BioOne COMPLETE

Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science

Authors: Verberk, W. C. E. P., van Noordwijk, C. G. E., and Hildrew, A. G.

Source: Freshwater Science, 32(2) : 531-547

Published By: Society for Freshwater Science

URL: https://doi.org/10.1899/12-092.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Freshwater Science, 2013, 32(2):531–547
© 2013 by The Society for Freshwater Science
DOI: 10.1899/12-092.1
Published online: 2 April 2013

PERSPECTIVES

This section of the journal is for the expression of new ideas, points of view, and comments on topics of interest to aquatic scientists. The editorial board invites new and original papers as well as comments on items already published in Freshwater Science (or J-NABS). Format and style may be less formal than conventional research papers; massive data sets are not appropriate. Speculation is welcome if it is likely to stimulate worthwhile discussion. Alternative points of view should be instructive rather than merely contradictory or argumentative. All submissions will receive the usual reviews and editorial assessments.

Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science

W. C. E. P. Verberk[1,2,3,7], C. G. E. van Noordwijk[1,2,4,8], AND A. G. Hildrew[5,6,9]

[1] *Department of Animal Ecology and Ecophysiology, Institute of Water and Wetland Research, Radboud University Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands*
[2] *Bargerveen Foundation, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands*
[3] *Marine Biology and Ecology Research Centre, University of Plymouth, Davy Building, Drake Circus, Plymouth PL4 8AA, UK*
[4] *Department of Biology, Terrestrial Ecology Unit, Ghent University, K. L. Ledeganckstraat 35, B-9000 Ghent, Belgium*
[5] *School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK*
[6] *Freshwater Biological Association, The Ferry Landing, Ambleside, Cumbria LA22 OLP, UK*

Abstract. The use of species traits in basic and applied ecology is expanding rapidly because trait-based approaches hold the promise to increase our mechanistic understanding of biological responses. Such understanding could transform descriptive field studies in community ecology into predictive studies. Currently, however, trait-based approaches often fail to reflect species–environment relationships adequately. The difficulties have been perceived mainly as methodological, but we suggest that the problem is more profound and touches on the fundamentals of ecology and evolution. Selection pressures do not act independently on single traits, but rather, on species whose success in a particular environment is controlled by many interacting traits. Therefore, the adaptive value of a particular trait may differ across species, depending on the other traits possessed by the species and the constraints of its body plan. Because of this context-dependence, trait-based approaches should take into account the way combinations of traits interact and are constrained within a species. We present a new framework in which trade-offs and other interactions between biological traits are taken as a starting point from which to develop a better mechanistic understanding of species occurrences. The framework consists of 4 levels: traits, trait interactions, trait combinations, and life-history strategies, in a hierarchy in which each level provides the building blocks for the next. Researchers can contribute knowledge and insights at each level, and their contributions can be verified or falsified using logic, theory, and empirical data. Such an integrated and transparent framework can help fulfill the promise of traits to transform community ecology into a predictive science.

Key words: biomonitoring, causal mechanism, filter, functional group, functional trait, life-history strategy, macroinvertebrates, natural selection, phylogeny, species sorting, trade-off, trait syndrome.

[7] E-mail addresses: wilco@aquaticecology.nl
[8] t.vannoordwijk@science.ru.nl
[9] a.hildrew@qmul.ac.uk

Ecologists seek to understand the relationships between organisms and their environment. How can spatial and temporal differences in species assemblages be explained by the varying abiotic and biotic conditions

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

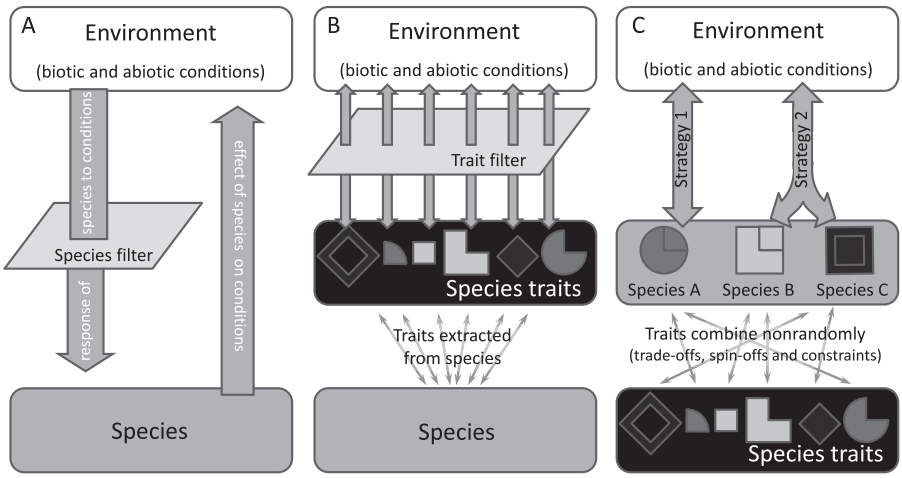


FIG. 1. Schematic representation of the taxon-based (A) and trait-based (B, C) approaches to understanding the differences in species assemblages resulting from abiotic and biotic conditions. Trait-based approaches are based on the notion that the habitat acts as a templet that mechanistically explains how major environmental drivers influence the fitness of the species, depending on the combination of traits they possess. Current trait-based approaches (B) do not incorporate relationships between traits, and traits are analyzed without considering how they are embedded within species. The proposed trait-based approach (C) stresses trait interactions and recognizes that selection pressures operate on whole organisms carrying multiple traits. Traits are important factors underlying species–environment relationships, but analyses should be focused on species grouped by life-history strategies and the relationships between strategies and the environment. A given strategy is characterized by a set of coevolved traits that enables a species to overcome similar environmental problems (e.g., species B and C). Thus, strategies condense species-rich assemblages into a few meaningful, easily interpreted relationships.

in their environment? Taxon-based approaches compare species assemblages (e.g., taxonomic composition, species richness, abundance measures) and relate them to differences in environmental conditions (Fig. 1A). They may accurately describe differences between localities in space or time. However, they do not provide mechanistic understanding because empirically fitted species–environment relationships need not reflect causation (Weiner 1995, Lawton 1999). In addition, differences in taxonomic composition between distant study sites may reflect regional differences in species pools rather than environmental differences (Lamouroux et al. 2002, Horrigan and Baird 2008). As such, empirically fitted species–environment relationships may be accurate only within a specific context or region (Lancaster et al. 2009, Hawkins et al. 2010).

Trait-based approaches focus on the attributes of a species that govern its ability to deal with environmental problems and opportunities (Fig. 1B). On ecological time scales, species sorting gives rise to differences in community structure because species are eliminated if they lack suitable adaptations whereas, on evolutionary time scales, natural selection may change the traits themselves (Webb et al. 2010). Thus, in species sorting and natural selection, traits govern the performance of the individual species in a given environment, albeit at different time scales.

