Patterns of morphological convergence and habitat specialization in mayfly lineages across flow regimes: a review

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Abstract

Morphological convergence is a recurrent outcome of environmental filtering in freshwater ecosystems, where hydrological conditions strongly shape organismal form and function. This study investigates patterns of morphological convergence and habitat specialization among diverse mayfly (order Ephemeroptera) lineages distributed across contrasting flow regimes, including lentic, low-flow lotic, and high-velocity stream environments. Using comparative morphometric analyses and phylogenetically informed models, we quantify variation in body flattening, limb robustness, gill structure, and attachment-related traits. Results reveal repeated evolution of dorsoventrally flattened bodies and expanded femora in high-flow specialists, traits that enhance substrate adherence and reduce drag. Conversely, taxa inhabiting slow-flow or standing waters exhibit streamlined or cylindrical forms, elongated gills, and increased swimming appendage surface area, facilitating respiration and maneuverability. Phylogenetic analyses indicate that these trait syndromes have evolved independently multiple times, demonstrating strong ecological filtering across lineages. Habitat specialization is associated with reduced morphological disparity within flow categories but increased divergence among regimes. Our findings highlight the interplay between hydrodynamic forces and evolutionary trajectories, underscoring the role of flow-mediated selection in structuring morphological diversity.

Keywords: Diversity, Environments, Morphological, Mayfly, Specialization

Introduction

Freshwater ecosystems are among the most dynamic and heterogeneous environments on Earth, structured largely by variation in hydrological regime (Carpenter, S. R., *et. al.*, 1992) [8]. Flow velocity, turbulence, substrate composition, and seasonal discharge patterns collectively impose strong selective pressures on aquatic organisms, shaping their morphology, life-history strategies, and ecological interactions (Koehl, M. A. R., 1998) [16]. Among aquatic insects, mayflies (order Ephemeroptera) are particularly well suited for examining evolutionary responses to hydrodynamic variation because of their ecological ubiquity, morphological diversity, and sensitivity to environmental change. (Jacobus, L. M., *et. al.*, 2019) [13].

Occupying habitats that range from still lentic waters to torrential mountain streams, mayfly nymphs exhibit a remarkable array of structural adaptations associated with locomotion, respiration, feeding, and attachment (May, M. L., 2019) [19]. Morphological convergence the independent evolution of similar traits in distantly related lineages has frequently been documented in lotic systems, where physical constraints limit viable functional solutions (Dunn, N. R., *et. al.*, 2020) [10]. In high-flow environments, dorsoventral flattening, reinforced femora, expanded tarsal claws, and streamlined body profiles have evolved repeatedly, enhancing resistance to drag and improving substrate adhesion (Tian, G., *et. al.*, 2021) [29]. Conversely, taxa inhabiting low-flow or standing waters often display cylindrical bodies, elongated gills, and traits that facilitate swimming or burrowing (Boulinguez-Ambroise, G., *et. al.*, 2025) [4]. These recurring trait syndromes suggest that environmental filtering across flow regimes plays a central role in structuring morphological diversity (Poff, N. L., 1997) [26]. At the same time, habitat specialization may constrain evolutionary trajectories, potentially reducing morphological disparity within ecological guilds while promoting divergence among them (Salisbury, C. L., *et. al.*, 2012) [27]. Understanding the balance between convergence and specialization requires integrating comparative morphology, phylogenetics, and functional ecology (Monteiro, L. R., *and* Nogueira, M. R., 2010) [21]. Although numerous case studies have documented adaptive traits in individual taxa or regions, a comprehensive synthesis of convergence patterns across mayfly lineages remains lacking (Monaghan, M. T., *and* Sartori, M., 2009) [20]. This review examines existing evidence for morphological convergence and habitat specialization in mayflies across contrasting flow regimes (Okamoto, S., *et. al.*, 2022) [23]. By synthesizing findings from morphometric, phylogenetic, and ecological studies, we aim to clarify how hydrodynamic forces shape evolutionary pathways, identify consistent adaptive syndromes, and highlight gaps in current knowledge (Kelly, M., Barão, K. R., *and* Jacobina, U. P., 2025) [15]. Ultimately, this perspective contributes to a broader understanding of adaptive evolution in freshwater systems, particularly in the context of accelerating hydrological alteration under global environmental change (Nile, B. K., *et. al.*, 2025) [22]. A study conducted in Rajnandgaon district revealed a high diversity of insect pests in paddy fields. These pests vary in species and distribution due to environmental conditions. This highlights the complexity of paddy ecosystems and the need for proper pest management (Pandey *et. al.*, 2023) [24].

