12-1-2006

Functional trait niches of North American lotic insects: Traits-based ecological applications in light of phylogenetic relationships

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Recommended Citation

Poff, N. LeRoy, Julian D. Olden, Nicole KM Vieira, Debra S. Finn, Mark P. Simmons, and Boris C. Kondratieff. "Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships." Journal of the North American Benthological Society 25, no. 4 (2006): 730-755.

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J. N. Am. Benthol. Soc., 2006, 25(4):730–755

ROSEMARY MACKAY FUND ARTICLE

The Rosemary Mackay Fund is intended to promote the publication of speculative, forward-looking, and philosophical articles on any aspect of benthology. The Fund was named to honor Rosemary Mackay, the first editor of J-NABS. Details for submissions under the Fund appear in J-NABS 17(4):381 and 25(2):269–270.

In this fourth article of the series, N. L. Poff and his co-authors explore the issue of inter-trait correlations for lotic insects and identify opportunities and challenges for advancing the theory and application of traits-based approaches in stream community ecology. N. LeRoy Poff is an Associate Professor in the Department of Biology at Colorado State University. His research focuses broadly on how riverine species and communities respond to natural and human-caused environmental variation across a range of spatial scales, from local to regional, and on how this information can be used both to test ecological theory and to inform stream management decisions.

Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships

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Abstract. The use of species traits to characterize the functional composition of benthic invertebrate communities has become well established in the ecological literature. This approach holds much potential for predicting changes of both species and species assemblages along environmental gradients in terms of traits that are sensitive to local environmental conditions. Further, in the burgeoning field of biomonitoring, a functional approach provides a predictive basis for understanding community-level responses along gradients of environmental alteration caused by humans. Despite much progress in recent years, the full potential of the functional traits-based approach is currently limited by several factors, both conceptual and methodological. Most notably, we lack adequate understanding of how individual traits are intercorrelated and how this lack of independence among traits reflects phylogenetic (evolutionary) constraint. A better understanding is needed if we are to make the transition from a largely univariate approach that considers single-trait responses along single environmental gradients to a multivariate one that more realistically accounts for the responses of many traits across multiple environmental gradients characteristic of most human-dominated landscapes. Our primary objective in this paper is to explore the issue of inter-trait correlations for lotic insects and to identify opportunities and challenges for advancing the theory and application of traits-based approaches in stream community ecology. We created a new database on species-trait composition of North American lotic insects. Using published accounts and expert opinion, we collected information on 20 species traits (in 59 trait states) that fell into 4 broad categories: life-history, morphological, mobility, and ecological. First, we demonstrate the importance of considering how the linkage of specific trait states within a taxon is critical to developing a more-robust traits-based community ecology. Second, we examine the statistical correlations among traits and trait states for the 311 taxa to identify trait *syndromes* and specify which traits provide unique (uncorrelated) information that can be used to guide trait selection in ecological studies. Third, we examine the evolutionary associations among traits by mapping trait states onto a phylogentic tree derived from morphological and molecular analyses and classifications from the literature. We examine the evolutionary *lability* of individual traits by assessing the extent to which they are unconstrained by phylogenic relationships across the taxa. By focusing on the lability of traits within lotic genera of Ephemeroptera, Plecoptera, and Trichoptera, taxa often used as water-quality indicators, we show how a traits-based approach can allow a priori expectations of the differential response of these taxa to specific environmental gradients. We conclude with some ideas about how specific trait linkages, statistical correlations among traits, and evolutionary lability of traits can be used in combination with a mechanistic understanding of trait response along environmental gradients to select *robust* traits useful for a more predictive community ecology. We indicate how these new insights can direct the research in statistical modeling that is necessary to achieve the full potential of models that can predict how multiple traits will respond along multiple environmental gradients.

Key words: species traits, functional trait niche, functional diversity, trait correlations, phylogenetic analysis, environmental gradients, environmental filters, predictive community ecology, biomonitoring.

A long-standing goal in benthic stream ecology has been to explain and predict species distributions according to key features of the environment (Theinemann 1954, Hynes 1970, Townsend and Hildrew 1994, Statzner et al. 2001b). This goal has proven challenging, not only because of taxonomic uncertainties, but also because environmental features in streams are embedded in a landscape context (Hynes 1975, Malmqvist 2002) that is both multiscaled (Frissell et al. 1986) and dynamic (Resh et al. 1988). Given the difficulties with predicting species composition in lotic systems, researchers have advanced functional classifications of species into groups with similar biological and ecological traits that are expected to respond consistently along specific environmental gradients. Cummins (1973) was the first to articulate fully the functional approach in stream biology by assigning insect species to feeding groups intended to reflect dominant modes of food acquisition. The River Continuum Concept (Vannote et al. 1980) built upon that work by presenting a theoretical construct for relating the trophic characteristics of species to the dominant longitudinal physical and energy gradients of rivers on a global scale. Over the past few decades, many species traits have been collated to facilitate further development of traits-based analyses of insect communities in stream benthic ecology (reviewed in Poff 1997, Statzner et al. 2001b).

The habitat template (templet) model of Southwood (1977, 1988) is the primary theoretical underpinning of traits-based approaches in stream ecology. This model predicts that where environmental conditions (drivers) are similar, species trait composition should converge, even across biogeographic boundaries where species pools differ (cf. Orians 1980, Schluter 1986). This model has been adapted to streams in several manifestations (e.g., Schlosser 1987, Poff and Ward 1990), but most extensively by Townsend and Hildrew (1994), who proposed that benthic communities should consist of species possessing traits well suited to the spatial and temporal heterogeneity of their habitat. The metaphor of environmental *filtering* (e.g., Tonn et al. 1990, Keddy 1991) entered the aquatic literature as community ecologists began to understand that local community composition reflects regional-scale processes (Ricklefs 1987, Ricklefs and Schluter 1993) and that multiscaled processes can be characterized in hierarchical terms (e.g., Allen and Starr 1982, Frissell et al. 1986). Building on this metaphor, Poff (1997) considered how species traits may be filtered at multiple landscape scales to influence the functional (trait) composition of local stream communities. The template model in benthic community ecology has been supported by numerous studies that explain trait composition of populations or invertebrate communities in terms of environmental drivers (e.g., Scarsbrook and Townsend 1993, Resh et al. 1994, Statzner et al. 1997, Townsend et al. 1997a, b, Robinson and Minshall 1998, Chessman and Royal 2004, Finn and Poff 2005, Heino 2005, Bêche et al. 2006). A handful of traits-based analyses conducted at multiple spatial scales (Richards et al. 1997, Parsons 2001, Weigel et al. 2003, Statzner et al. 2004, Lamouroux et al. 2004, NLP, unpublished data) also give credence to the multiscale filtering concept in lotic systems.

The mechanistic basis for understanding and predicting trait–environment relationships underlying the template model has encouraged some to argue that traits-based approaches could be used in the burgeoning field of stream biomonitoring (Dolédec et al. 1999, Hawkins et al. 2000, Statzner et al. 2001a, Bady et al. 2005). The strong theoretical framework for linking benthic community responses to environmental alteration (especially by anthropogenic stressors) could be used to create ecologically meaningful biometrics that are broadly applicable across multiple spatial scales and that span biogeographic boundaries. Furthermore, for benthic invertebrates, traits may be more time- and cost-efficient than taxonomic methods of defining assemblages. Taxonomic identification at coarser levels than species (e.g., genera and families) can provide an accurate description of the trait diversity at a locality (Dolédec et al. 2000, Gayraud et al. 2003) and, therefore, taxonomic expertise and time-consuming lab work are minimized. The application of traits-based biomonitoring approaches has been best developed in Europe (Dolédec et al. 1999, 2000, Charvet et al. 2000, Usseglio-Polatera et al. 2000b, Statzner et al. 2001a, Gayraud et al. 2003, Bady et al. 2005, Ducrot et al. 2005), although there are also examples from North America (e.g., Merritt et al. 2002, Vieira et al. 2004), Australia (Chessman and Royal 2004), and New Zealand (Dolédec et al. 2006). Trait applications in biomonitoring thus far include defining *assemblage types*, determining expected trait diversity under reference conditions, and developing metrics to detect environmental gradients.

The traits-based perspective presents a powerful paradigm for broad-scale stream community ecology (both basic and applied) because it offers a framework for mechanistically linking traits in a community to major environmental drivers that influence the fitness of the species possessing those attributes. However, even where such mechanistic linkages can be made easily, fundamental challenges confront the development of a more predictive traits-based approach to community ecology. The overarching need is to develop a more robust multivariate framework, in which the responses of multiple, independent traits can be related to multiple environmental gradients characteristic of most landscapes. Univariate approaches consider single trait responses along individual environmental gradients (e.g., Lamouroux et al. 2004), whereas most multivariate approaches aggregate multiple traits into groups (e.g., Poff and Allan 1995) or ordinate them to reduce dimensionality (e.g., Finn and Poff 2005) and then examine how they vary along environmental gradients. However, these multivariate approaches do not account for statistical or phylogenetic relationships among the traits, and neither do more formal multivariate-based techniques that test for statistical relationships between environmental variables and individual trait responses (e.g., Dolédec et al. 1996, Legendre et al. 1997).

The implicit challenge in adopting such a multifaceted approach is to account quantitatively for the fact that traits are often linked together by evolution and, therefore, cannot necessarily be treated as independent entities. That traits can be linked together into *syndromes* has been known for some time, e.g., the classic *r*–*K* strategies in life-history traits (Pianka 1970). Stream ecologists also have recognized such linkages and pointed out that these linkages may cause individual traits to appear decoupled from environmental conditions (see Resh et al. 1994, Townsend and Hildrew 1994, Statzner et al. 2004). This linkage is analogous to the concept of pleiotropy in genetics, in which selection for a particular gene may alter the frequency of other, linked genes. However, to date, virtually no effort has been expended to disentangle trait linkages quantitatively to reveal the unique information available in each trait and, thus, to allow development of more-informed models relating responses of multiple traits to environmental condition(s).

Our primary objective in this paper is to explore the issue of inter-trait correlations for lotic insects and to identify opportunities and challenges for advancing the theory and application of traits-based approaches in stream community ecology. We pursue this objective in 4 sections. First, we analogize a taxon's specific combination of traits to the ecological niche to conceptualize how linked traits may dictate the response of whole communities to the environment. Second, we quantify the statistical correlations of traits for a large collection of families and genera of North American lotic insect taxa. This analysis allows us to identify highly correlated traits that may influence how entire benthic communities respond along environmental gradients. Third, we use an inferred phylogeny of all taxa based on molecular and morphological data to identify traits that are least constrained by phylogenetic history and, therefore, that can be used to test hypotheses regarding community responses to environmental change. As a subset of this analysis, we focus on the Ephemeroptera, Plecoptera, Trichoptera (EPT taxa), orders often used as water-quality indicators (e.g., Resh and Jackson 1993), to show how a traits-based approach can allow a priori expectations of how these particular taxa may respond differentially to specific environmental gradients. Fourth, we conclude with a brief discussion of some of the analytical limitations to advancing the multivariate traits-based approach, and we recommend future research directions.

The *Functional Trait Niche*—Linkage among Traits within Taxa

Traits are characteristics of species that are often used to define some biological feature of the organism or its direct relation to the environment. As such, the combination of traits an organism possesses is thought to be the product of natural selection by the environmental conditions in which a species or population has evolved (Southwood 1977). Any individual organism itself possesses multiple traits, and traits are not necessarily concordant with phylogeny (e.g., not all members of the Plecoptera are predators, and not all predators are Plecoptera). Because traits are not necessarily dependent on phylogeny, a traits-based approach can, in principle, be applied across biogeographic boundaries to examine issues such as community convergence under similar selection regimes (e.g., Lamouroux et al. 2002). From this point forward, we use the term *trait* to indicate some attribute, such as voltinism, that has multiple potential *states* (e.g., multivoltine, univoltine, or semivoltine) or, in some cases, that can be characterized in a continuous fashion (e.g., absolute body size). The delineation of states for each trait may be arbitrary and reflect either the ability to characterize a discrete state or the ecological question of interest.