Two key advantages of trait-based over taxon-based approaches are: 1) improved mechanistic understanding of species–environment relationships (Keddy 1992, Townsend and Hildrew 1994, Kearney and Porter 2009) and, consequently, 2) greater generality of such relationships because of applicability across regions. Trait-based approaches may further facilitate regional comparisons because they rely on commonality in traits rather than species identity. Because of this potential, the use of species traits in basic and applied ecology is a rapidly expanding research area (Dolédec and Statzner 2010, Menezes et al. 2010, Webb et al. 2010, VandeWalle et al. 2010).

The attributes of a species are usually termed biological species traits, or simply traits, and they relate to physiological, morphological, and life-history features that are inherent to the organism and, therefore, can be measured at the individual level without making reference to the external environment (Violle et al. 2007). This definition of traits excludes species-specific descriptors of habitat use by a species (e.g., preferences for flow velocity, substratum, or pH), which are sometimes referred to as ecological traits in the literature on aquatic invertebrates (Usseglio-Polatera et al. 2000). The preference of a species is not a trait or attribute in itself, but rather the result of how a trait has interacted with environmental conditions (e.g.,

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

suckers are the attribute that helps Blephariceridae larvae deal with high flow, underlying their ecological trait of rheophily). Labeling these habitat preferences as traits is somewhat misleading because preferences are essentially the species–environment relationships that one seeks to understand in trait-based approaches.

Trait-based approaches hold the promise of transforming descriptive field studies into a predictive science of communities because traits capture the causal mechanisms underlying species–environment relationships. However, trait-based approaches have not yet fully delivered on this promise. Progress has been made in using traits to calculate species relative abundances in a specific habitat from prior knowledge of the aggregated trait values of the community, by using a principle of maximizing entropy (e.g., Shipley et al. 2006), but here we are interested in understanding and predicting the distribution of particular species along an environmental gradient based on the traits it possesses without such prior knowledge.

Two principal problems in trait-based approaches are low discriminatory power and low mechanistic understanding. Many investigators have found differences in trait representation when comparing species assemblages across environmental gradients (e.g., Statzner et al. 1994, Townsend et al. 1997, Bonada et al. 2007). However, such studies typically represent trait values as assemblage means and the differences in representation of traits across assemblages are often small (e.g., Statzner et al. 2001). The small magnitude of differences in trait values across gradients gives rise to the 1st problem of low discriminatory power. At the same time, the ability of trait-based approaches to provide a mechanistic understanding of biological responses appears limited (e.g., Webb et al. 2010). Testing hypotheses by making a priori predictions has had some success (Dolédec and Statzner 2008, Pollard and Yuan 2010), but in general, consistently strong traits–environment relationships are uncommon (Statzner and Bêche 2010). Instead, the complex patterns of environmental conditions, species occurrences, and species traits are described first and a causal link is inferred a posteriori (i.e., hypothesis generation) (Usseglio-Polatera et al. 2000, Ilg and Castella 2006).

The limited success of current trait-based approaches suggests that the data on species traits or the way in which they are currently analyzed do not reflect adequately the species–environment relationship. Here, we analyze the causes underlying these 2 problems. We argue that a better recognition of interactions between traits and consideration of their adaptive value is a central building block needed to move the field forward. An evolutionary perspective of how traits have coevolved in response to natural selection would allow a better understanding of the current match between species and their environment (species sorting). We present an open and flexible conceptual framework based on these fundamentals of ecology and evolution that we think can remedy many short-comings of current trait-based approaches. We identify the main challenges that must be overcome and outline the various levels at which researchers can contribute to render community ecology more predictive. The examples upon which we draw are mainly from ecological studies in freshwaters that focus on macroinvertebrates because aquatic invertebrates are 1 of 2 groups for which trait approaches are best developed (the other is terrestrial plants). Because of this advanced position, challenges and limitations may be more apparent in this group, but their resolution is likely to be relevant to other fields and groups as well.

Why Have Current Trait-Based Approaches Performed Relatively Poorly?

The low discriminatory power and poor mechanistic understanding of current trait-based approaches have been related to: 1) lack of knowledge regarding which traits are most important and how they are related to the scale on which species use their habitat, 2) failure to take into account linkages and interactions among traits, and 3) functional equivalence of alternative suites or combinations of traits (see Resh et al. 1994, Statzner et al. 1997, Verberk et al. 2008b, van Noordwijk et al. 2012). Attempts to resolve these issues have been mainly methodological in nature (Table 1), and investigators have proposed that future advances will require improved methods. Dolédec and Statzner (2010) saw new statistical techniques as the key to improved prediction of how ecological integrity differs between natural and impacted conditions, Webb et al. (2010) argued that new model development is critical for exploiting fully the power of trait-based approaches, and Menezes et al. (2010) called for development of methodological approaches to diminish the effects of trade-offs and alternative combinations of traits.

We do not deny the existence of methodological obstacles, but we think the main problem of how to analyze multiple, interacting traits extends beyond methods. The trait-based approach is rooted in the habitat templet theory of Southwood (1977), which holds that the habitat provides the templet on which evolution forges characteristic life-history strategies (through natural selection). As a result, major

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 1. Methodological innovations proposed to circumvent some of the problems associated with current trait-based approaches and their shortcomings.

Problem	Solution (source)	Description	Shortcoming
How to deal with heterogeneity in biological data, i.e., differences in level of detail across species and lack of data on certain traits for certain groups of taxa (arises particularly when considering species differing in body plan)	Fuzzy coding (Chevenet et al. 1994)	A common coding method to code and arrange qualitative and quantitative information	1. Focuses on absolute differences in trait categories, rather than relative differences 2. Does not incorporate constraints set by a species' body plan on the set of possible trait categories 3. Linkages among trait categories are not made explicit (e.g., through trait interactions), but arise indirectly through species having affinities for multiple trait categories)
How to analyze 3 matrices simultaneously: L (species × sites); R (environmental data × sites); Q (species × traits)	RLQ analysis (Dolédec et al. 1996, Dray and Legendre 2008)	A statistical technique developed to incorporate species traits (Q matrix) into the analysis of species–environment relationships	Does not accommodate a priori linkages between traits arising from phylogeny or from interactions between traits (trade-offs, spin-offs, body-plan constraints)
Statistical nonindependence of closely related species	Phylogenetic independent contrasts (Felsenstein 1985) or focus analyses towards labile traits (Poff et al. 2006)	A method to use phylogenetic information to transform mean values for species into values that are statistically independent; direct analysis toward traits that are unconstrained by phylogenic relationships on the basis that environmental filtering should have more predictable effects on those traits	1. May overlook significant information that is associated with phylogeny; traits may be conserved for an ecological reason (sensu Westoby et al. 1995, Powell 2010) 2. Information on phylogeny may be valuable as a context to derive trait function
How to link traits to whole community without modeling population dynamics on a species by species basis	Maximum Entropy (MaxEnt) Modeling (Shipley et al. 2006)	Statistical mechanistic approach that maximizes the Shannon Entropy within the boundaries given by the measured community-aggregated trait values	Some element of circularity involved because community-aggregated trait values are needed to constrain calculations; limits the ability to extrapolate to new conditions
Complexity of trait–environment relationships (nonlinear with different optima and minima) complicates hypothesis testing and prediction of trait-based approaches	Quantitative trait-based analyses (Webb et al. 2010)	Combination of statistical mechanics models, Bayesian multilevel models, and dynamical systems models proposed to project trait responses across environmental gradients by means of a hierarchically structured performance filter	Difficult to see how contingency of trait function can be realistically incorporated when developing performance filters because the number of potential interactions increases rapidly when considering more traits