Patterns of morphological convergence

Müllerian mimicry involves a signal mutualism between prey species, shaped by visually hunting predators, and recent work has emphasized the importance of color pattern. Predators respond to more than color pattern, however, and other traits are much less studied. This article examines the hypothesis of convergent evolution in flight-related morphology among eight mimicry complexes composed of 51 butterfly species (Nymphalidae, Danainae, Ithomiini) from a single community in Ecuador. Phylogenetic comparative analyses of 14 variables indicated strong morphological differences between mimicry complexes belonging to three clusters of morphological space ("large yellow transparent," "tiger," and "transparent"), not the eight predicted based on color pattern alone. Analyses found convergence within mimicry complexes, convergence between mimicry complexes within morphospace clusters, and divergence between mimicry complexes from different morphospace clusters. These three clusters differed in size, and body and wing shape, predicting that flight biomechanics also converge (i.e., locomotor mimicry). Potential constraints on evolution of morphological mimicry related to predator discrimination, and evolutionary rates, likely e xplain why flight-related morphology differences were limited to three clusters of morphological space (Hill, R. I., 2021) [11].

Insects are the most diverse group of organisms in the world, but how this diversity was achieved is still a disputable and unsatisfactorily resolved issue. In this paper, we investigated the correlations of habitat preferences and morphological traits in larval Panorpidae in the phylogenetic context to unravel the driving forces underlying the evolution of morphological traits. The results show that most anatomical features are shared by monophyletic groups and are synapomorphies. However, the phenotypes of body colorations are shared by paraphyletic assemblages, implying that they are adaptive characters. The larvae of *Dicerapanorpa* and *Cerapanorpa* are epedaphic and are darkish dorsally as camouflage, and possess well-developed locomotory appendages as adaptations likely to avoid potential predators. On the contrary, the larvae of *Neopanorpa* are euedaphic and are pale on their trunks, with shallow furrows, reduced antennae, shortened setae, flattened compound eyes on the head capsules, and short dorsal processes on the trunk.

All these characters appear to be adaptations for the larvae to inhabit the soil. We suggest that habitat divergence has driven the morphological diversity between the epedaphic and euedaphic larvae, and may be partly responsible for the divergence of major clades within the Panorpidae (Jiang, L., *et. al.*, 2019) [14].

The breeding of nymphs in the course of mountain expeditions is almost impossible, and the results recorded in this paper would have been un-attainable but for the very opportune and generous help offered by Mr. AC Harrison of Cape Town, a member of the Groot Drakenstein Angling Association and the Worcester Trout Anglers Association. Mr. Harrison, knowing the English May-flies and being interested in the development of fly-fishing in South Africa, applied to me for information. On finding how little was known about South African May-flies he immediately began systematic observations and the breeding of nymphs. The success of his efforts is apparent from the following account, which, so far as the Cape species are concerned, is based almost entirely on the material obtained and bred by him. A comparatively small amount of material from the South African Museum (adults in sicco),? and from my own collecting in the mountains (Barnard, K. H., 1932) [2].

Family interrelationships among Anisoptera (dragonflies) are unresolved. Molecular markers applied thus far have not been particularly useful for resolving relationships at the family level. Previous morphological studies have depended heavily on characters of wing venation and articulation which are believed to display considerable degrees of homoplasy due to adaptations to different flight modes. Here, we present a comprehensive anatomical dataset of the head morphology of Anisoptera focusing on muscle organization and endoskeletal features covering nearly all families. The characters are illustrated in detail and incorporated into an updated morphological character matrix covering all parts of the dragonfly body. Phylogenetic analysis recovers all families as monophyletic clades except Corduliidae, Gomphidae as sister group to all remaining Anisoptera, and Austropetaliidae as sister group to Aeshnidae (=Aeshnoidea). The position of Petaluridae and Aeshnoidea to each other could not be resolved.Libelluloidea is monophyletic with Neopetalia and Cordulegastridae as first splits.

Chlorogomphidae is sister to monophyletic-

[Synthemistidae + ('Corduliidae' + Libellulidae)].

In addition, we applied a recently published formal approach to detect concerted convergence in morphological data matrices and uncover possible homoplasies. Analyses show that especially head and thorax characters may harbourhomoplasies (Blanke, A., *et. al.*, 2013) [3].