The specific states making up some given set of traits can be identified for any species (or higher taxon). We define this specific combination of trait states as a taxon's *functional trait niche* (FTN), which is analogous to the ecological niche of a species, i.e., the totality of attributes defining its unique relation to its environment and other species. (See Chase and Leibold 2003 for a cogent discussion of the ecological niche and Rosenfeld 2002 for the related concept of the functional niche. Also see McGill et al. 2006 for a discussion of the relationship between functional traits and the realized and ecological niches of species.) Generally speaking, FTNs are nonrandom because they have been structured by evolution and, accordingly, closely related taxa are more likely to have similar FTNs than are distantly related taxa (discussed further below).

The FTN is an important concept because trait linkages at the individual species level represent a specific, evolutionarily constrained structure within the aggregate community trait composition. This structure has some important implications for predictive traits-based community ecology. First, the trait states comprising a community cannot be treated as independent statistical entities, a fact well understood by both ecologists (e.g., Townsend and Hildrew 1994) and statisticians (e.g., Legendre et al. 1997). Second, and more subtly, the response of a benthic community along some environmental gradient(s) may depend on the specific collection of FTNs represented by members of the community. As a consequence, composite measures of community trait composition that do not explicitly account for the evolutionary linkage of trait states (e.g., functional diversity; Charvet et al. 2000, Bady et al. 2005) are unlikely to be adequate indicators of traits-based community response to environmental change.

The simple hypothetical example presented in Fig. 1 illustrates the utility of the FTN concept. In this example, 2 communities each consist of 3 taxa. Each taxon is described by a specific combination of 3 traits (a, b, and c), each of which has 3 states (e.g., trait a has states a_1, a_2, and a_3). Note that the 6 taxa making up

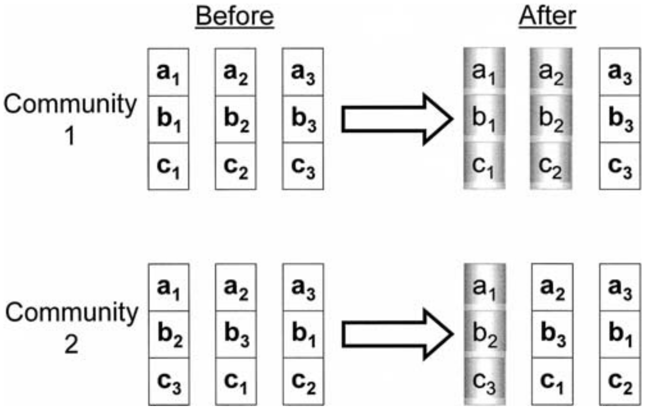

FIG. 1. A simple hypothetical example of how the specific sequences of trait states (functional trait niches [FTNs]) of the taxa in a community can dictate community response to an environmental selective force or filter. In this illustration, each of 2 communities has 3 taxa, whose FTNs are defined in terms of the specific sequence of trait states for each of 3 traits: a, b, and c. Before an environmental filtering event, both communities have the same taxonomic richness ($n = 3$) and functional diversity (same 9 trait states present across all taxa), but the functional identity of each community is unique (i.e., no taxa share the same FTN). The arrow represents a hypothetical environmental change that specifically selects against (filters) trait states a_1 and b_2. Because the linkage of these 2 trait states differs among the members of the 2 communities, 2 taxa are lost (shading) from community 1, whereas only 1 taxon is lost from community 2. Thus, the FTNs of the 2 communities dictate the taxonomic and functional diversity of the communities subsequent to the filtering event.

the 2 communities are, in fact, unique in terms of their FTNs, i.e., no 2 taxa share an identical combination of trait states. However, each community has the same functional diversity, i.e., number of unique trait states. If we now impose on both communities a strong environmental filter that specifically selects against trait states a_1 and b_2, we see a differential response between the communities as a function of their constituent FTNs. In the 1st community, trait states a_1 and b_2 occur in separate taxa, both of which are subsequently lost from the community. By contrast, in the 2nd community, trait states a_1 and b_2 occur in only 1 taxon, and only that taxon is eliminated. Thus, under the same environmental selection regime, the specific combinations of trait states (i.e., the FTNs of the constituent species) can directly influence the resultant functional diversity of the whole community. Of course, a different selection event that, say, selects for a_1 and b_1 would have the opposite consequence regarding the functional diversity of these hypothetical communities.

We present this simple example to make 2 important points. First, it is possible to achieve the same functional diversity with different sets of contributing taxa, an observation that underscores the point that functional and taxonomic diversity need not be equivalent. Second, linkage among traits and trait states (as represented by FTNs) raises the possibility that the overall functional diversity of a community may change in unanticipated ways in response to some environmental selective force acting on a specific trait or trait state. These observations emphasize the importance of considering multiple traits and their linkages in developing a traits-based predictive ecology. The most informative traits and trait states in broad-scale analyses of community responses along environmental gradients would be those that are relatively independent, i.e., weakly correlated and not strongly linked by evolution. Such traits might be particularly useful for biomonitoring applications, a theme we return to below. Another insight afforded by these observations is that an FTN represents a multidimensional response potential for a species along some environmental gradient(s). Therefore, the FTN concept may help ecologists improve our presently limited understanding of how *combinations* of trait states may interact with the environment by providing an evolutionarily informed, multivariate framework for exploring how particular trait combinations are associated with different selection regimes.

Correlations among Traits across Taxa

We characterized 311 taxa in 75 families of North American lotic insect taxa (from Merritt and Cummins 1996, with nomenclature updates) according to 20 traits coded in 59 states that are broadly categorized as life-history, mobility, morphological, and ecological traits (Table 1). We selected all traits that were readily available in the literature or that could be evaluated confidently by expert opinion and applied to the entire set of North American lotic insect taxa. Our trait matrix was cross-referenced with a comprehensive meta-database of traits for North American invertebrates that we developed for the US Geological Survey (USGS; see Vieira et al. 2006 for database and extensive documentation). The USGS meta-database can be used to express traits quantitatively or as multistate, fuzzy categories (e.g., Resh et al. 1994). However, we assigned each taxonomic unit to only one trait state (i.e., a binary approach) using literature and expert opinion for several reasons. First, detailed trait information typically is not available for invertebrate taxa at the continental scale in North America (unlike in Europe). Second, our goal was to use the trait matrix to explore some dominant relationships among taxa that could guide future research, rather than to provide an exhaustive and authoritative listing of lotic insect traits. Third, this approach greatly simplifies our phylogenetic analysis (see below), which is a novel approach for examining the evolutionary relationships among traits and trait states for a continental invertebrate fauna. Furthermore, the highest taxonomic resolution we considered was the genus level (except for some Chironomidae where tribe was used) because of great taxonomic uncertainty at the species level (for aquatic juveniles) and because congeneric species are often functionally equivalent and arguably can be viewed as ecologically equivalent (Wiggins and Mackay 1978). We also completed analyses at the family level, where we used a majority rule to assign the most common genus-level trait state to the family (regardless of species diversity within genera). The assignments to specific trait states for each taxon are provided in the Appendix. Hereafter, we will refer to the various taxonomic levels as "genus" or "genera" only.

There are >350,000 theoretical combinations of the 59 various states (based on multiplying number of possible trait states for each of the 20 traits) in our trait matrix. However, by definition, a maximum of only 311 unique sequences has been realized during evolution among the 311 extant taxa we considered (at the genus/tribe level of resolution). Of this number, 233 unique combinations of trait states actually occur, i.e., some genera have identical FTNs at the level of trait resolution used in the analysis. In this section, we explore in more detail how these trait states are associated across the North American lotic insect taxa to identify which trait states are only weakly correlated across taxa and, thus, make particularly good candidate traits for use in predictive community ecology.

We used multivariate ordination and cluster analyses to explore relationships among the 20 biological traits at 2 taxonomic resolutions: the genus (or tribe) level ($n = 311$) and the family level ($n = 75$). For both levels of taxonomic resolution, we conducted 2 analyses using Gower's similarity coefficient (Gower 1971), which calculates similarity between 2 taxa according to categorical traits. First, we examined the similarity of the taxa in terms of the multistate biological traits. We used Principal Coordinates Analysis (PCoA) on the genus and family similarity matrices to reduce dimensionality and to summarize the dominant patterns of variation among the biological traits (Legendre and Legendre 1998). We retained the first 2 PCoA dimensions to facilitate visual interpretation of the resulting plots. Second, we used Gower's similarity index to construct a dendogram showing similarity in traits across all taxa.

The multivariate summary of the 311 genera (Fig. 2A) shows strong separation in 2-dimensional space, where the 1st and 2nd PCoA axes explained 17.8% and 13.6% of the variation in trait space, respectively (both components were statistically significant based on the broken-stick model; Jackson 1993). Genera were distributed in this ordination space with discernible separation among orders in most cases, although some orders (Coleoptera, Plecoptera) contain genera that span much of the ordination space and overlap in their trait composition with other orders (Fig. 2B). These patterns suggest that most genera can be separated according to 3 major trait gradients based on combinations of traits that explain dominant levels of variation among the genera in this 2-dimensional space (Fig. 2C).

The 1st trait gradient (positive axis I and negative axis II scores) primarily represents genera of Hemiptera and Odonata, although some Coleoptera and Plectoptera genera are included. The primary trait states are high crawling rate (Crwl3), long adult life span (Life3), semivoltinism (Volt1), strong adult flight (Flgt2), and predatory feeding mode (Trop4). Two other traits important to some genera in this group are lack of attachment to the benthos (Atch1) and large adult body size (Size3). The 2nd trait gradient (negative axis I scores and negative axis II scores) primarily represents Ephemeroptera and some Plecoptera genera. The primary trait states are fast seasonal life cycles (Devl1), no body armoring (Armr1), very short adult life span (Life1), and small adult size (Size1). These genera are common or abundant in the drift (high negative loading on Drft1; see Table 1). The 3rd trait gradient (positive axis II scores) mainly describes Trichoptera and some Diptera and Coleoptera genera that are characterized primarily by no swimming ability (Swim1), some attachment (Atch2), high rheophily (Rheo3), body armoring (Armr3), and short adult life span (Life2).

The trait gradients shown in Fig. 2 can be viewed essentially as trait *syndromes* in which specific trait states co-occur across the range of North American lotic insect taxa. Specific sets of trait states are strongly associated with particular groups of genera and families, a finding similar to that reported for European lotic insect taxa using different traits (see Usseglio-Polatera et al. 2000a). We note that these syndromes are interpreted in only a 2-dimensional space that explains <⅓ of the variation in trait states across all the taxa. Adding additional axes would probably better define particular groups (e.g., some of the Plecoptera that cluster with the Trichoptera), but

TABLE 1. Description of the 20 traits (59 states) applied to 311 genera/tribes in 75 families of North American lotic insects, categorized into 4 trait groups (bolded). The letter in each code refers to the trait and the number refers to the trait state.