environmental drivers influence the fitness of the species in a consistent manner (resulting in species sorting), depending on the traits they possess (Southwood 1977, McGill et al. 2006, Webb et al. 2010). The interplay between traits and environmental conditions is sometimes conceptualized as a filter (e.g., Keddy 1992, Poff 1997, Webb et al. 2010), such that the representation of traits in the regional species pool is filtered to yield the trait composition and, therefore, species composition and relative abundance, of local communities. Essentially, natural selection and species sorting do not operate at the level of single traits,

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

but on whole organisms carrying multiple traits. Consequently, species performance will be a function of combinations of traits that together present an adaptive response to the prevailing environment (Stearns 1976, Grime 1977, Southwood 1977, Winemiller and Rose 1992, Verberk et al. 2008b). As a result, a specific combination of traits may have more adaptive value than the constituent traits separately. An important repercussion is that the context of the remainder of an organism's biology could be critically important for the adaptive value of a particular trait (see Box 1). If so, traits cannot be analyzed as separate units, and the filter concept—while useful when applied to species—cannot be freely extended to single traits.

We suggest that the problems with current trait-based approaches are interlinked and can be traced back to a disproportionate focus on trait–environment relationships. Habitats do not primarily filter on the basis of separate traits. Instead, they filter species and only incidentally filter (sets of) traits because species can be represented as combinations of traits (Fig. 1A–C). Essentially, in current trait-based approaches, species identity is not the main focus, but is primarily a way of obtaining lists of traits and their representation (Fig. 1B). Representing species implicitly only as combinations of traits may not seem to be a profound conceptual simplification, but it shifts attention away from the species themselves, and with this shift we may have lost sight of the fact that traits are to some extent coupled and that they may interact.

The Importance of Trait Linkages and Context-Dependence for Mechanistic Understanding and Discriminatory Power

The ordination plots used to visualize multivariate analyses might suggest that traits float freely in trait ordination space, but in fact, traits are firmly bound together in the organisms themselves (Fig. 1C). Linkages among traits are well recognized and can come about in different ways. Poff et al. (2006)

Box 1. Trait function is contingent on the remainder of an organisms' biology.

A presumption underlying many trait-based approaches is the existence of general trait–environment relationships, where a single trait consistently constitutes a functional adaptation to a particular environmental gradient (see also Horrigan and Baird 2008). Various statements in the traits literature allude to this presumption. Bremner (2008, pp. 37–38) stated that an analysis starts ''with the identification of key aspects of … the ecosystem and the selection of suitable indicator traits'', Statzner and Bêche (2010, p. 87) considered that traits could act as a ''multi-probe for different stressor types (i.e. individual trait categories may respond differently to various stressors)''; whereas Poff et al. (2006, p. 733) called for an ''effort … to disentangle trait linkages quantitatively to reveal the unique information available in each trait''.

However, many traits did not evolve in isolation and in response to a single selection pressure, but rather as linked sets. A specific combination of traits may have more adaptive value than the constituent traits separately. Consider, for example, a habitat with predictable but short periods of suitable conditions. Only the *combination* of rapid growth and obligate diapause provides an effective adaptation. Thus, for a given species, the adaptive value of a specific trait (e.g., diapause) depends on the rest of its biology (e.g., does it also have rapid growth?). Evolution is a blind process and species survive by making do with the traits they have. Therefore, we suggest that traits do not have a fixed adaptive value. Instead the adaptive value of traits is context dependent. This idea is further illustrated by changes in trait function over time. During a species' evolutionary history and during its ontogeny, organs may have one function, only to be repurposed over time for any number of new uses. In extreme cases, traits may no longer have any adaptive value, representing body-plan spandrels of the past (see Gould and Lewontin 1979). Changes in trait function may follow ontogenetic changes in the individual (e.g., allometric scaling may change how environmental conditions are experienced or can affect internal body-plan constraints). For example, gills may be used mainly for osmoregulation in early life, but become more important for gas exchange as the organism grows (Maltby 1995, Spicer and McMahon 1994, Rombough 2007). Their dual function (respiration and osmoregulation) also yields different predicted responses to temperature. Buchwalter et al. (2003) suggested that organisms with gill respiration may be susceptible to temperature-induced changes in gill permeability, giving rise to higher costs involved in maintaining homeostasis in warmer water. Conversely, Bonada et al. (2007) predicted that gill respiration is favored in the warmer Mediterranean streams to facilitate O_2 uptake.

Because traits may take on different functions (i.e., have different adaptive value) during ontogeny or over evolutionary time, an evolutionary solution to an ecological problem encountered by a species may have repercussions for other aspects of its biology or may open up new possibilities. For example, drought-resistant eggs also may facilitate wind-driven or zoochorous dispersal (Bilton et al. 2001). Similarly, synchronous emergence in aquatic insects, which increases encounter frequency with potential mates, also can swamp predators. Thus, the importance of a species trait for a species ecological performance is variable and contingent upon the overall body plan of that species. This argument forms the basis for our call for a better recognition of interactions between traits and consideration of their adaptive value as central building blocks for trait-based approaches.