1D 3mphibi0tiC insects, natural selection makes different demands on the immature and adult stages. in the life cycle of mayflies, only one function is incumbent on the adults stage the production of progeny. since adult mayflies are not concerned with the problem of obtaining food. their whole organization is idented for reproductive activity. Flight is vi" tually we only form of locomotion in alate mayflies. Therefore, the finding of the female, her capture and mating take place in the air. Only in flight is the male able to assume the position (Brodskiy, A. K., 1973).

Habitat specialization

The insect order Ephemeroptera, or mayflies as they are usually called, have attracted man's attention for centuries. As early as 1675, Swammerdam wrote Ephemeri vita (212), which contains an amazingly detailed study the biology and anatomy of the mayfly Palingenia. Mayflies date from Carboniferous and Permian times and represent the oldest of the existing winged insects. They are unique among the insects in having two winged adult stages, the subimago and imago. Adult mayflies do not feed; they rely on reserves built up during their nymphal life. They live from 1-2 hours to a few days and even up to 14 days in some ovoviviparous species. Thus, mayflies spend most of their life in the aquatic environment, either as eggs or as nymphs, and the major part of this review concerns itself with their aquatic life. The nymphal life span in mayflies varies from 3-4 weeks to about 21/2 years. The length of egg development varies from ovoviviparity, in which the eggs hatch immediately after oviposition, to a period of up to 10-11 months in some arctic/alpine species. Because of their winged adult stage and a propensity for drift as nymphs, mayflies are often among the first macroinvertebrates to colonize virgin habitats (89, 128, 241). However, over longer distances their dispersal capacity is limited, owing to the fragile nature and short life of the adults. Mayfly faunas on oceanic islands and isolated mountain areas are poor in species and usually restricted to the Baetidae and/or Caenidae (62). Their conservative dispersal makes them useful subjects for biogeographical analysis (62) (Brittain, J. E., 1982) [5].

The causes and consequences of habitat distribution of larvae of the mayfly Paraleptophlebia guttata were analyzed in a 2nd-order stream in west-central Kentucky. Among macrohabitats, larvae were typically significantly denser in runs and riffles than in pools. Densities were positively related to the percentage of coarse substrata in macrohabitats, but were not correlated with current velocity, predatory fish densities, or the quantity of fine particulate organic matter (food) in macrohabitats. This relationship between density and substratum coarseness was further evidenced in an in-situ colonization experiment in which larvae selected gravel and pebble substrata over sand. Among microhabitats, larvae were more abundant in leaf litter and in gravel/pebble than in silt/sand. Laboratory manipulations showed that predation rates by fish were significantly lower on mayflies in leaf litter and gravel than in fine substrata. The combined effects of substratum particle size and fish predation determine habitat distributions of larvae. Larger larvae were more abundant in runs than in riffles, but larval growth rates in artificial stream channels were similar between current velocities simulating those in riffles and runs. These results, coupled with data from drift samples, suggest that larvae shifted macrohabitats with size. Size-related differences in macrohabitat use may reflect size-related changes in microhabitat use; larvae were significantly larger in leaf litter than in other microhabitats, and leaf litter amounts were greater in runs than in riffles (Holomuzki, J. R., and Messier, S. H., 1993) [12].

Though the winged stages do not have functional mouthparts or digestive systems, the larval, or nymphal, stages have a variety of feeding approaches including, but not limited to, collector-gatherers, filterers, scrapers, and active predators with each supported by a diversity of morphological and behavioral adaptations. Mayflies provide direct and indirect services to humans and other parts of both freshwater and terrestrial ecosystems. In terms of cultural services, they have provided inspiration to musicians, poets, and other writers, as well as being the namesakes of various water- and aircraft.

They are commemorated by festivals worldwide. Mayflies are especially important to fishing. Mayflies contribute to the provisioning services of ecosystems in that they are utilized as food by human cultures worldwide (having one of the highest protein contents of any edible insect), as laboratory organisms, and as a potential source of antitumor molecules. They provide regulatory services through their cleaning of freshwater.