Trait	Trait state (modality)	Code
Life history		
Voltinism	Semivoltine (<1 generation/y)	Volt1
	Univoltine (1 generation/y)	Volt2
	Bi- or multivoltine (>1 generation/y)	Volt3
Development	Fast seasonal	Devl1
	Slow seasonal	Devl2
	Nonseasonal	Devl3
Synchronization of emergence	Poorly synchronized (wk)	Sync1
	Well synchronized (d)	Sync2
Adult life span	Very short (<1 wk)	Life1
	Short (<1 mo)	Life2
	Long (>1 mo)	Life3
Adult ability to exit	Absent (not including emergence)	Exit1
	Present	Exit2
Ability to survive desiccation	Absent	Desi1
	Present	Desi2
Mobility		
Female dispersal	Low (<1 km flight before laying eggs)	Disp1
	High (>1 km flight before laying eggs)	Disp2
Adult flying strength	Weak (e.g., cannot fly into light breeze)	Flgt1
	Strong	Flgt2
Occurrence in drift	Rare (catastrophic only)	Drft1
	Common (typically observed)	Drft2
	Abundant (dominant in drift samples)	Drft3
Maximum crawling rate	Very low (<10 cm/h)	Crwl1
	Low (<100 cm/h)	Crwl2
	High (>100 cm/h)	Crwl3
Swimming ability	None	Swim1
	Weak	Swim2
	Strong	Swim3
Morphology		
Attachment	None (free-ranging)	Atch1
	Some (sessile, sedentary)	Atch2
	Both	Atch3
Armoring	None (soft-bodied forms)	Armr1
	Poor (heavily sclerotized)	Armr2
	Good (e.g., some cased caddisflies)	Armr3
Shape	Streamlined (flat, fusiform)	Shpe1
	Not streamlined (cylindrical, round, or bluff)	Shpe2
Respiration	Tegument	Resp1
	Gills	Resp2
	Plastron, spiracle (aerial)	Resp3
Size at maturity	Small (<9 mm)	Size1
	Medium (9–16 mm)	Size2
	Large (>16 mm)	Size3
Ecology		
Rheophily	Depositional only	Rheo1
	Depositional and erosional	Rheo2
	Erosional	Rheo3
Thermal preference	Cold stenothermal or cool eurythermal	Ther1
	Cool/warm eurythermal	Ther2
	Warm eurythermal	Ther3
Habit	Burrow	Habi1
	Climb	Habi2
	Sprawl	Habi3
	Cling	Habi4
	Swim	Habi5
	Skate	Habi6

TABLE 1. Continued.

Trait	Trait state (modality)	Code
Trophic habit	Collector-gatherer	Trop1
	Collector-filterer	Trop2
	Herbivore (scraper, piercer, and shedder)	Trop3
	Predator (piercer and engulfer)	Trop4
	Shredder (detritivore)	Trop5

the major components of the FTNs of the insect taxa are reasonably depicted by these 2 dimensions, and our goal here is simply to show general patterns.

We found similar patterns for the 75 families of North American lotic insects. The first 2 PCoA components explained 18.0% and 13.8% of the variation in the original traits, respectively (both statistically significant), and the families were distinguished basically according to the same 3 major trait gradients identified in the analysis of genera (results not shown). This finding, which is consistent with other studies showing similarities in trait analyses between genus and family levels (Dolédec et al. 2000, Gayraud et al. 2003) suggests that a substantial

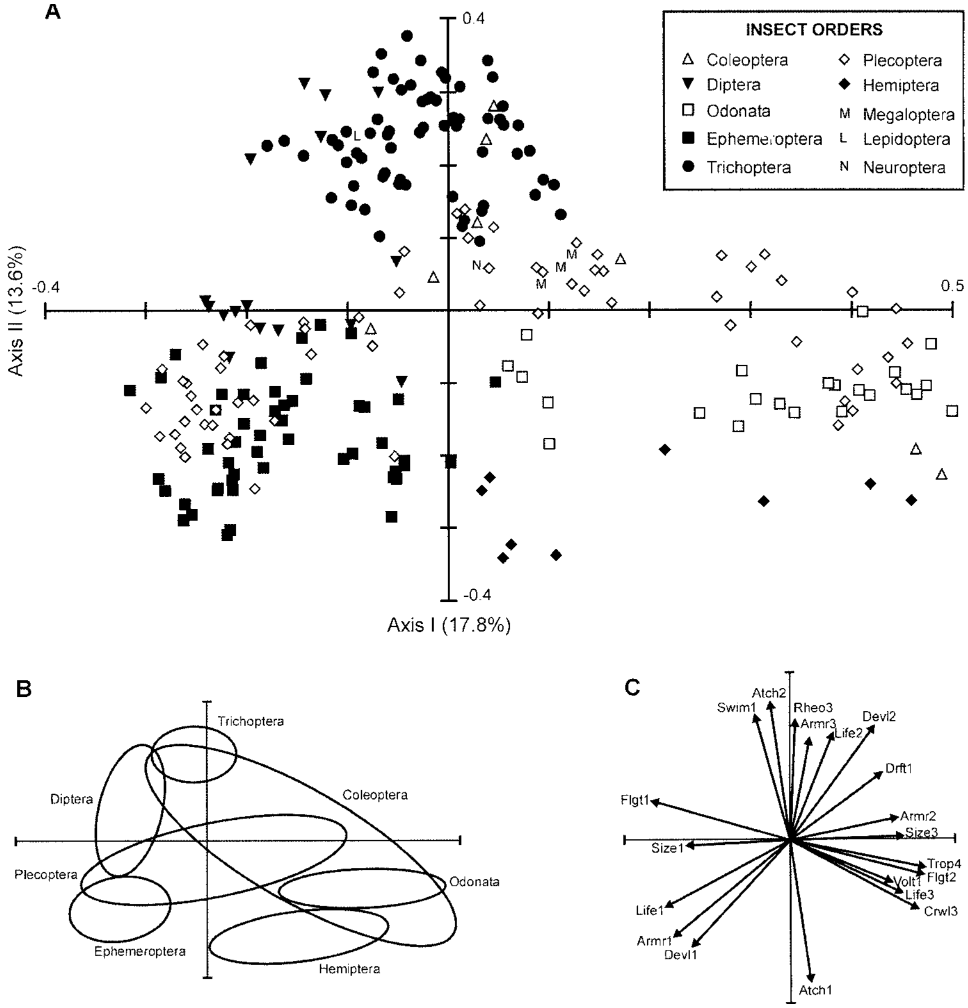

FIG. 2. Ordination plot resulting from a Principal Coordinates Analysis (PCoA) of 311 macroinvertebrate genera and 20 biological traits according to Gower's similarity coefficient. A.—Position of each genus in relation to the first 2 principal components. B.—95% confidence intervals for genera according to their order. C.—Dominant trait contributions (eigenvector loading >0.25), where the length of the vector is related to the strength of its contribution to the principal coordinate.

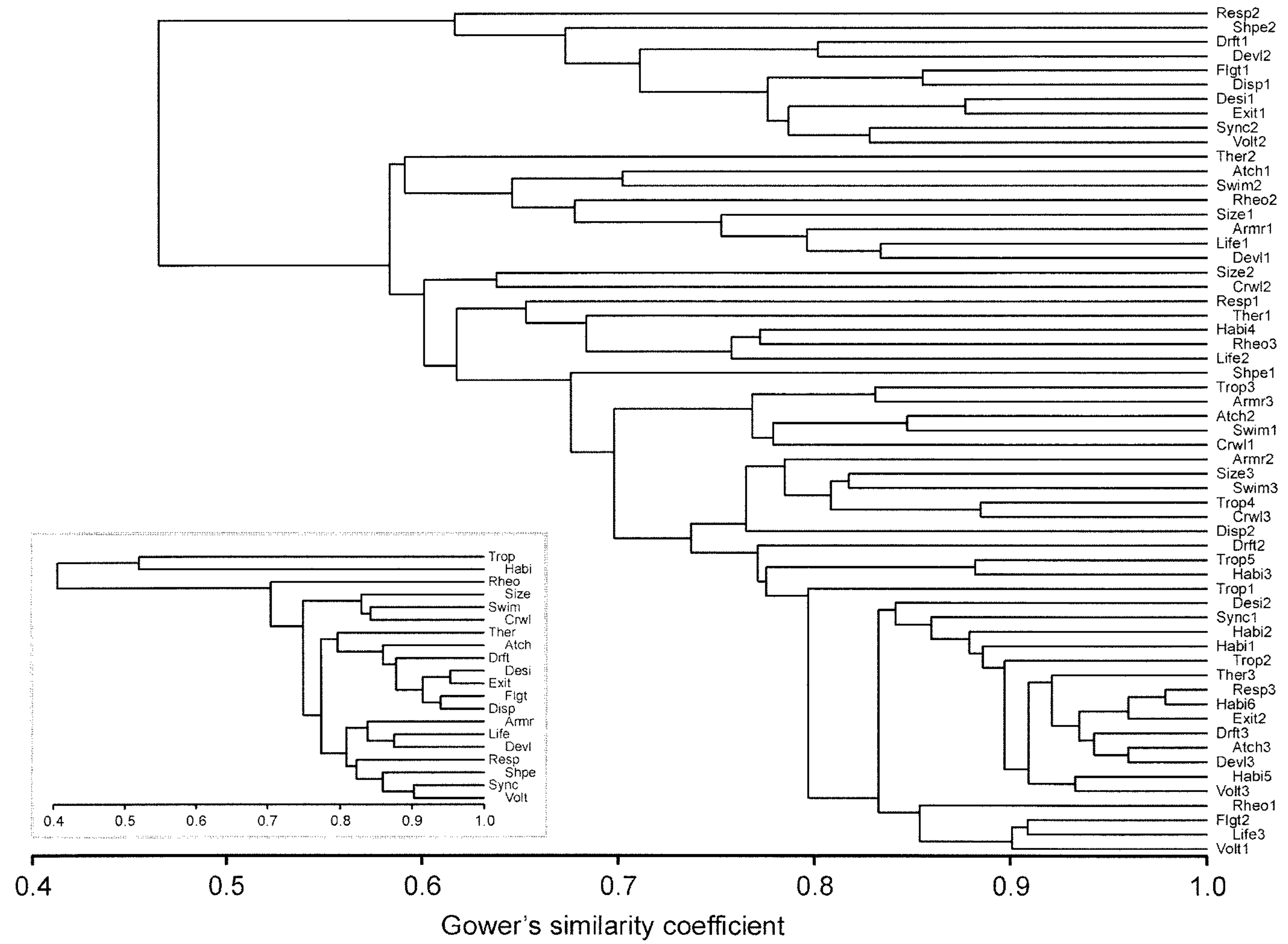

FIG. 3. Dendrogram showing similarities among the 59 trait states, and 20 trait values (inset) for 311 genera, according to Gower's similarity coefficient. Traits codes are described in Table 1.

amount of variation in trait diversity within benthic communities can be captured by a coarse taxonomic (family-level) resolution. However, use of family-level could result in the loss of some potentially important resolution, especially for the many families that possess a diversity of trait characteristics among the constituent genera. For example, 17 of the 20 limnephild genera in the database (Appendix) have unique FTNs, i.e., they differ in their unique combinations of trait states. Diversity is reasonably high among baetids (10 of 13 genera have unique FTNs), heptageneiids (9 of 12), and perlids (12 of 14), whereas diversity is less pronounced among groups such as hydropsychids (4 of 11) and gomphids (6 of 13). Thus, when attempting to explore community responses to complex and multiple environmental gradients, use of genus-level information is expected to provide more sensitivity to detection of subtle biological and ecological responses.