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

illustrated linkage of traits within species by proposing an analogy with pleiotropy in genetics, whereby selection for a particular gene (trait) increases the frequency of other, linked genes (traits) on the same chromosome (species). Across species, traits may be phylogenetically linked through a common ancestry so that, in a set of closely related species, traits are similarly combined. In addition, traits may be ecologically linked across species that occupy similar habitats, giving rise to recurrent combinations of traits that represent a suitable adaption to particular environmental conditions (e.g., the r–K continuum; Pianka 1970). A consequence of linkages among traits is that, out of all the combinations of traits that are theoretically possible, only a small subset is represented (Winemiller and Rose 1992, Usseglio-Polatera et al. 2000, Poff et al. 2006, Horrigan and Baird 2008, Verberk et al. 2008a, b). Ordination plots may show an association between 2 traits (e.g., trait A, trait B) but cannot show the complete complexity of the relationships among traits. For example, a particular association can arise because both traits are necessary to prevail in a given habitat (A + B) or because successful species fall into 2 classes, each with 1 particular trait representing alternative solutions (A or B). In addition, spurious trait–environment relationships may arise when the occurrence of a species is governed by another (unmeasured) trait that is strongly correlated with the measured trait for which the relationship was found. In both cases, information on trait linkages can help provide a better mechanistic understanding. For example, Statzner et al. (2004) pointed out that the relationship between altitude and ovoviviparity was confounded by a physiological mechanism. Ovoviviparity is prevalent in crustaceans, mollusks, and the leeches feeding on them, but all of these taxa have a high physiological demand for Ca. Thus, their low numbers at high altitude were not related to reproduction but to the low Ca content of waters at high altitude.

Beyond the well recognized linkages among traits lies the notion presented here that the function of a trait, and hence its relevance in overcoming a particular ecological problem, is context dependent (Box 1). Thus, analyses must extend beyond the simultaneous action of multiple traits (A + B; see e.g., Statzner et al. 2008, Poff et al. 2010) to take into account the possibility that one trait may change the relevance of another trait (i.e., to include the interaction term A × B). This procedure is not straightforward because the number of interaction terms increases rapidly with multiple factors. However, failure to address this context dependence may cause an averaging effect when calculating trait responses (e.g., traits associated with a certain set of environmental conditions or a habitat). This averaging effect arises because the function, and hence relevance, of a trait is assumed to be identical across species, ignoring context dependence. Thus, the calculated trait response will be an average across all species in the assemblage, including those for whom the trait is not decisive in their occurrence (e.g., species that lack that trait but are present because of another trait and vice versa). For example, in a recolonization study, flight capability was not important (Van Kleef et al. 2006). This counterintuitive result arose because many species with active flight were *also* carnivorous, and their recolonization was delayed by scarcity of prey. This interaction obscured the association between active flight and recolonization success because the calculated trait response constituted an average across both carnivores and noncarnivores. This averaging effect may explain why differences among trait categories are often very small, even though they are usually highly significant (Statzner et al. 2001, Bonada et al. 2007). It may also obscure causal mechanisms and cause problems for making (accurate) predictions.

In short, remedying the poor performance of current trait-based approaches is more than a methodological challenge and is related to fundamentals of ecology and evolution, such as trait linkages and the context dependence of the relevance of a trait for a species' survival. The aim of trait-based analyses is to gain a mechanistic understanding of differences in habitat use among species. We suggest that the way forward is to consider traits explicitly within their context, recognizing that species and organisms as a whole are the units that modify and respond to environmental conditions (Fig. 1C). At the same time, we need to achieve generality beyond individual species if we are to progress beyond taxon-based approaches. So can we find a way that takes into account that traits are contained within organisms without having to explain relationships at the level of species?

Integrating Species Traits to Advance Trait-based Ecology

To incorporate the context dependence of trait function, we present an alternative framework (Fig. 2) in which trait linkages are studied explicitly to resolve the context dependence of trait function and to accommodate combinations of traits that are functionally equivalent. This integrated and transparent framework consists of 4 hierarchical levels: 1) traits, 2) trait interactions, 3) combinations or suites of traits, and 4) life-history strategies.

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

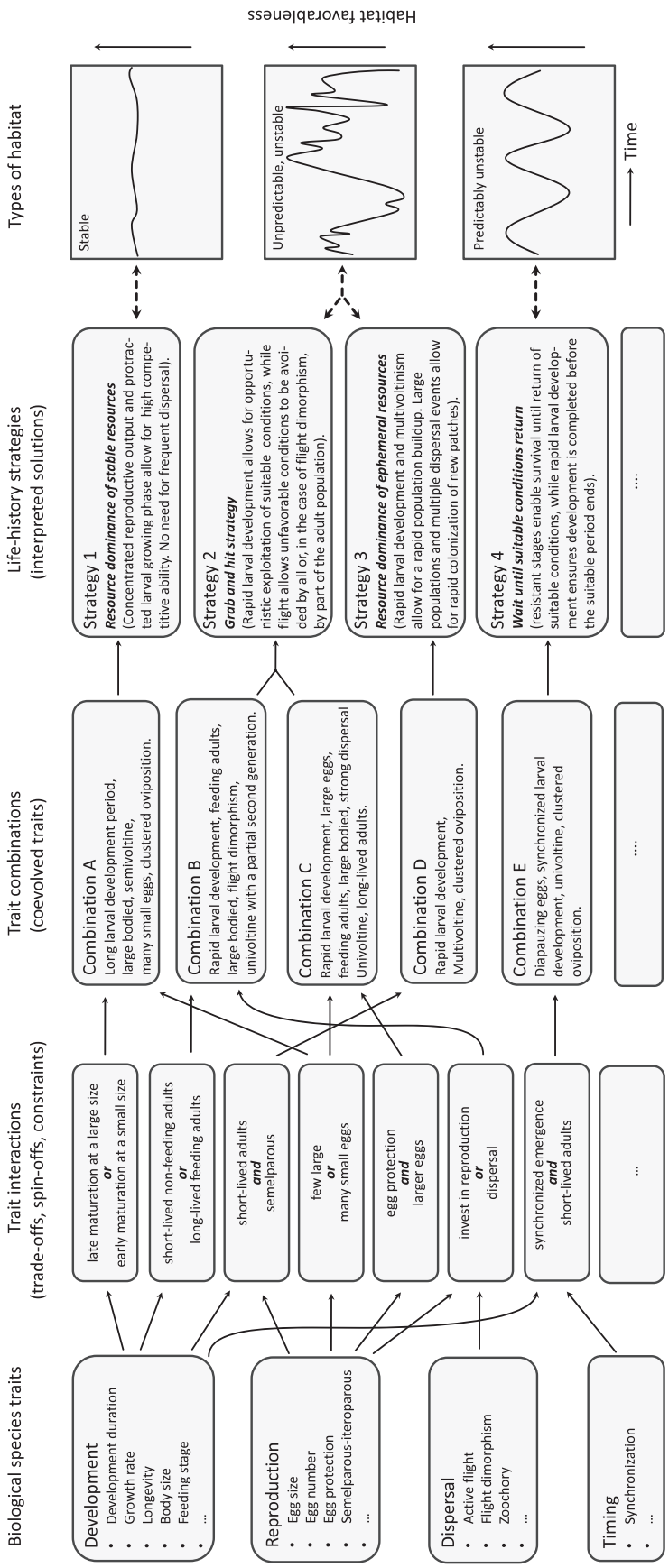


FIG. 2. Overview of the 4 hierarchical levels (traits, trait interactions, combinations of traits, and life-history strategies) of the strategy approach. Traits are classified into 4 domains related to 1) survival, growth, and development; 2) reproduction; 3) dispersal; and 4) timing of growth, reproduction, and dispersal (Siepel 1994, Verberk et al. 2008b). Traits interact to give rise to suites of coevolved traits. Combination of traits allows better interpretation of their adaptive value within an environmental context. Such functional interpretations are represented by life-history strategies. Lower levels of the hierarchy are the building blocks for the next level, allowing a flexible framework.

