in groups largely confined to the water surface (Gerromorpha), cooler habitats (Plecoptera), or a relict range (Megaloptera). Feeding niche diversity allows for more sympatric lineages: Although it may restrict the richness of mostly generalist predatory or scavenging groups (Odonata, Gerromorpha, many Coleoptera), feeding niche diversity may explain why Diptera and Trichoptera are so rich. Reinforcing factors such as sexual selection, important in Odonata, are probably also relevant in other groups but remain poorly studied.

SUMMARY POINTS

1. Freshwaters cover less than 1% of the Earth's surface, but more than 6% of all insect species spend one or more life stages in aquatic habitats. This diversity occurs across 12 orders and has arisen following more than 50 terrestrial invasions of freshwaters and subsequent diversification. The myriad adaptations to life in freshwaters comprise a remarkable example of convergence.
2. Diversification is poorly understood, largely because we lack species-level phylogenies suitable for hypothesis testing in most groups. Nonetheless, evidence for allopatry, sexual selection, and ecological diversification into microhabitats and feeding modes suggests these have been critical processes.
3. Aquatic insects are excellent models for research on diversification. Their habitats exhibit marked spatial and temporal gradients in stability and their amphibiotic lifestyles link strong habitat dependence with response to change via dispersal. This has likely led to varying contributions of extinction as well as allopatric and ecological speciation.
4. The habitat stability hypothesis was developed for macroecology and has been successfully applied to predict ecological and population-genetic patterns. How exactly it applies to diversification is not clear, although it should lead to higher speciation and extinction rates (i.e., greater turnover) in stable habitats because the species there are less dispersive. The single test of this hypothesis to date found equivocal evidence.
5. Highly dispersive (mostly lentic) species probably respond better to environmental changes than lotic species do. Subsequently lower extinction rates and more frequent and extensive geographic range reconfigurations are probably the main drivers of lentic diversification. However, genetic isolation may occur more erratically and over larger spatial scales and be obscured by recolonization patterns, making comparative work difficult.

FUTURE ISSUES

1. The foremost research priorities are to obtain a better understanding of the impact of habitat stability and dispersal ability on freshwater diversification and to quantify the relative importance of the diversification mechanisms and key innovations in the insect groups.
2. The large number of studies stimulated by basic research on lake and stream ecosystems, as well as by the use of aquatic insects as bioindicators, has produced an enormous amount of ecological trait data. These are useful for studying the evolution of ecological characters in combination with species-level phylogenies.
3. Population-genetic studies should be used to integrate intraspecific and species-level examination of diversity patterns and to infer diversification mechanisms from both historic (phylogeny, trait evolution) and contemporary (dispersal limitation, genetic diversity patterns) perspectives.

4. The ecology and evolutionary biology of aquatic insects are rarely studied in both aquatic and terrestrial stages. Research should focus on whether their amphibiotic life cycles place different evolutionary constraints and selective pressures on aquatic and terrestrial life-history stages, i.e., whether ecological segregation in one or both stages enhances diversification.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This review benefited from conversations with Michael Balke, Wolfram Graf, Herman de Jong, Vincent Kalkman, Mike May, and Nico Nieser. MTM's research is partially supported by the European Union FP7 Project BioFresh (**http://www2.freshwaterbiodiversity.eu/**). SUP's research is funded by the "LOEWE - Landes-Offensive zur Entwicklung wissenschaftlich-ökonomischer Exzellenz" program of Hesse's Ministry of Higher Education, Research, and the Arts, DFG grant PA1617/2-1, and FWF grant P 23687-B17.

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