In Fig. 3 we show the quantitative similarity among the 59 trait states (and 20 average trait values–inset) as defined by the 311 taxa used in the analysis. Trait states that have high similarity in the dendogram do not necessarily show close association in Fig. 2C, which is only a 2-dimensional representation of relationships among trait states (as compared to the 311-dimensional representation of Fig. 3). Several sets of trait states show high similarity (>80%) across the dendogram. For example, at the bottom of the of the dendogram, a suite of trait states describing semivoltinism (Volt1) with a preference for depositional habitats (Rheo1) and long-lived (Life3), strong-flying adults (Flight2) occurs. This syndrome is represented mostly by members of the Odonata and corresponds closely to the trait gradients observed in Fig. 2. Immediately above this cluster are some groups of trait states that have similarity >90%. One consists of air breathing (Resp3) taxa, with skating habit (Habi6) and ability of the adult to exit the stream (Exit2), i.e., mainly hemipterans. Another consists of the trait states high juvenile drift occurrence (Drft3), ability to both attach and range freely (Atch3), and nonseasonal development (Devl3). Both of these clusters are closely allied with the warm eurythermal trait state (Ther3) as well as with the trait states of swimming habit (Habi5), bi/multivoltinism (Volt3), and collector-filterer feeding mode (Trop2). If the similarity threshold is dropped to 80% the additional trait states of desiccation tolerance (Desi2), poorly synchronized emergence (Sync1), and habits of climbing (Habi2) and burrowing (Habi1) are included. The trait states in the remainder of the dendrogram (i.e., above the trait state Desi2) generally show low similarity; however, scattered throughout this region are sets of trait states with >80% similarity across the 311 taxa. These sets include the following associations: sprawling (Habi3) and shredder/detritivore (Trop5); strong crawler (Crwl3) and predator (Trop4) along with large size (Size3) and strong swimmer (Swim3); no swimming (Swim1) with some attachment (Atch2); strong armoring (Armr3) and herbivore (Trop3); short adult life (Life1) with fast seasonal development (Devl1); univoltine (Volt2) with well-synchronized emergence (Sync2); low tolerance to desiccation (Desi1) with inability of adult to exit water (Exit1); weak adult flyer (Flgt1) with short aerial dispersal (Disp1); and rare in drift (Drft1) with slow-seasonal development (Devl2).

The analysis of trait similarity across all genera also revealed a number of interesting patterns for average trait correlations (Fig. 3 inset). Traits associated with larval dispersal and potential resilience to disturbance occur together (Drft, Desi, Exit, Flgt, Disp), and life-history traits have some strong affinities (Life, Devl and Sync, Volt). Some traits within our 4 general trait groups (Table 1) show low similarity across the 311 taxa. For example, the morphological traits Size, Atch, Armr, and Shpe are only about 80% correlated. Trophic (Trop) and habit (Habi) traits are only weakly correlated with other traits, a pattern that may reflect, in part, the fact that these traits have a relatively large number of trait states or that these traits are more evolutionarily labile than other traits (see below).

Evolutionary Lability among Traits across Taxa

Given the fact that many trait states occur together as tightly-linked syndromes that have apparently strong taxonomic affinities, the question arises as to how one might go about identifying traits that could be used generally for any benthic community. Ideally, we would like to use traits and associated states that are relatively unconstrained by phylogeny. A focus on such *evolutionarily labile* traits could help avoid the problems raised in Fig. 1. Specifically, convergent evolution is expected among highly labile traits because they are responsive to local selection; therefore, similarity among taxa with respect to these traits often will be largely independent of their phylogenetic relationships (e.g., Cavender-Bares et al. 2004). Indeed, environmental filtering has been shown to act more predictably on evolutionarily labile traits than on other traits in plants (Patterson and Givnish 2002, Cavender-Bares et al. 2004).

Speculation among ecologists about lability of traits through evolutionary time has a long history (e.g., Gause 1947, Mayr 1974, Diamond 1986), but this topic has received only brief attention in the stream ecology literature. Townsend and Hildrew (1994) noted it as an issue for predictive traits-based community ecology, and Usseglio-Polatera et al. (2000a) noted qualitatively that biological traits (e.g., morphology, physiology, life history) appear to be much more constrained by phylogeny than ecological traits (e.g., behavior, habitat preference). However, to date, no one has formally mapped aquatic insect traits onto an inferred phylogeny of North American lotic insects to quantify evolutionary lability and, thus, identify which traits may be applied most robustly to broad-scale community analyses. Furthermore, if phylogenetically unconstrained traits can be related directly to important environmental gradients (filters), then they could provide a good starting point for mechanistic hypothesis testing of a priori expectations about community-level responses to certain types of environmental change. In this section, we describe a formal approach to quantifying the phylogenetic constraint of trait states of North American lotic insect taxa, with the intent of identifying independent (more labile) traits that can be used in predictive community ecology.

Measuring trait lability across a phylogeny of North American lotic insects

We constructed a phylogenetic tree for North American lotic insects based on a compilation from the literature of morphological and molecular phylogenetic analyses and classifications. We also constructed a subtree consisting of the EPT taxa only, because this group is commonly used in water-quality biomonitoring programs (Resh and Jackson 1993). Phylogenetic relationships among insect orders followed Wheeler et al. (2001), the most comprehensive phylogenetic analysis available at this level of taxonomy. We typically favored information from molecular-based studies over morphology-based phylogenetic analyses

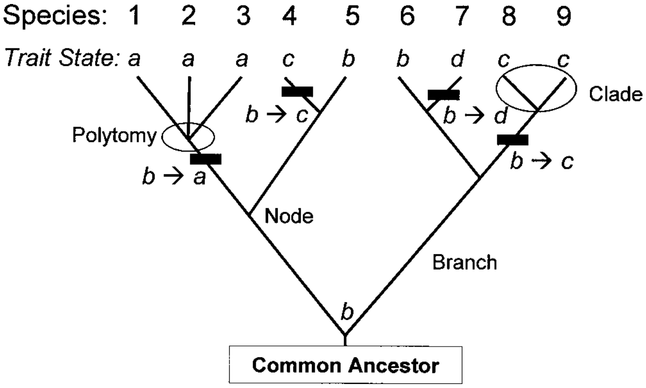

FIG. 4. Hypothetical phylogenetic tree for 9 extant species (numerals) that express 4 states of a given trait (italicized letters *a–d*). The branching structure is based on inferred phylogenies from the literature (see text). The most parsimonious evolution of this trait is shown, based on the inferred relationships among the 9 extant species. Dark bars indicate the inferred changes among trait states. In this illustrative tree, there are 3 state changes (number of steps $=$ 4) out of a possible 3 for this 4-state trait (Consistency Index [CI] is $3/4 = 0.75$). Clade, polytomy, and CI are defined in the text.

or classifications to resolve relationships among families and genera.

We used MacClade software (D. R. Maddison and W. P. Maddison. 2001. MacClade: analysis of phylogeny and character evolution, version 4.03, Sinauer, Sunderland, Massachusetts) to integrate information derived from the literature to reconstruct evolutionary relationships among insect taxa in the form of a hierarchical branching tree (cladogram) with extant taxa at the terminal nodes (Fig. 4 is an illustrative hypothetical example). We resolved orders, families, subfamilies, and tribes into clades (i.e., monophyletic groups of taxa sharing a common ancestor). We removed 3 plecopteran genera (*Alaskaperla*, *Bisancora*, and *Diploperla*) from the analysis because of a lack of information on phylogenetic relationships. Unfortunately, we were unable to resolve relationships within some taxonomic groups, resulting in several polytomies (clades within which relationships are ambiguous; Fig. 4) in our trees. For example, the 13 genera of Baetidae, formed a polytomy because of their unresolved phylogeny. Complete documentation of data matrices, guidelines used for tree construction, tree topologies, and relevant supporting literature are available at http://rydberg.biology.colostate.edu/Research/poff-etal-2006.

Each of the 20 traits was individually mapped onto both the full and the EPT-only trees in MacClade using the parsimony criterion to infer the minimum number of evolutionary changes in state needed to achieve the observed distribution, given the consensus phylogenetic trees. All trait states were treated as unordered (i.e., one step between every state change; Fitch 1971) and both parsimony-informative and parsimony-uninformative states were included in the analysis (see Davis et al. 1998). Evolutionary lability of each trait was estimated by calculating: 1) the inferred minimum number of evolutionary steps that would result in the observed distribution of trait states from a single ancestral state (Fig. 4), and 2) the consistency index (CI; Kluge and Farris 1969) for each trait. The CI measures homoplasy (convergence or reversal events) by calculating the ratio of the minimum possible number of steps (e.g., a 4-state trait would have a minimum of 3 steps from a single ancestral state) to the observed number of steps for each trait. As such, the CI ratio ranges from 0 to 1 and provides a standardized value for comparison among traits having different numbers of states. Lower CI values suggest traits (with the same number of alternative states) that are less consistent and, therefore, more evolutionarily labile.

Our analyses revealed a broad range of lability in terms of the number of steps for both the full tree (5–62 steps) and the EPT-only tree (1–52 steps) (Table 2). CI values also demonstrated differences in lability of traits, but CI values were all relatively low (≤ 0.20 for the full tree and ≤ 0.33 for the EPT-only tree). This result suggests that convergence and reversal events are fairly prevalent in lotic insect traits. Among the 4 trait groups (defined in Table 1), ecological traits had higher lability whereas life-history traits were more evolutionarily constrained. This pattern makes intuitive sense because taxonomic constraints in life-history traits may aid in reproductive success (e.g., maintaining synchronous emergence) and, thus, preservation of a species, whereas diversification of ecology-related traits allows species to use spatially and temporally variable resources. Across all traits, the most labile traits are thermal preference, rheophily, and size at maturity (all with >50 steps and CI <0.05; Table 2). Other labile traits (e.g., with >25 steps and CI <0.11) include trophic habit, habit, occurrence in drift, maximum crawling rate, armoring, and voltinism. For the EPT-only tree, some traits, such as voltinism and armoring, are less labile, a result that reflects the fact that some taxonomic groups show less variation among genera (e.g., univoltinism in Trichoptera) than other groups.

Phylogenetic correlations among traits

Groups of traits that are highly labile and statistically uncorrelated ought to be evolutionarily unlinked,

TABLE 2. Evolutionary lability of traits grouped into 4 categories (see Table 1 for list of trait states within each of the 20 traits) for phylogenetic trees for all North American lotic insects (311 taxa) and for Ephemeroptera, Plecoptera, and Trichoptera (EPT) genera only. Mean (±1 SD) number of steps and consistency index (CI) across all traits in a group are also presented. See text for details. The higher the number of steps and the lower the CI value, the greater the evolutionary lability.

		All-insects tree		EPT-only tree	
Trait group	Trait	No. steps	CI	No. steps	CI
Life history	All	17 (6.6)	0.10 (0.05)	11 (4.9)	0.28 (0.36)
	Voltinism	25	0.08	13	0.15
	Development	20	0.10	13	0.15
	Emergence synchrony	18	0.06	12	0.08
	Adult life span	18	0.11	10	0.20
	Adult exiting ability	5	0.20	1	1.00
	Desiccation resistance	17	0.06	14	0.07
Mobility	All	23 (9.5)	0.07 (0.02)	17 (10.6)	0.11 (0.06)
	Female dispersal	19	0.05	12	0.08
	Adult flying strength	12	0.08	6	0.17
	Occurrence in drift	32	0.06	29	0.07
	Maximum crawling rate	34	0.06	28	0.07
	Swimming Ability	18	0.11	11	0.18
Morphology	All	24 (17.1)	0.11 (0.07)	15 (12.6)	0.17 (0.10)
	Attachment	10	0.20	6	0.33
	Armoring	26	0.08	14	0.14
	Shape	15	0.07	8	0.13
	Respiration	17	0.18	11	0.18
	Size at maturity	53	0.04	37	0.05
Ecology	All	55 (7.30)	0.07 (0.05)	41 (11.4)	0.09 (0.06)
	Rheophily	57	0.04	36	0.06
	Thermal preference	58	0.02	52	0.02
	Habit	45	0.11	27	0.15
	Trophic habit	62	0.11	48	0.13

i.e., one trait would not be constrained to change state given an adaptive state change in another. We tested this prediction by identifying traits that had both low statistical correlation (Fig. 3) and high degrees of lability (Table 2) and by conducting paired-comparison analyses with these traits using the Mesquite program (W. P. Maddison and D. R. Maddison. 2003. Mesquite: a modular system for evolutionary analysis, version 1.06, http://mesquiteproject.org/mesquite/mesquite.html) to examine whether a shift in state of one trait corresponded to a state shift in its paired trait. For each paired comparison, we calculated a statistical probability to test the null hypothesis that changes in these states are correlated across the phylogenetic tree (see Maddison 2000 for more details).