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Traits

Any species trait potentially yields useful information about the match between a species and its environment, so how do we decide which traits are most relevant? For aquatic macroinvertebrates, detailed data frequently are missing for many taxa, and taxa display variability in certain traits (e.g., voltinism). To deal with lack of data and heterogeneity in data, traits are often categorized in discrete categories or states, delineated by absolute threshold values (Table 1). However, the same number of eggs (e.g., 50) may be considered high for some species (e.g., iteroparous species with brood care) but low for other species (e.g., semelparous species). Similarly, a development period of 12 wk may be considered slow for a small carnivore but very rapid for a large detritvore. This problem is the reason life-history studies typically deal with comparisons rather than absolutes (Begon et al. 1996) and makes comparisons among related species a powerful tool (see also Harvey and Pagel 1991). Whether some trait is strongly pronounced (high or low trait investment) becomes clear in view of the constraints and opportunities set by the rest of a species' life history, body plan, and feeding guild (Gould and Lewontin 1979). Such a context of trait interactions allows redefinition of (absolute) trait categories as (relative) trait investments. Comparing energy and resource partitioning among various traits within a set of closely related species provides information on what constitutes a (relatively) high or a low investment or a strongly or weakly pronounced trait. Such differences in relative trait investments are forged during the evolutionary history of a species and reflect responses to (historically) important environmental conditions. This perspective enables us to see more clearly the world as it is experienced by the organisms themselves, reflected in relatively large investment in those traits that are most relevant for dealing with challenges in their environment.

Trait interactions

Trait interactions arise when possession of a certain trait predisposes a species to have certain other traits. They underlie the ecological and evolutionary linkages among traits and give rise to the recurrent combinations of traits that provide mechanistic links between species abundance and environmental conditions (see e.g., Olden et al. 2006, Verberk et al. 2010b). Traits may interact through trade-offs and spin-offs, or interactions may arise because of biophysical and body-plan constraints. Trade-offs constitute a powerful direct interaction, in which investment in one trait leaves fewer resources available for another. The term trade-off is often used loosely in the literature, but here we restrict the term to internal trade-offs in resource allocation, i.e., a limited amount of resource that can be spent in different ways. Investment in one trait axiomatically reduces the resources left for other traits. Examples include the trade-off between few large or many small eggs; maturing early at a small size or later at a larger size; investing resources in reproduction at the expense of adult survival; and investing resources in dispersal or reproduction, giving rise to the oogenesis–flight syndrome in which flight is limited to individuals with immature reproductive systems (Johnson 1969). These trade-offs are inescapable and increase the likelihood that the way species partition investments in one trait or the other is relevant to overcoming a particular ecological problem. Trait investments could help us discover which traits are most important because traits important for survival are likely to be those most strongly pronounced or requiring relatively high investment, as inferred from a comparison of a set of closely related species (see also section on traits above).

Spin-offs are a 2nd way in which species traits may interact. In this case, selection favors individuals with both traits because they act in concert. Investment in one trait may reduce the cost or increase the benefit of investment in the other. For example, when species have traits that increase egg survival, e.g., endophytic oviposition (some damselflies) or parental care (glossiphonid leeches and belostomatid water bugs), laying larger eggs also may be advantageous.

The 3rd way in which traits may interact is via constraints. For example, the eggs of small amphipods are relatively large for the adult body size, presumably because a minimum egg size is needed for a developing embryo (Sainte-Marie 1991). Body-plan constraints (e.g., minimum egg size) may cause 2 traits to become associated (small body size and relatively large eggs).

Trait combinations

The theoretical number of ways in which traits can be combined can be large. For example, Poff et al. (2006) distinguished 20 traits with 59 trait categories, giving rise to 1,020,366,720 unique ways in which trait categories could be combined. They called these possible combinations functional trait niches (FTNs). If trait categories were combined randomly, the 311 genera studied by Poff et al. (2006) would each be expected to fall into their own FTN, but Poff et al. (2006) found only 233 realized FTNs. Thus, some

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

genera had identical FTNs, a result that reflects generation of ecological and evolutionary linkages among traits by trait interactions. The ecological performance of a species is controlled by multiple traits, so explaining its numerical abundance requires consideration of the factors that drive mortality and reproduction across all life stages (Stearns 1992, Lancaster and Downes 2010). By considering multiple, interacting traits, we unite key events throughout the life cycle (from egg diapauses to adult longevity) to gain a fuller understanding of how differences in reproduction, survival, and dispersal limit or regulate populations. Traits can be grouped into trait combinations (based on their interactions) and species can be grouped subsequently into strategies (based on the functional interpretation of trait combinations; see below). Thus, species that have a comparable biology as adults may be grouped differently if their larvae have different traits. By studying trait combinations, rather than separate traits, investigators can avoid the averaging effect (see above). Species can be grouped according to trait combinations (e.g., flight capacity and development period), and responses can be analyzed separately for each group. For example, consider 2 species similar in one trait (good flight capacity) but differing in another (a carnivore and an algivore) and that show contrasting recolonization success. Analysis of data at the level of trait combinations prevents averaging of their responses, even though they share a common trait.

Life-history strategies

The life-history strategy of a species can be viewed as the combination of traits that maximizes fitness in the face of a range of ecological problems (e.g., periodic harsh conditions, predation pressure, strong competition) (Verberk et al. 2008b). The assignment of species to strategies involves an interpretation of how trait combinations could function to overcome the challenges of a given environmental arena. Relative trait investments can be helpful in deciding the relevance of a trait, especially when comparing species that differ widely in body plan and, therefore, for which comparisons of absolute values are less meaningful. Different combinations of traits can provide a similar overall solution to ecological problems and, thus, constitute the same strategy. For example, similar types of adaptations involving different traits can be envisaged that reduce egg mortality, i.e., endophytic oviposition, egg guarding, or ovovivipary. The notion of strategies combining similar evolutionary solutions, enables investigators to deal with alternative suites or combinations of traits that are functionally equivalent. Radically different evolutionary solutions to a threat would constitute a different strategy (e.g., one massive synchronized reproductive event that swamps egg predation and increases the probability of some juvenile survival in the face of high mortality). Alternative adaptations may fit organisms to the same environmental arena, leading to the coexistence of species with different life-history strategies (Hildrew 1986, Winemiller and Rose 1992; Fig. 2).