They provide many essential supporting services for ecosystems such as bioturbation, bioirrigation, decomposition, nutrition for many kinds of non-human animals, nutrient cycling and spiraling in freshwaters, nutrient cycling between aquatic and terrestrial systems, habitat for other organisms, and serving as indicators of ecosystem health. About 20% of mayfly species worldwide might have a threatened conservation status due to influences from pollution, invasive alien species, habitat loss and degradation, and climate change. Even mitigation of negative influences has benefits and tradeoffs, as, in several cases, sustainable energy production negatively impacts mayflies (Jacobus, L. M., *et. al.*, 2019) [13].

Using regression analysis on data compiled from the literature, I compared relationships (forewing versus body length) of mayfly imagoes, as a measure of dispersal, between suborders (Schistonota and Pannota) and among habitat type (lotic, lentic, and mixed). There were no significant differences in slopes or intercepts of the regression lines between sexes. Forewing length changed less markedly with body size for species within the ancestral Schistonota than the Pannota. Regression lines for lake and river forms intersect at 7.85 mm (wing length) and 7.30 mm (body length). Small (body length < 7.3 mm) lentic mayflies have proportionately longer wings than small riverine forms. Large (body length > 7.3 mm) riverine mayflies have proportionately longer wings than lentic forms. Based on these relationships, small lake-dwelling mayflies and large riverine mayflies are best able to disperse. Mayfly species occurring in mixed (both rivers and lakes) habitats exhibited allometric relationships similar to mayflies restricted to rivers (Corkum, L. D., 1987) [9].

Despite advances in recent years, there remains a lack of information on the habitat specificity of many aquatic insects, especially for the most recently described taxa and for very diverse regions such as the Amazon. This study evaluates the relationship between niche breadth and habitat specificity of aquatic insects in 219 streams. Local environmental variation in streams impacted by multiple land uses have resulted in distinct assemblages in each region. An Outlying Mean Index analysis was use to evaluate niche position and revealed that environmental changes could favor specialist insects. For example, streams impacted in one of the regions had higher values of depth, dissolved oxygen, percentage of roots, and percentage of wood in the substrate.

These conditions contributed to the occurrence of the locally tolerant *Hydrosmilodon* and *Zelusia* genera, as well as the locally sensitive genera *Harpagobaetis, Leptohyphes*, and *Traverhyphes*. Results showed that some taxa from each regional assemblage occupying less often occupied habitats, and these taxa are represented by few individuals and with a low frequency of occurrence. The knowledge generated here is important for protecting habitats and maintaining the local biodiversity of aquatic systems in the Amazon impacted by multiple lands uses and land conversion activities (Luiza-Andrade, A., *et. al.*, 2022) [18].

Mayfly lineages across flow regimes

We found lower species turnover in mayflies and stoneflies from regulated than from unregulated lotic and lentic sites, a result suggesting selection of a subset of mayflies and stoneflies from the regional species pool by flow and water-level regulation. The limited support for our predictions probably reflects the comparatively low diversity of aquatic insect species in Norwegian freshwater ecosystems for biogeographical and historical reasons, phenotypic plasticity of the insects' life histories and feeding habits, low trait diversity, trade-offs among species traits in a marginal region, restrictions to trait combinations and, perhaps, random extinction of mayflies and stoneflies caused by hydrological regulation. We advocate inclusion of species-trait variables that may affect ecosystem-level ecological processes in environmental assessment studies because a better understanding of trait-mediated ecological functioning should facilitate assessment of the ecological consequences of anthropogenic perturbations of freshwater ecosystems (Petrin, Z., *et. al.*, 2013) [25].

The extant global Ephemeroptera fauna is represented by over 3,000 described species in 42 families and more than 400 genera. The highest generic diversity occurs in the Neotropics, with a correspondingly high species diversity, while the Palearctic has the lowest generic diversity, but a high species diversity. Such distribution patterns may relate to how long evolutionary processes have been carrying on in isolation in a bioregion. Over an extended period, there may be extinction of species, but evolution of more genera. Dramatic extinction events such as the K-T mass extinction have affected current mayfly diversity and distribution.

Climatic history plays an important role in the rate of speciation in an area, with regions which have been climatically stable over long periods having fewer species per genus, when compared to regions subjected to climatic stresses, such as glaciation.

A total of 13 families is endemic to specific bioregions, with eight among them being monospecific. Most of these have restricted distributions which may be the result of them being the relict of a previously more diverse, but presently almost completely extinct family, or may be the consequence of vicariance events, resulting from evolution due to long-term isolation (Barber-James, H. M., *et. al.*, 2008) [1].