For the purpose of demonstration, we restricted the paired-comparison analyses to 4 traits (voltinism, occurrence in drift, thermal preference, and trophic habit) for the EPT genera. These traits often are used in traits-based studies and met our initial requirements (high lability and low statistical correlation). We removed trait states represented by only a few taxa (e.g., piercer-predators and piercer-herbivores within the trophic habit trait) from the analysis to reduce the total number of correlations investigated, and compared the remaining states of each trait against each other. States of these 4 traits were not phylogenetically correlated or were only weakly correlated for EPT taxa ($p > 0.063$ for all state × state comparisons, without Bonferroni's correction, which would greatly increase p values). This finding suggests that phylogenetic correlations (Mesquite output) and statistical correlations (Fig. 3) of our categorical traits provide similar information.

New Insights and Continuing Challenges

Traits-based approaches have a rich (though relatively recent) history in both basic and applied stream ecology and are attractive because they represent evolutionary responses to environmental selective forces that often can be quantified across broad geographic extents. The theoretical underpinnings of how various benthic invertebrate traits will respond to environmental gradients have been well established (e.g., Townsend and Hildrew 1994, Poff 1997, Statzner et al. 2001b). However, we remain limited in our ability to predict community functional composition empirically. One problem has been that investigators have focused on univariate responses of particular traits to single environmental gradients or, in cases using multivariate approaches, have ignored the FTNs of individual taxa, which often consist of a group of trait states that are closely linked evolutionarily. We have offered the beginnings of an approach for disentangling the series of traits making up individual FTNs as a way to identify which traits have the greatest potential for a predictive ecology, i.e., those with relatively low statistical correlation to other traits and with higher evolutionary lability across taxonomic groups.

Selecting what might be considered the most robust traits for use in predictive community ecology seems to require balancing 3 important constraints: 1) Ideally, traits with high evolutionary lability should be selected because they can be used for a variety of taxa. Several such traits were identified in Table 2. 2) Low statistical and phylogenetic correlations (which are inherently related) among traits are desirable to ensure statistical independence among traits and to maximize information content when multiple traits are to be used. We identified several labile traits (e.g., voltinism and trophic habit) that were statistically and phylogenetically uncorrelated. For our categorical trait states, statistical correlations provided an adequate approximation of phylogenetic constraint among trait states. The next obvious step would be to explore lability and phylogenetic/statistical correlations among trait states with more informative coding, such as quantitative values or fuzzy coding. 3) The ability to link the trait mechanistically to a specific environmental gradient (preferably one that is quantifiable) also is desirable. This quality may not be feasible for all traits with high evolutionary lability where little is known about trait response to environmental change, e.g., maximum crawling rate is not obviously related to any quantifiable environmental gradient. However, it may be achievable for such traits as voltinism, which has been reported to vary among sites having different disturbance regimes (e.g., Richards et al. 1997) in conformance to theoretical expectations (Townsend and Hildrew 1994).

Figure 5 presents a simple conceptual model that places phylogenetically labile traits into a mechanistic framework given several important environmental gradients. This model provides a way to visualize how individual traits, or combinations of traits, may change under different environmental conditions. In principle, taxa in any regional species pool could be positioned in this 3-dimensional space to provide a priori expectations of community composition in multivariate space.

The preceding discussion offers a way forward in predictive community ecology, but we raise the point that our ability to identify robust traits is currently limited by our incomplete understanding of how traits may *interact* in a given environmental context. For example, the degree to which single vs multiple traits may be involved in species replacements along the hypothetical disturbance gradient in Fig. 5 is unknown. Disturbance traits may interact with other, less labile traits to confer some resistance or resilience to environmental change, but we have limited understanding of these relationships in nature. Given this knowledge gap, we view the FTN framework as providing a basis for examining, on a taxon-by-taxon basis, how combinations of trait states may be assorted along different environmental gradients. This area is in much need of empirical research. Compiling this type of information also may help inform contemporary theoretical questions about the relationships between functional diversity and taxonomic diversity (e.g., Díaz and Cabido 2001, Petchy and Gaston 2002, Mouillot et al. 2005) or ecosystem function (e.g., Naeem and Wright 2003, Petchey et al. 2004) in biotic communities, and how these relationships may change along environmental gradients (Heino 2005, Stevens et al. 2003). Indeed, the systematic analysis of how functional traits vary along environmental gradients is a promising approach to defining the quantitative relationship between species' fundamental and realized niches, thereby allowing community ecology to become a more predictive science (McGill et al. 2006).

To achieve the full potential of a functional, traits-based ecology, we believe that several challenges must yet be met. A fundamental need exists for a more comprehensive characterization of organismal traits and a more-mechanistic understanding of organism–environment relationships (Poff 1997). For example, many of the traits available to benthic ecologists are based simply on convenience of characterization, not necessarily on some underlying functional relationship with demonstrated or inferred adaptation to the environment. Even for those traits that are most robust for predictive modeling, uncertainties arise from ontogenetic shifts in trait states, such as trophic habit, changes in mobility, etc. An unstated assumption of traits-based analyses at this time is that characterizing traits for late instars is adequate to examine organism–environment relations, but this may not always be the case.

Another assumption of current traits-based analyses is that biotic traits, i.e., those that reflect intensity of ecological interactions among organisms, are typically unimportant. For example, subtle differences in terms of resource acquisition can exist among species in the

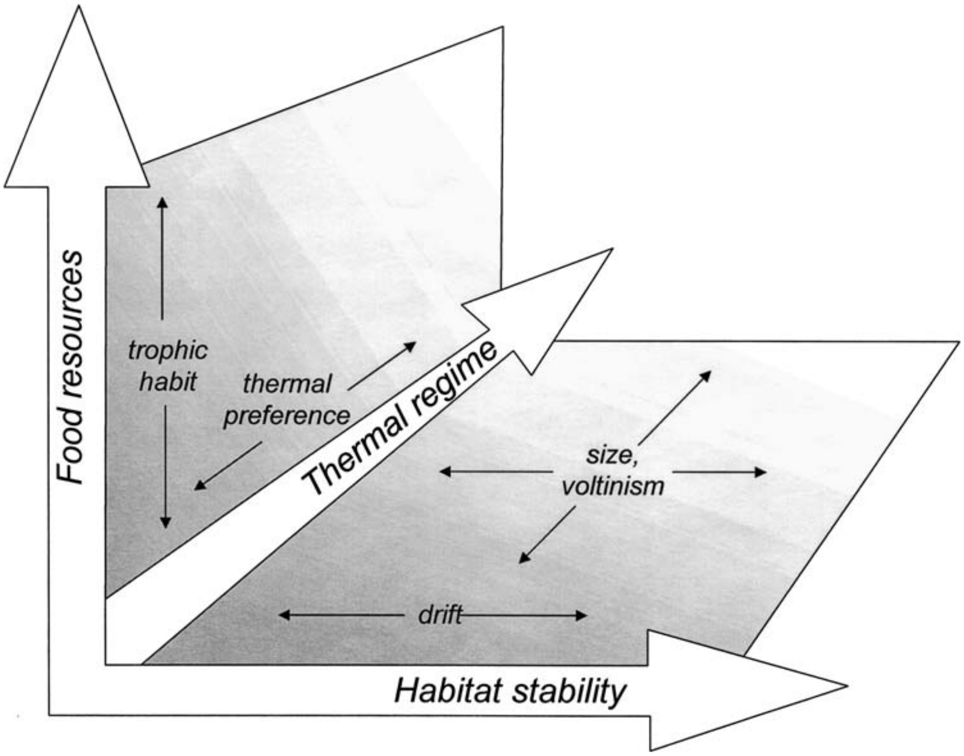

FIG. 5. Conceptual representation of how phylogentically labile traits (from Table 2) for North American lotic insects may respond along gradients of 3 dominant environmental selective forces (axes of graph) characteristic of natural stream habitats. Orthogonal axes are drawn to emphasize relative independence of these selective forces. Traits are named and associated with the environmental axis (or axes) along which that trait is predicted to respond most strongly. For environmental gradients that consist of more than one dominant selective force, combinations of traits would be expected to change, and species that possess sensitive trait states along both environmental axes will probably be most responsive.

same trophic guild (e.g., Kohler 1992), and these subtleties can vary along environmental gradients (Poff et al. 2003). Likewise, foodweb structure and ecosystem energy flow can be mediated by behavioral traits of predators and prey (e.g., McIntosh and Peckarsky 1999, Power and Dietrich 2002, Schmitz et al. 2004). Certainly, this kind of trait information is difficult to develop in general, as it typically is derived from more experimental studies; however, development of such traits could add increased resolution to predictive community ecology.

Last, even assuming that all of these biological issues can be resolved, a basic statistical challenge remains. Current multivariate analyses seeking to describe community trait composition such as RLQ analysis (Dolédec et al. 1996) and the 4th-corner method (Legendre et al. 1997) do not explicitly account for evolutionary linkage of traits; therefore, metrics derived from such analyses may not be adequate indicators of traits-based community response to environmental change. Furthermore, these approaches consider only a single trait at a time, and some can analyze only binary species data (e.g., Legendre et al. 1997). In short, new multivariate statistical methods that account for inter-trait correlations and that can be applied to multiple environmental gradients also are needed to advance a predictive traits-based ecology.

In conclusion, we hope that the approach presented here will encourage more mechanistic, traits-based analyses to advance the predictive ability of trait applications. We believe our approach for defining traits relevant to a specific environmental gradient and for reducing the number of traits (variables) to a more tractable and robust subset for analyses (by filtering out noninformative and intercorrelated/redundant traits) will be useful in many practical applications, as well as in basic stream community ecology. Furthermore, by examining how trait states are linked within various taxa (the FTN), we may gain insight into trait interactions that influence species' responses along multiple environmental gradients.

Acknowledgements

This paper represents the fruition of a long process. NLP would especially like to thank David Yount, Penny Firth, and Rosemary Mackay for encouraging the genesis of this work back in the early 1990s, as well as Chuck Hawkins, Will Clements, Margaret Palmer, Dave Allan, Bernhard Statzner, Vincent Resh, and David Rosenberg for encouraging its completion along the way. Additional comments and discussions with John Wenzel and Stan Sczytko were helpful, and the comments of 3 anonymous referees helped improve the final version of our paper. Daren Carlisle and Stephen Moulton provided support through a USGS grant toward the end of this project. Angie Moline helped with Fig. 5. We also thank various funding agencies for support of DSF (NSF graduate research fellowship), JDO (Canadian NSERC fellowship), and NKMV (USGS grant).

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Received: 16 September 2005
Accepted: 5 July 2006

APPENDIX. Trait matrix for genera, tribes, and families. Trait abbreviations and descriptions are provided in Table 1.