We have presented an example of successful characterization of life-history strategies in aquatic macroinvertebrates in 2 companion papers. First, we defined 13 strategies a priori from theory (Verberk et al. 2008b). These strategies expressed differences in adult longevity and dispersal, partitioning of reproductive effort over space and time, and the degree of synchronization of juvenile development and adult emergence. We combined traits according to trait interactions. For example, high per capita investment was associated with long-lived, feeding adults, small eggs frequently were deposited in clusters and entailed prolonged juvenile development, and synchronous juvenile development was frequent when development was rapid and reproduction occurred only once (univoltine). Differences in species assigned to these theoretically defined strategies could be related to the prevailing environmental conditions through mechanistic explanations (Verberk et al. 2008a). Subsequently, we applied the characterization of life-history strategies to predict differences in abundance, shedding light on the fundamental macroecological pattern that widespread species are also generally abundant and vice versa (Gaston 2003, Verberk et al. 2010b). In an applied context, strategies explained macroinvertebrate responses to changes in environmental conditions following rewetting measures in a bog remnant (Verberk et al. 2010a). This approach also has been applied to ants, a rather different taxonomic group. Here, traits related to the foundation and overwintering of colonies were hypothesized to underlie differences in thermal requirements and sensitivity to fragmentation. Field data on the distribution of ants in calcareous grasslands supported these hypotheses and yielded clear recommendations on how to improve conservation management (van Noordwijk et al. 2012).

Aggregating species into a smaller number of strategies might reduce analytical discriminatory power compared to using separate trait categories as a ''multi-probe for different stressor types'' (Statzner and Bêche 2010). However, each trait does not always contribute unique information because of the context dependence of trait function. In this respect, use of a

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

smaller number of strategies capturing the most relevant differences in trait combinations could help improve the signal-to-noise ratio, resulting in higher discriminatory power. Verberk et al. (2008a) found that differences in strategy composition across types of water body were quite large. A limited number of strategies does not necessarily entail a loss of discriminatory power because several strategies can coexist in a given type of habitat (Hildrew 1986, Verberk et al. 2008a; Fig. 2) and the representation of specific combinations of strategies can be diagnostic of environmental change (Verberk et al. 2010a). The utility of increasing the signal-to-noise ratio by aggregating alternative trait combinations is also exemplified by the SPEcies At Risk (SPEAR) approach. In this approach, combinations of traits are used to predict which species are at risk from pesticides (Liess et al. 2008). Pesticides are usually applied as pulses, so their influence is best diagnosed by the absence of species that cannot avoid such events, tolerate them, or recover quickly. Thus, for their purposes, Liess et al. (2008) considered species at risk if they possessed a combination of traits related to their: 1) sensitivity (high sensitivity to pesticide, making species vulnerable), 2) life cycle (aquatic stages coincide with the main period of agrochemical application, exposing the species to the pesticide), 3) dispersal (poor dispersal, reducing the potential for recolonization), and 4) generation time (low voltinism, reducing the potential for recolonization). Species not at risk (i.e., not possessing *all* of the above traits) probably differed in how they combined traits, but for the purposes of the assessment were considered equivalent and were grouped together. Essentially, combining species with equivalent trait combinations (those at risk or not) is similar to the strategy approach we advocate, but without the emphasis on trait interactions.

A Hierarchical Transparent Framework for Integrating Traits

Grouping species based on their traits is not new, and previous investigators developed groups for a range of organisms including higher plants, fish, aquatic invertebrates, and algae (Grime 1977, Winemiller and Rose 1992, Steneck and Dethier 1994, Usseglio-Polatera et al. 2000, Verberk et al. 2008b). However, here we propose an encompassing trait-based framework that is hierarchical. Trait interactions give rise to adaptive combination of traits whose function, in turn, is interpreted by applying logic and life-history theory (Fig. 2). Several investigators already have used one or more steps from this approach. For example, Usseglio-Polatera et al. (2000) grouped species by trait categories, but they did not specifically incorporate trait interactions. Winemiller and Rose (1992) used trait interactions as the basis for their life-history groupings, but they did not generally incorporate the context dependence of traits. Instead, they assumed that one trait had the same function across species with different life histories. However, they did adopt the perspective of relative trait investments when noting that the small eggs of small fish could be considered large relative to fish body size, thus, making them more akin to the equilibrium strategy for which a large egg size is characteristic.

The strategy approach we advocate is based on relative trait investments and the context dependence of trait function, which allow complex, biodiverse assemblages to be condensed to a few meaningful, easily interpretable relationships (Fig. 1C). Based on a hierarchical structure of traits, trait interactions, trait combinations, and strategies, our open framework allows both analytical flexibility and scientific rigor (Fig. 2).

Scientific rigor

Scientific rigor and objectivity are ensured by rooting analytical choices in fundamental trade-offs known from life-history theory. Thus, logic and theory can be used to construct hypotheses regarding which factors are likely to be important to a species, given its suite of traits, which can then be tested empirically (Siepel 1995, Verberk et al. 2008a, 2010b, van Noordwijk et al. 2012). Essentially, life-history strategies focus on those trait combinations that are specified beforehand to reflect a meaningful adaptation. This step is analogous to assigning different weights to a single trait across species in multivariate analysis. For example, rapid development may be particularly important and, therefore, be given more weight, for species that combine it with a diapausing life stage (presenting an adaptive solution to periodically favorable habitats). One could argue that conventional multivariate analyses, which do not explicitly account for such context dependency, are more liberal and objective than our strategy approach because they do not constitute such a constrained analysis. Nevertheless, weighting a trait equally across species and using the same coarse trait categories is only one of many possible ways to analyze data, and is one that does not necessarily make the most sense ecologically. The ability to construct testable hypotheses at the level of individual species based on their strategy is a powerful tool,

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

which may be particularly valuable in applied biodiversity studies where few pristine, unimpacted sites may be left as control sites (van Noordwijk et al. 2012). Species can be grouped based on their traits, which are hypothesized to underlie their ability to cope with a particular stressor. Subsequently, statistical replication across species, rather than across sites, could be used to determine if species groups show different responses, indicating the action of that stressor (Downes 2010).