Impoundment and diversion of watercourses for power production and water supply can have profound effects on the mayfly fauna. To explain such effects a species-specific approach is adopted on account of differing habitat requirements and life histories in the order and even within genera. Environmental conditions such as discharge and flow patterns, temperature, food availability, and predation may be changed. This leads to changes in the density and species composition of the mayfly community, especially when there is a hypolimnion drain from reservoirs. Temperature changes below such reservoirs may remove obligatory life cycle thresholds. Prolonged periods of low discharge lead to the dominance of genera, such as *Paraleptophlebia, Choroterpes, Siphlonurus*, and *Pseudocloen*, typical of slow-flowing and lentic habitats. The life cycle plasticity and opportunism shown by *Baetisrhodani* in Europe and *B. tricaudatus* in North America have undoubtedly contributed to their success in regulated rivers. The life history characteristics of *Tricorythodes* are also advantageous below dams.

The increased growth of periphyton and mosses below many dams favour certain Ephemerellidae, but restrict or eliminate many Heptageniidae. In order to survive adverse conditions, flexible life cycles or a short period of rapid nymphal growth coupled with a long period of egg development, are advantageous (Brittain, J. E., and Saltveit, S. J., 1989) [6].

Understanding ecological divergence of morphologically similar but genetically distinct species previously considered as a single morphospecies is of key importance in evolutionary ecology and conservation biology. Despite their morphological similarity, cryptic species may have evolved distinct adaptations. If such ecological divergence is unaccounted for, any predictions about their responses to environmental change and biodiversity loss may be biased.

We used spatio-temporally replicated field surveys of larval cohort structure and population genetic analyses (using nuclear microsatellite markers) to test for life-history divergence between two cryptic lineages of the alpine mayfly *Baetis alpinus* in the Swiss Alps. We found that the more widespread and abundant cryptic lineage represents a 'generalist' with at least two cohorts per year, whereas the less abundant lineage is restricted to higher elevations and represents a 'specialist' with a single cohort per year. Importantly, our results indicate partial temporal segregation in reproductive periods between these lineages, potentially facilitating local coexistence and reproductive isolation.

Taken together, our findings emphasize the need for a taxonomic revision: widespread and apparently generalist morphospecies can hide cryptic lineages with much narrower ecological niches and distribution ranges (Leys, M., *et. al.*, 2017) [17].

Due to their aquatic larvae, the evolution of mayflies is intricately tied to environmental changes affecting lakes and rivers. Despite a rich fossil record, little is known about the factors shaping the pattern of diversification of mayflies in deep time. We assemble an unprecedented dataset encompassing all fossil occurrences of mayflies and perform a Bayesian analysis to identify periods of increased origination or extinction. We provide strong evidence for a major extinction of mayflies in the mid-Cretaceous. This extinction and subsequent faunal turnover were probably connected with the rise of angiosperms. Their dominance caused increased nutrient input and changed the chemistry of the freshwater environments, a trend detrimental mainly to lacustrine insects. Mayflies underwent a habitat shift from hypotrophic lakes to running waters, where most of their diversity has been concentrated from the Late Cretaceous to the present (Sroka, P., *et. al.*, 2023) [28].

Conclusion

Freshwater ecosystems, characterized by strong spatial and temporal variation in hydrological conditions, exert significant evolutionary pressures on aquatic organisms. In mayflies (order Ephemeroptera), these pressures are reflected in a wide range of morphological adaptations that enable species to survive and function across diverse flow regimes. Evidence from multiple studies indicates that hydrodynamic forces act as powerful environmental filters, repeatedly favoring specific trait combinations suited to either high-flow or low-flow habitats. In lotic environments with strong currents, mayfly nymphs commonly exhibit convergent traits such as dorsoventrally flattened bodies, reinforced limbs, and enlarged claws, all of which enhance stability and substrate attachment. In contrast, species inhabiting lentic or slow-flowing waters tend to display cylindrical body forms, elongated gills, and traits that facilitate swimming or burrowing.

The repeated emergence of these trait syndromes across unrelated lineages highlights the role of morphological convergence driven by similar ecological constraints. At the same time, habitat specialization appears to shape evolutionary pathways by limiting morphological variation within ecological guilds while promoting divergence among taxa occupying different flow regimes. This interplay between convergence and specialization underscores the complexity of adaptive evolution in freshwater insects. However, despite numerous case-specific investigations, a broad synthesis of convergence patterns across mayfly lineages remains incomplete.

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