	Life history						Mobility					Morphology					Ecology			
Order/Family/Genus	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
COLEOPTERA																				
Dryopidae																				
Helichus	1	2	1	3	1	1	1	1	1	1	1	1	3	2	3	1	3	2	4	3
Pelonomus	1	3	1	3	1	1	1	1	1	1	1	1	3	2	3	1	2	2	2	3
Dytiscidae																				
Agabus	1	2	1	3	2	1	2	2	1	3	3	1	3	1	3	2	2	2	5	4
Hydroporus	1	2	1	3	2	1	2	2	1	3	3	1	3	1	3	2	1	2	5	4
Oreodytes	1	2	1	3	2	1	2	2	1	3	3	1	3	1	3	2	1	2	5	4
Elmidae	1	3	1	3	1	2	1	1	2	2	1	1	2	2	1	1	2	2	4	1
Haliplidae																				
Brychius	2	2	2	3	2	1	1	2	1	2	2	1	3	2	2	1	3	1	4	3
Psephenidae																				
Ectopria	1	2	2	2	1	1	1	1	1	1	1	2	3	1	2	2	3	2	4	3
Psephenus	1	2	2	2	1	1	1	1	1	1	1	2	2	1	2	2	3	2	4	3
DIPTERA																				
Athericidae																				
Atherix	2	2	2	1	1	1	1	1	1	2	1	1	2	2	1	2	2	2	3	4
Blephariceridae																				
Agathon	2	2	2	1	1	1	1	1	1	1	1	2	3	1	2	1	2	1	4	3
Bibiocephala	2	2	2	1	1	1	1	1	1	1	1	2	3	1	2	2	3	1	4	3
Blepharicera	2	2	2	1	1	1	1	1	1	1	1	2	3	1	2	1	3	1	4	3
Philorus	2	2	2	1	1	1	1	1	1	1	1	2	3	1	2	1	3	1	4	3
Ceratopogonidae	2	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	2	2	3	4
Chironomidae																				
Chironominae	3	1	2	1	2	1	2	1	3	1	1	1	1	2	2	1	1	2	1	1
Diamesinae	2	1	2	1	2	1	2	1	3	1	1	1	1	2	2	1	2	1	3	1
Orthocladiinae	2	1	2	1	2	1	2	1	3	1	1	1	1	2	2	1	2	1	1	1
Prodiamesinae	2	1	2	1	2	1	2	1	3	1	1	1	1	2	2	1	2	1	3	1
Tanypodinae	2	1	2	1	2	1	2	1	3	1	1	1	1	2	2	1	2	2	3	4
Deuterophlebiidae																				
Deuterophlebia	2	2	2	1	1	1	1	1	1	1	1	2	3	1	1	1	3	1	4	3
Empididae	2	2	2	1	2	1	1	1	1	2	1	1	1	2	1	2	2	2	3	4
Psychodidae																				
Maruina	2	1	2	1	1	1	1	1	1	1	1	2	2	1	1	1	3	1	4	3
Pericoma	2	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	2	1	1
Simuliidae	3	1	2	1	1	1	1	2	2	2	1	2	1	2	1	1	3	2	4	2
Tipulidae	2	2	1	2	1	2	1	1	1	2	1	1	1	2	2	2	2	2	3	5
Tipulidae2	2	2	1	2	1	2	1	1	1	2	1	1	1	2	2	2	2	2	1	5
EPHEMEROPTERA																				
Acanthametropodidae																				
Acanthametropus	2	2	2	2	1	1	1	1	1	3	2	1	1	2	2	1	1	1	5	4
Ametropodidae																				
Ametropus	2	1	2	1	1	1	1	1	2	1	1	1	1	1	2	1	2	1	1	2
Ameletidae																				
Ameletus	2	1	2	2	1	1	1	1	1	3	3	1	1	1	2	1	2	1	5	1

APPENDIX. Continued.

	Life history						Mobility					Morphology					Ecology			
Order/Family/Genus	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
Baetidae																				
Acentrella	3	1	1	1	1	1	1	1	2	1	3	1	1	1	2	1	2	2	5	1
Acerpenna	3	1	1	1	1	1	1	1	3	1	3	1	1	1	2	1	2	2	5	1
Apobaetis	3	1	1	1	1	1	1	1	1	1	3	1	1	1	2	1	2	2	5	1
Baetis	3	1	1	1	1	1	1	1	3	1	3	1	1	1	2	1	2	2	5	1
Callibaetis	3	1	1	1	1	1	1	1	1	2	3	1	1	1	2	1	1	2	5	1
Centroptilum/ Procloeon	3	1	1	1	1	1	1	1	1	2	3	1	1	1	2	1	2	2	5	1
Cloeodes	3	1	1	1	1	1	1	1	1	2	3	1	1	1	2	1	2	2	5	1
Camelobaetidius	3	1	1	1	1	1	1	1	3	2	3	1	1	1	2	1	1	2	5	1
Diphetor	3	1	1	1	1	1	1	1	1	2	3	1	1	1	2	1	2	2	5	1
Fallceon	3	1	1	1	1	1	1	1	3	2	3	1	1	1	2	1	2	2	5	1
Heterocloeon	3	1	1	1	1	1	1	1	1	2	3	1	1	1	2	1	3	2	5	3
Paracloeodes	3	1	1	1	1	1	1	1	1	2	3	1	1	1	2	1	1	3	5	3
Pseudocloeon	3	1	1	1	1	1	1	1	3	2	2	1	1	1	2	1	2	2	5	1
Baetiscidae																				
Baetisca	2	1	2	1	1	1	1	1	1	1	1	1	2	2	2	2	1	2	3	1
Caenidae																				
Amercaenis	2	1	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	2	3	2
Brachycercus	2	2	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	2	3	1
Caenis	3	2	2	1	1	1	1	1	1	2	2	1	1	2	2	1	1	3	3	1
Ephemeridae																				
Ephemera	1	2	1	1	1	1	1	1	1	2	2	1	1	2	2	2	1	2	1	1
Hexagenia	1	2	1	1	1	1	1	1	1	2	2	1	1	2	2	2	1	2	1	1
Litobrancha	1	2	1	1	1	1	1	1	1	2	2	1	1	2	2	2	1	1	1	1
Pentagenia	1	2	1	1	1	1	1	1	1	2	2	1	1	2	2	2	1	3	1	1
Ephemerellidae																				
Attenella	2	2	2	1	1	1	1	1	1	2	2	1	1	2	2	2	3	2	4	1
Caudatella	2	2	2	1	1	1	1	1	1	2	2	1	1	2	2	2	2	1	4	1
Caurinella	2	2	2	1	1	1	1	1	1	2	2	1	1	2	2	2	2	1	4	1
Drunella	2	2	2	1	1	1	1	1	1	2	2	1	1	2	2	2	2	2	4	3
Ephemerella	2	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	2	4	1
Eurylophella	2	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	2	4	1
Serratella	2	2	2	1	1	1	1	1	2	2	2	1	1	2	2	2	2	2	4	1
Timpanoga	2	2	2	1	1	1	1	1	2	2	2	1	1	2	2	1	2	1	4	1
Heptageniidae																				
Cinygma	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	2	2	1	4	3
Cinygmula	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	1	2	1	4	3
Epeorus	2	1	2	1	1	1	1	1	1	2	2	1	1	1	2	2	2	1	4	1
Heptagenia	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	2	2	1	4	3
Ironodes	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	2	2	2	4	3
Leucrocuta	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	2	2	1	4	3
Macdunnoa	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	1	2	2	4	3
Nixe/Ecdyonurus	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	1	2	2	4	3
Raptoheptagenia	2	1	2	1	1	1	1	1	1	2	2	1	1	1	2	1	2	1	5	4

APPENDIX. Continued.

Order/Family/Genus	Life history						Mobility					Morphology					Ecology			
	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
Rhithrogena	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	2	2	1	4	1
Maccaffertium/Stenonema	2	1	1	2	1	1	1	1	2	2	2	1	1	1	2	2	2	2	4	3
Stenacron	2	1	2	1	1	1	1	1	2	2	2	1	1	1	2	2	2	2	4	1
Isonychiidae																				
Isonychia	2	2	1	1	1	1	1	1	3	3	3	1	1	1	2	2	3	2	5	2
Leptophlebiidae																				
Choroterpes	2	1	1	2	1	1	1	1	2	2	2	1	1	1	2	1	2	3	4	1
Habrophlebia	2	1	2	1	1	1	1	1	2	1	2	1	1	1	2	1	2	1	5	1
Habrophlebiodes	2	1	2	1	1	1	1	1	2	1	2	1	1	1	2	1	2	1	5	3
Leptophlebia	2	2	1	1	1	1	1	1	2	2	2	1	1	1	2	1	3	2	5	1
Neochoroterpes	2	1	1	1	1	1	1	1	2	2	2	1	1	1	2	1	2	3	4	1
Paraleptophlebia	2	1	1	1	1	1	1	1	2	2	2	1	1	1	2	2	2	2	5	1
Thraulodes	2	1	1	1	1	1	1	1	2	2	2	1	1	1	2	2	2	3	4	1
Traverella	2	1	1	1	1	1	1	1	2	2	2	1	1	1	2	2	2	3	4	2
Metretopodidae																				
Siphloplecton	2	1	2	1	1	1	1	1	1	3	3	1	1	1	2	2	2	2	5	1
Oligoneuriidae																				
Homoeoneuria	2	2	2	1	1	1	1	1	1	3	3	1	1	1	2	1	1	2	1	2
Polymitarcyidae																				
Ephoron	2	2	1	1	1	1	1	1	1	2	2	1	1	1	2	2	2	3	1	1
Tortopus	2	2	1	1	1	1	1	1	1	2	2	1	1	1	2	2	3	2	1	1
Pseudironidae																				
Pseudiron	2	2	2	1	1	1	1	1	1	2	2	1	1	2	2	2	1	3	3	4
Potamanthidae																				
Anthopotamus	2	2	1	1	1	1	1	1	1	2	2	1	1	2	2	2	1	2	1	2
Siphlonuridae																				
Siphlonurus	2	2	1	1	1	1	1	1	2	3	3	1	1	1	2	2	1	2	5	1
Leptohyphidae																				
Leptohyphes	2	1	1	1	1	1	1	1	2	2	2	1	1	2	2	1	1	3	4	1
Tricorythodes	2	1	1	1	1	1	1	1	3	2	2	1	1	2	2	1	1	2	3	1
HEMIPTERA																				
Belostomatidae																				
Abedus	2	1	2	2	2	2	2	2	1	3	3	1	3	1	3	3	1	3	2	4
Belostoma	2	1	2	3	2	2	2	2	1	3	3	1	3	1	3	3	1	3	2	4
Corixidae	3	1	2	3	2	2	2	2	1	3	3	1	3	1	3	1	1	2	5	3
Gerridae																				
Aquarius	3	1	2	3	2	2	1	1	1	3	3	1	1	2	3	2	1	2	6	4
Gerris	3	1	2	3	2	2	1	1	1	3	3	1	1	2	3	2	1	2	6	4
Metrobates	2	1	2	3	2	2	1	1	1	3	3	1	1	2	3	1	2	2	6	4
Rheumatobates	2	1	2	3	2	2	1	1	1	3	3	1	1	2	3	1	1	2	6	4
Trepobates	2	1	2	3	2	2	1	1	1	3	3	1	1	2	3	1	1	2	6	4
Nepidae																				
Curicta	2	2	1	3	2	2	1	1	1	3	1	1	2	2	3	3	1	2	2	4
Nepa	2	2	1	3	2	2	1	1	1	3	1	1	2	2	3	3	1	2	2	4
Veliidae																				
Microvelia	3	1	2	3	2	2	1	1	1	3	3	1	1	2	3	1	1	2	6	4

APPENDIX. Continued.