Analytical flexibility

The concept we put forward permits more analytical flexibility than traditional approaches because the level of detail of information on traits can be adjusted depending on the taxonomic scope and the research question addressed. In addition, because of the linkages between traits, exhaustive data on each and every trait may not be necessary to assign a species with confidence to a certain strategy, thereby solving the issue of data heterogeneity (Table 1). Trait information that differs in the level of detail can be brought together because each piece of information gives clues about the strategy that is key to survival. In this way, the rich body of knowledge on natural history can be tapped (Keddy 1992). Identifying which species can be grouped and why has been suggested as an area in great need of targeted research (Downes 2010). We think this area of research would greatly benefit from the study of traits, trait interactions, and strategies (see also Poff et al. 2006). We see no reason to adopt a rigid structure regarding the number of species groups or strategies. For some questions, species could be quite coarsely aggregated into a few strategies, whereas other questions might require a finer resolution. For example, when interested in a single factor, such as a pesticide, species could be aggregated into just 2 groups, those at risk and those not at risk (Liess et al. 2008).

Taxonomic resolution

Trait-based analyses often use coarse trait categories that are qualitatively very similar at different taxonomic levels (e.g., species, genus, or family) (e.g., Gayraud et al. 2003). This similarity in trait–environment relationships across different taxonomic levels suggests that trait information at higher taxonomic levels (genera or even family) is sufficient to discriminate among the effects of different environmental stressors. *Descriptions* of communities using trait data at the generic level may be sufficiently accurate to delineate environmental effects. The choice of resolution would reflect the need for detail and practical limitations (Schmidt-Kloiber and Nijboer 2004). However, the conclusion that trait data at the generic level are sufficient (Statzner and Bêche 2010) may not be valid in general. If the aim is to *explain* patterns in invertebrate assemblages from environmental conditions, rather than describe such patterns, information is required at the level of the species because causal mechanisms operate at the level of species, not genera or families (see also Lenat and Resh 2001). For example, at the family level, glossiphonid leeches engage in brood care, whereas erpobdellid leeches do not. However, within the Glossiphoniidae, species differ in the degree of care. *Helobdella stagnalis* (Linnaeus) carry the eggs, feed the young upon hatching, and carry the young, whereas *Glossiphonia complanata* (Linnaeus) guard the eggs, but do not carry them (Kutschera and Wirtz 2001). Incorporating such variations on a theme is difficult, either because such detailed information simply is not available for many species in a study or because such detail is lost when coarse trait categories based on absolute values are used. Nevertheless, such variations on a theme provide important information on whether a trait is strongly pronounced in view of the constraints and opportunities set by the remainder of a species' body plan. Use of relative trait investments can help incorporate more detailed trait information at the level of the species (the variations on a theme), basically rescaling the absolute trait values to relative investments. By doing so, the obvious differences among higher taxonomic units are diminished. More focus is placed on the variations on the theme, rather than the theme itself because these themes may be constrained phylogenetically (see below).

Phylogeny

Phylogeny can confound analyses that attempt to use traits to link species to their environments when coexisting species also share a common ancestry. Intact, fast flowing, oxygenated, permanent streams are invariably dominated by insects of 3 clades (Ephemeroptera, Plecoptera, and Trichoptera). Therefore, in comparisons of running and standing waters, patterns in community composition will have a strong phylogenetic signature. If a trait is associated with these 3 clades it is likely to be related to fast flow conditions, but that relationship may or may not be spurious. Disentangling causation from coincidence then becomes difficult. Traits of related species cannot be used as independent pieces of evidence for an association between a certain trait and the habitat (Harvey and Pagel 1991).

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Poff et al. (2006) suggested a focus on evolutionarily labile traits, i.e., traits that are uncorrelated with phylogeny, as a way to deal with the confounding effects of phylogeny. Labile traits could provide unique information because they are independent of phylogeny. Examples of labile traits given by Poff et al (2006) include thermal preferences, size, voltinism, and trophic habit (encompassing feeding behavior and trophic position). Such traits may vary more widely than phylogenetically correlated traits among closely related species because they are less constrained by phylogeny. Thus, labile traits are akin to those studied in plant ecology, such as water-use efficiency and leaf characteristics (e.g., Wright et al. 2004). For such traits, linking back to species before linking to the environment may not always be necessary, and a shortcut linking traits directly to the environment might be possible (Fig. 1B). In addition, if a clear, direct mechanistic trait–environment relationship can be demonstrated, issues pertaining to trait linkages and context-dependency of function would be circumvented. The call to focus on labile traits (Poff et al. 2006) makes good sense within this context and fits with the proposal of Statzner and Bêche (2010) to search for traits that have a direct relationship with stressors and are stressor-specific. An important prerequisite for the shortcut to link traits directly to the environment is that labile traits do not interact with other traits. Labile and other traits might be phylogenetically uncorrelated, but they could still be linked ecologically, thereby giving rise to recurrent combinations of traits. For example, trophic habit does affect duration of larval development. In addition, labile traits may vary more widely than phylogenetically correlated traits among closely related species, but they also vary within species. Measuring labile traits under controlled conditions could reduce this variability and make data more comparable across species. Use of independently collected data to explain field distributions also circumvents the criticism made of preferences or ecological traits. Controlled measurements of traits, such as sensitivity to pesticides (e.g., Liess et al. 2008), thermal tolerance, and O_2 consumption (e.g., Verberk and Bilton 2011), could explain the selective effect of pesticides on assemblages or variation in the preferences of species for a certain thermal regime or flow conditions, respectively. Gathering information on labile traits extends the basis for trait-based approaches and can be used simultaneously to test whether such traits are truly independent from the remainder of an organisms' biology. Labile traits also could reflect variations on a theme (see taxonomic resolution above).

Whether labile traits could be sufficient to explain species occurrences remains an open question. Phylogenetically correlated traits could still be the most ecologically important traits (Westoby et al. 1995), which would explain why they are phylogenetically conserved in the first place. The phylogenetic context, or more broadly, trait interactions (including those arising from trade-offs and spin-offs), can be very helpful in linking species to their environment via their trait combinations (Fig. 1C). By interpreting trait function within the context of the rest of the traits (including the phylogenetically conserved ones), phylogeny may become an ally, rather than a confounding factor.

Taxonomic scope

Taxonomic scope, i.e., the range in body plans considered, is related to the issue of phylogeny and differences in body plan. Studies with a rather narrow taxonomic scope, such as those of aquatic insects (Statzner et al. 1997, Townsend et al. 1997) or fish (Winemiller and Rose 1992), have been relatively more successful in predicting trait relationships with the environment compared to studies with a wider taxonomic scope. This success could be related to the fact that species perceive their habitat differently and respond to properties of the habitat at different spatial and temporal scales (Giller et al. 1994, Resh et al. 1994, Statzner et al. 1997, Mokany and Roxburgh 2010). These perceptual scales of a species are themselves altered by traits, such as those related to dispersal and dormancy (Levin 1992, McLachlan 1983). Therefore, a given habitat may not act as a templet in a uniform way for species with different body plans (e.g., Southwood 1977). Thus, making statements about the adaptive value and function of traits requires comparison of like with like. Restricting the analysis to aquatic insects or fish, where similarity in body plan causes them to experience more similar constraints and trade-offs, increases the chance that the same trait will have the same adaptive value across species and that the spatial and temporal scale at which the studied organisms operate will be similar.