	Life history						Mobility					Morphology					Ecology			
Order/Family/Genus	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
Rhagovelia	3	1	2	3	2	2	1	1	1	3	3	1	1	2	3	1	2	2	6	4
LEPIDOPTERA																				
Pyralidae																				
Petrophila (*Paragyractis*)	2	2	2	1	1	1	1	1	1	1	1	2	2	2	2	2	3	2	4	3
MEGALOPTERA																				
Corydalidae																				
Corydalus	1	2	2	2	1	1	1	1	1	3	1	1	2	2	1	3	2	2	4	4
Nigronia	1	2	2	2	1	1	1	1	1	3	1	1	2	2	1	3	2	2	4	4
Sialidae																				
Sialis	2	2	2	2	1	1	1	1	1	3	1	1	2	2	1	2	2	2	1	4
NEUROPTERA																				
Sisyridae																				
Climacia	2	2	2	2	1	1	1	1	1	3	1	1	2	2	1	1	2	2	2	4
Sisyra	2	2	2	2	1	1	1	1	1	3	1	1	2	2	1	1	2	2	2	4
ODONATA																				
Aeshnidae																				
Aeshna	1	2	2	3	1	1	2	2	1	3	3	1	2	2	2	3	2	2	2	4
Basiaeschna	1	2	2	3	1	1	2	2	1	3	3	1	2	2	2	3	1	2	2	4
Boyeria	1	2	2	3	1	1	2	2	1	3	3	1	2	2	2	3	2	2	2	4
Epiaeschna	1	2	2	3	1	1	2	2	1	3	3	1	2	2	2	3	2	2	2	4
Nasiaeschna	1	2	2	3	1	1	2	2	1	3	3	1	2	2	2	3	3	2	2	4
Calopterygidae																				
Calopteryx	1	2	2	2	1	1	1	2	1	3	2	1	1	1	2	3	2	2	2	4
Hetaerina	1	2	2	2	1	1	1	2	1	3	2	1	1	1	2	3	2	2	2	4
Corduliidae																				
Didymops	1	2	2	3	1	1	2	2	1	3	1	1	2	2	2	3	2	2	3	4
Epicordulia	1	2	2	3	1	1	2	2	1	3	2	1	2	2	2	3	1	2	3	4
Epitheca	1	2	2	3	1	1	2	2	1	3	2	1	2	2	2	3	1	2	2	4
Helocordulia	1	2	2	3	1	1	2	2	1	3	2	1	2	2	2	2	1	2	3	4
Neurocordulia	1	2	2	3	1	1	2	2	1	3	2	1	2	2	2	2	1	2	2	4
Somatochlora	1	2	2	3	1	1	2	2	1	3	2	1	2	2	2	3	1	2	3	4
Coenagrionidae																				
Argia	2	2	2	2	1	1	1	1	1	3	2	1	1	1	1	2	2	2	4	4
Chromagrion	2	2	2	2	1	1	1	1	1	3	2	1	1	1	1	2	3	2	2	4
Coenagion	2	2	2	2	1	1	1	1	1	3	2	1	1	1	1	2	2	2	2	4
Enallagma	2	2	2	2	1	1	1	1	1	3	2	1	1	1	1	2	1	2	2	4
Hesperagrion	2	2	2	2	1	1	1	1	1	3	2	1	1	1	1	2	1	2	2	4
Ischnura	2	2	2	2	1	1	1	1	1	3	2	1	1	1	1	2	1	2	2	4
Cordulegastridae																				
Cordulegaster	2	2	2	3	1	1	2	2	1	3	2	1	2	2	2	2	1	2	1	4
Gomphidae																				
Aphylla	1	2	2	3	1	1	2	2	1	3	2	1	2	2	2	3	2	2	1	4
Arigomphus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	2	1	4
Dromogomphus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	2	1	4

APPENDIX. Continued.

Order/Family/Genus	Life history						Mobility					Morphology					Ecology			
	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
Erpetogomphus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	3	1	2	1	4
Gomphus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	2	1	4
Hagenius	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	2	3	4
Lanthus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	1	1	4
Octogomphus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	3	1	1	1	4
Ophiogomphus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	2	1	4
Phyllogomphoides	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	3	1	2	1	4
Progomphus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	2	1	4
Stylogomphus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	2	1	4
Stylurus	1	2	2	3	1	1	1	2	1	3	2	1	2	2	2	2	1	2	1	4
Lestidae																				
Archilestes	2	1	2	2	1	1	1	1	1	3	2	1	1	1	1	3	1	2	2	4
Lestes	2	1	2	2	1	1	1	1	1	3	2	1	1	1	1	3	1	2	2	4
Libellulidae																				
Macromia	1	2	2	3	1	1	2	2	1	3	1	1	2	2	2	3	2	2	3	4
PLECOPTERA																				
Capniidae																				
Allocapnia	2	1	2	1	1	2	1	1	2	2	2	1	1	2	1	1	2	2	4	5
Capnia	2	1	2	1	1	2	1	1	2	2	2	1	1	2	1	1	2	1	3	5
Capnura	2	1	2	1	1	2	1	1	1	2	2	1	1	2	1	1	2	2	3	5
Eucapnopsis	2	1	2	1	1	2	1	1	1	2	2	1	1	2	1	1	2	1	3	5
Isocapnia	2	1	2	1	1	2	1	1	1	2	2	1	1	2	1	1	3	1	3	5
Mesocapnia	2	1	2	1	1	2	1	1	1	2	2	1	1	2	1	1	2	2	3	5
Nemocapnia	2	1	2	1	1	2	1	1	1	2	2	1	1	2	1	1	2	3	3	5
Paracapnia	2	1	2	1	1	2	1	1	1	2	2	1	1	2	1	1	2	1	3	5
Utacapnia	2	1	2	1	1	2	1	1	1	2	2	1	1	2	1	1	2	1	3	5
Chloroperlidae																				
Alaskaperla	2	2	2	2	1	1	1	1	1	2	2	1	1	2	1	2	3	1	4	4
Alloperla	2	2	2	2	1	1	1	1	2	2	2	1	1	2	1	2	2	1	4	1
Bisancora	2	2	2	2	1	1	1	1	1	2	2	1	1	2	1	1	2	2	4	1
Haploperla	2	2	2	2	1	1	1	1	3	2	2	1	1	2	1	1	2	2	4	4
Kathroperla	2	2	2	2	1	1	1	1	1	2	2	1	2	2	1	3	3	1	4	1
Paraperla	2	2	2	2	1	1	1	1	1	2	2	1	2	2	1	2	3	1	4	4
Plumiperla	2	2	2	2	1	1	1	1	2	2	2	1	1	2	1	1	2	1	4	1
Suwallia	2	2	2	2	1	1	1	1	2	2	2	1	1	2	1	2	2	2	4	4
Sweltsa	1	2	2	2	1	1	1	1	2	2	2	1	1	2	1	2	2	2	4	4
Triznaka	2	2	2	2	1	1	1	1	2	2	2	1	1	2	1	2	2	1	4	4
Utaperla	2	2	2	2	1	1	1	1	1	2	2	1	1	2	1	2	2	1	4	4
Leuctridae																				
Despaxia	2	1	2	1	1	1	1	1	2	2	2	1	1	2	1	1	2	1	3	5
Leuctra	2	1	2	1	1	1	1	1	2	2	2	1	1	2	1	1	2	2	3	5
Moselia	2	1	2	1	1	1	1	1	2	2	2	1	1	2	1	1	2	2	3	5
Paraleuctra	2	1	2	1	1	2	1	1	2	3	2	1	1	2	1	1	2	2	3	5
Perlomyia	2	1	2	1	1	2	1	1	2	2	2	1	1	2	1	1	2	1	3	5
Zealeuctra	2	1	2	1	1	2	1	1	2	2	2	1	1	2	1	1	2	1	3	5
Nemouridae																				
Amphinemura	2	1	2	1	1	2	1	1	2	1	2	1	1	2	2	1	2	2	3	5
Malenka	2	1	2	1	1	1	1	1	2	1	2	1	1	2	2	1	2	2	3	5

APPENDIX. Continued.

	Life history						Mobility					Morphology					Ecology			
Order/Family/Genus	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
Nemoura	2	1	2	1	1	2	1	1	2	1	2	1	1	2	1	1	2	1	3	5
Paranemoura	2	1	2	1	1	1	1	1	2	1	2	1	1	2	1	1	2	1	3	5
Podmosta	2	1	2	1	1	1	1	1	1	1	2	1	1	2	1	1	2	1	3	5
Prostoia	2	1	2	1	1	2	1	1	2	1	2	1	1	2	1	1	2	1	3	5
Shipsa	2	1	2	1	1	2	1	1	2	1	2	1	1	2	1	1	2	2	3	5
Soyedina	2	1	2	1	1	2	1	1	1	1	2	1	1	2	1	1	2	1	3	5
Visoka	2	1	2	1	1	1	1	1	1	1	2	1	1	2	2	1	2	1	3	5
Zapada	1	1	2	1	1	1	1	1	2	1	2	1	1	2	2	1	2	1	3	5
Perlidae																				
Acroneuria	2	2	1	2	1	1	2	2	1	3	2	1	2	1	2	3	3	2	4	4
Agnetina	1	2	1	2	1	1	2	2	1	3	2	1	2	1	2	3	3	2	4	4
Attaneuria	1	3	2	2	1	1	2	2	1	3	2	1	2	1	2	3	3	3	4	4
Beloneuria	1	3	2	2	1	1	2	1	1	3	2	1	2	1	2	3	3	1	4	4
Calineuria	1	2	1	2	1	1	2	2	1	3	2	1	2	1	2	3	3	2	4	4
Claassenia	1	3	1	2	1	1	2	2	1	3	2	1	2	1	2	3	3	1	4	4
Doroneuria	1	2	2	2	1	1	2	1	1	3	2	1	2	1	2	3	3	1	4	4
Eccoptura	2	2	2	2	1	1	2	2	1	3	2	1	2	1	2	3	3	1	4	4
Hansonoperla	2	2	2	2	1	2	1	1	1	3	2	1	2	1	2	3	3	1	4	4
Hesperoperla	1	3	2	2	1	1	2	2	1	3	2	1	2	1	2	3	3	1	4	4
Neoperla	2	2	1	2	1	1	2	2	1	3	2	1	2	1	2	2	3	1	4	4
Paragnetina	1	3	1	2	1	2	2	2	1	3	2	1	2	1	2	2	3	2	4	4
Perlesta	2	2	1	2	1	1	2	2	1	3	2	1	2	1	2	3	2	2	4	4
Perlinella	2	2	2	2	1	2	2	2	1	3	2	1	2	1	2	3	2	2	4	4
Perlodidae																				
Calliperla	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	2	2	2	4	4
Clioperla	2	2	2	2	1	1	2	1	1	2	2	1	2	1	1	2	2	1	4	4
Cascadoperla	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	2	3	2	4	4
Cultus	2	2	2	2	1	1	1	1	1	3	2	1	2	1	1	2	3	1	4	4
Diploperla	2	2	2	2	1	1	1	1	1	3	2	1	2	1	1	2	3	1	4	4
Diura	2	2	2	2	1	1	1	1	1	3	2	1	2	1	1	2	3	2	4	3
Frisonla	2	2	2	2	1	1	1	1	1	3	2	1	2	1	1	2	3	1	4	4
Helopicus	2	2	2	2	1	1	2	1	1	3	2	1	2	1	1	3	3	1	4	4
Hydroperla	2	2	2	2	1	1	2	1	1	3	2	1	2	1	1	3	2	1	4	4
Isoperla	2	2	2	1	1	2	1	1	2	3	2	1	2	2	1	2	2	2	4	4
Isogenoides	2	2	2	2	1	1	2	1	1	3	2	1	2	1	1	3	2	2	4	4
Kogotus	2	2	2	2	1	1	1	1	1	3	2	1	2	1	1	2	3	1	4	4
Malirekus	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	3	2	1	4	4
Megarcys	2	2	2	2	1	1	1	1	1	2	2	1	2	1	2	3	3	1	4	4
Oroperla	2	2	2	2	1	1	1	1	1	2	2	1	2	1	2	3	3	1	4	4
Osobenus	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	2	3	1	4	4
Pictetiella	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	3	3	1	4	4
Perlinodes	2	2	2	2	1	1	1	1	1	2	2	1	2	1	2	3	3	1	4	4
Remenus	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	2	2	1	4	4
Rickera	2	2	2	2	1	2	1	1	1	2	2	1	2	2	1	2	2	1	4	4
Setvena	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	3	2	1	4	4

APPENDIX. Continued.

	Life history						Mobility					Morphology					Ecology			
Order/Family/Genus	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
Skwala	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	3	3	1	4	4
Susulus	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	3	2	1	4	4
Yugus	2	2	2	2	1	1	1	1	1	2	2	1	2	1	1	3	2	1	4	4
Pteronarcyidae																				
Pteronarcys	1	2	2	3	1	1	2	2	2	3	1	1	3	2	2	3	2	1	4	5
Pteronarcella	1	2	2	2	1	1	1	1	1	2	1	1	2	2	2	2	2	2	4	5
Taeniopterygidae																				
Bolotoperla	2	1	2	1	1	2	1	1	1	1	2	1	1	2	1	2	2	2	3	3
Doddsia	2	1	2	1	1	2	1	1	1	2	2	1	1	2	1	2	2	1	3	3
Oemopteryx	2	1	2	1	1	2	1	1	2	2	2	1	1	2	1	2	2	1	3	3
Strophopteryx	2	1	2	1	1	2	1	1	2	2	2	1	1	2	1	2	2	1	3	3
Taeniopteryx	2	1	2	1	1	2	1	1	1	1	2	1	1	2	2	2	2	2	3	5
Taenionema	2	1	2	1	1	2	1	1	2	2	2	1	1	2	1	2	2	1	3	3
TRICHOPTERA																				
Apataniidae																				
Allomyia	2	2	2	2	1	1	1	1	1	2	1	2	3	2	1	2	3	1	4	3
Moselyana	2	2	2	2	1	1	1	1	1	2	1	2	3	2	1	2	3	1	3	1
Pedomoecus	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	3	1	4	3
Brachycentridae																				
Adicrophleps	2	2	2	2	1	1	1	1	1	1	1	3	3	2	1	2	3	1	4	5
Amiocentrus	2	2	2	2	1	1	1	1	1	1	1	3	3	2	2	2	3	1	4	1
Brachycentrus	2	2	2	2	1	1	1	1	1	1	1	3	3	2	2	2	3	2	4	2
Micrasema	2	2	2	2	1	1	1	1	1	1	1	3	3	2	2	1	3	2	4	3
Calamoceratidae																				
Heteroplectron	2	2	2	2	1	1	1	1	1	1	1	2	3	2	2	2	2	1	3	5
Phylloicus	2	2	2	2	1	1	1	1	1	1	1	2	2	2	2	2	2	1	3	5
Glossosomatidae																				
Agapetus	2	2	2	2	1	2	1	1	1	2	1	1	3	2	1	1	3	1	4	3
Anagapetus	2	2	2	2	1	1	1	1	1	2	1	1	3	2	1	1	3	1	4	3
Culoptila	2	2	2	2	1	1	1	1	1	2	1	1	3	2	1	1	3	1	4	3
Glossosoma	2	2	2	2	1	1	1	1	1	2	1	1	3	2	1	1	3	2	4	3
Matrioptila	2	2	2	2	1	1	1	1	1	2	1	1	3	2	1	1	3	2	4	3
Protoptila	2	2	2	2	1	1	1	1	1	2	1	1	3	2	1	1	3	1	4	3
Goeridae																				
Goeracea	2	2	2	2	1	1	1	1	1	1	1	1	3	2	1	2	3	1	4	3
Goera	2	2	2	2	1	1	1	1	1	1	1	1	3	2	2	2	3	1	4	3
Hydroptilidae																				
Agraylea	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	2	2	2	3
Alisotrichia	2	2	2	1	1	1	2	1	1	1	1	2	2	1	2	1	2	2	4	3
Dibusa	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	2	2	4	3
Hydroptila	2	2	2	1	1	1	2	1	2	1	1	2	2	1	2	1	2	2	4	3
Ithytrichia	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	3	2	4	3
Leucotrichia	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	3	2	4	3
Mayatrichia	2	2	2	1	1	1	2	1	2	1	1	2	2	1	1	1	3	3	4	3
Neotrichia	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	3	2	4	3
Ochrotrichia	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	2	2	4	1

Appendix. Continued.

Order/Family/Genus	Life history						Mobility					Morphology					Ecology			
	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
Orthotrichia	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	2	2	4	3
Oxyethira	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	2	2	2	3
Paucicalcaria	2	2	2	1	1	1	2	1	1	1	1	2	2	1	2	1	2	2	4	3
Stactobiella	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	2	2	4	5
Zumatrichia	2	2	2	1	1	1	2	1	1	1	1	2	2	1	1	1	2	2	4	3
Helicopsychidae																				
Helicopsyche	2	2	2	2	1	2	2	1	1	2	1	2	3	2	2	1	3	2	4	3
Hydropsychidae																				
Arctopsyche	2	2	2	2	1	1	1	1	1	2	1	2	1	2	2	2	3	1	4	2
Ceratopsyche	2	2	2	2	2	1	2	2	2	2	1	2	1	2	2	2	3	2	4	2
Cheumatopsyche	2	2	2	2	1	1	2	2	2	2	1	2	1	2	2	2	3	2	4	2
Diplectrona	2	2	2	2	1	1	1	1	1	2	1	2	1	2	2	2	3	1	4	2
Homoplectra	2	2	2	2	1	1	1	1	1	2	1	2	1	2	2	2	3	1	4	2
Hydropsyche	2	2	2	2	2	1	2	2	2	2	1	2	1	2	2	2	3	2	4	2
Macrostemum	2	2	2	2	1	1	2	2	2	2	1	2	1	2	2	2	3	3	4	2
Oropsyche	2	2	2	2	1	1	1	1	1	2	1	2	1	2	2	2	3	1	4	2
Parapsyche	2	2	2	2	1	1	1	1	1	2	1	2	1	2	2	2	3	1	4	2
Potamyia	2	2	2	2	1	1	2	2	2	2	1	2	1	2	2	2	3	2	4	2
Smicridea	2	2	2	2	1	1	2	2	2	2	1	2	1	2	2	2	3	3	4	2
Leptoceridae																				
Ceraclea	2	2	2	2	1	1	2	1	1	1	2	2	2	2	2	2	2	2	3	1
Nectopsyche	2	2	2	2	1	1	2	1	1	1	2	2	2	2	2	2	2	2	2	3
Oecetis	2	2	2	2	1	1	2	1	1	1	2	2	2	2	2	2	2	2	4	4
Setodes	2	2	2	2	1	1	2	1	1	1	2	2	2	2	2	1	2	1	3	1
Limnephilidae																				
Allocosmoecus	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	2	1	3	3
Amphicosmoecus	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	2	1	3	5
Apatania	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	3	1	4	3
Asynarchus	2	2	2	1	1	2	1	1	1	1	1	2	2	2	2	2	2	1	2	5
Chyranda	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	1	1	3	5
Cryptochia	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	3	1	3	3
Dicosmoecus	1	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	3	1	3	3
Ecclisocosmoecus	1	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	3	1	1	3
Ecclisomyia	1	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	3	1	4	1
Eocosmoecus	1	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	2	1	3	5
Hesperophylax	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	2	2	3	5
Homophylax	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	2	1	4	5
Hydatophylax	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	1	2	3	5
Onocosmoecus	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	1	1	3	5
Pycnopsyche	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	2	1	3	5
Pseudostenophylax	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	2	2	3	5
Philocasca	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	2	1	4	5
Platycentropus	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	3	1	2	2	5
Psychoglypha	2	2	2	3	1	1	1	1	1	2	1	2	3	2	2	3	3	1	3	1
Psychoronia	2	2	2	2	1	1	1	1	1	2	1	2	3	2	2	2	2	1	3	5

APPENDIX. Continued.

	Life history						Mobility					Morphology					Ecology			
Order/Family/Genus	Volt	Devl	Sync	Life	Exit	Desi	Disp	Flgt	Drft	Crwl	Swim	Atch	Armr	Shpe	Resp	Size	Rheo	Ther	Habi	Trop
Lepidostomatidae																				
Lepidostoma	2	2	2	2	1	1	1	1	1	1	1	1	1	2	2	2	2	1	2	5
Theliopsyche	2	2	2	2	1	1	1	1	1	1	1	1	1	2	2	1	3	1	2	5
Odontoceridae																				
Pseudogoera	2	2	2	2	1	1	1	1	1	1	1	2	3	2	2	2	2	1	3	4
Psilotreta	2	2	2	2	1	1	1	1	1	1	1	2	3	2	2	2	2	3	3	3
Philopotamidae																				
Chimarra	2	2	2	2	1	1	1	1	1	1	1	2	1	2	1	1	3	2	4	2
Dolophilodes	2	2	2	2	1	1	1	1	1	1	1	2	1	2	1	1	3	2	4	2
Wormaldia	2	2	2	2	1	1	1	1	1	1	1	2	1	2	1	1	3	2	4	2
Polycentropodidae																				
Cyrnellus	2	2	2	2	1	1	2	1	1	1	1	2	1	2	1	2	3	2	4	2
Neureclipsis	3	2	2	2	1	1	2	1	1	1	1	2	1	2	1	2	3	2	4	2
Nyctiophylax	2	2	2	2	1	1	2	1	1	1	1	2	1	2	1	2	2	2	4	4
Polycentropus	2	2	2	2	1	1	2	1	1	1	1	2	1	2	1	2	3	2	4	4
Psychomyiidae																				
Lype	2	2	2	2	1	1	1	1	1	1	1	2	1	2	1	1	3	2	4	3
Psychomyia	2	2	2	2	1	1	2	1	1	1	1	2	1	2	1	1	3	2	4	1
Rhyacophilidae																				
Rhyacophila	2	2	2	2	1	1	1	1	1	3	2	2	2	2	1	2	3	2	4	4
Rossianidae																				
Rossiana	2	2	2	2	1	1	1	1	1	2	2	3	3	2	2	2	3	1	4	3
Sericostomatidae																				
Gumaga	2	2	2	2	1	1	1	1	1	2	1	2	2	2	2	2	3	1	3	5
Uenoidae																				
Farula	2	2	2	2	1	1	1	1	1	1	2	2	2	2	2	1	3	1	4	3
Neothremma	2	2	2	2	1	1	1	1	1	1	2	2	2	2	2	1	3	1	4	3
Neophylax	2	2	2	2	1	1	1	1	1	1	2	2	3	2	2	2	3	2	4	3
Oligophlebodes	2	2	2	2	1	1	1	1	1	1	2	2	3	2	2	2	3	1	4	3