Taxonomic scope has repercussions for trait-based analyses. For example, Winemiller and Rose (1992) were able to plot detailed continuous data using absolute values for various traits to distill the most important patterns for a large range of fish species. When a greater range of body plans is considered (i.e., a wider taxonomic scope), problems arise with context dependency. Winemiller and Rose (1992) found that traits were not equally relevant across different groups of fishes. For example, clupeiforms achieve larger clutches by delaying reproduction until a larger body size is achieved, rather than by packaging reproductive biomass into smaller eggs.

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Thus, taxonomic scope will influence the taxonomic resolution that should be adopted and the degree to which phylogeny may have confounding effects. A wider taxonomic scope will increase the need to tackle the issue of context dependence. Taxonomic scope also may explain the observation by Chown (2012) that trait-based methods are less contentious in physiology than in ecology. Comparative physiology focuses on intra- and interspecific variation in traits, usually of related species or at least species with a comparable body plan. In contrast, ecological endeavors frequently focus on assemblages comprising species with widely varying body plans. The use of relative trait investments can resolve absolute differences in trait values among disparate systematic groups, whereas context-dependent interpretations may help deal with flexibility in trait function and may accommodate differences in level of detail across species and lack of data on certain traits for certain groups of taxa.

Future Perspectives: Toward an Open Framework

We have proposed a different way of investigating trait–environment relationships: trade-offs between traits and underlying adaptive value of traits are central in evolutionary ecology and are viewed as the core of our approach rather than as obstacles that must be circumvented. Calls have been made for a common analytical framework (Webb et al. 2010) that could advance trait-based ecology and improve biomonitoring tools to identify (multiple) stressors, functional impairment, and management priorities (Statzner and Bêche 2010). We agree that a framework is necessary to bring together the different approaches. We have presented an open and integrative framework that goes beyond methodological approach (Table 1) to foster understanding of how species traits can shape species–environment relationships. Selection has led to sets of traits that work well together (spin-offs), do not exclude each other or render each other irrelevant (trade-offs), and are available to an organism (i.e., no body-plan constraints). These suites of traits provide a complex adaptive solution (strategy) to the multitude of historical and contemporary challenges faced by an organism in its environment (the multidimensional niche). Our proposed framework builds on evolutionary and ecological principles to gain a better mechanistic understanding of the link between species and their environment.

Understanding causality is a prerequisite for any biomonitoring or decision-support tool (Kearney and Porter 2009, Friberg et al. 2011). Our framework is a foundation for development of future biomonitoring tools, rather than a ready-made tool. We agree with Statzner et al. (1997) and Resh and Rosenberg (2010) that the expansion and integration of existing trait databases is a good idea because information on species traits is the necessary basis for any trait-based approach. However, care must be taken to prevent strong prescriptions regarding the taxonomic level (species, genera), traits, and trait categories for which information should be gathered. Collecting new data on more labile traits, such as thermal tolerance and O_2 consumption, could be very informative. The information contained in continuous traits and traits coded at the level of species or populations could provide important clues about the interpretation of species–environment relationships. The approach adopted by Baird et al. (2011) seems promising in this respect. They outlined a novel way to collate trait information of different detail and to use query tools to operationalize the data for application. We suggest 3 ways to improve the utility of efforts to collect trait data. First, present the raw continuous data instead of reducing information content by condensing data into classes. Second, make comparisons when studying a trait. Its relevance can be better interpreted when 2 or, even better, more species are compared. Third, make comparisons within species. Many traits vary along environmental gradients (e.g., development time along a latitudinal gradient). Reporting intraspecific variability provides information on the flexibility of a trait or the constraints governing it. The degree of intraspecific variability itself can be an important trait, particularly if the variability is caused by plasticity or genetic variation (Flenner et al. 2010).

Our framework starts from fundamentals of ecology and evolution and could be instrumental in transforming and coordinating the efforts taken in collecting additional data. A central notion is acknowledging that the function of a trait is contingent upon the rest of a species' biology, as opposed to assuming the existence of general trait–environment relationships in which a given trait consistently constitutes a functional adaptation to a particular environmental gradient. Therefore, future efforts to generate and test hypotheses may be more fruitfully directed by taking this flexibility of trait function into account. We expect analysis of differences in strategy composition between water bodies to provide better discriminatory power and increased mechanistic understanding than traditional analyses, which do not take into account trait linkages and context dependence. The added value of our approach should be especially evident when considering a wide range of body plans (wide taxonomic scope) and when

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

analyzing traits data of high detail (high trait resolution). Researchers can contribute at various levels (Fig. 2): 1) expanding the basis of traits by providing or collating information on traits, 2) reporting on ways in which traits interact, 3) synthesizing interacting traits into trait combinations and strategies for one or more taxonomic groups, and 4) testing these combinations and strategies with field data. Within the integrated and transparent framework presented here, these contributions can be verified or falsified using logic and theory to help fulfill the promise that traits can transform community ecology into a predictive science.

Acknowledgements

Two anonymous referees made critical, much appreciated comments that improved our manuscript. WCEPV was in receipt of a Marie-Curie Fellowship (no. FP7-PEOPLE-2009-IEF). CGEVN received financial support from Ghent University and from the O+BN program of the Dutch ministry of Economics, Agriculture and Innovation (project no. 2010-04).

Literature Cited

BAIRD, D. J., C. J. O. BAKER, R. B. BRUA, M. HAJIBABAEI, K. MCNICOL, T. J. PASCOE, AND D. DE ZWART. 2011. Towards a knowledge infrastructure for trait-based ecological risk assessment. Integrated Environmental Assessment and Management 7:209–215.

BEGON, M., J. L. HARPER, AND C. R. TOWNSEND. 1996. Ecology: individuals, populations, and communities. 3rd edition. Blackwell Science, Oxford, UK.

BILTON, D. T., J. R. FREELAND, AND B. OKAMURA. 2001. Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics 32:159–181.

BONADA, N., S. DOLÉDEC, AND B. STATZNER. 2007. Taxonomic and biological trait differences of stream macroinvertebrate communities between Mediterranean and temperate regions: implications for future climatic scenarios. Global Change Biology 13:1658–1671.

BREMNER, J. 2008. Species' traits and ecological functioning in marine conservation and management. Journal of Experimental Marine Biology and Ecology 366:37–47.

BUCHWALTER, D. B., J. J. JENKINS, AND L. R. CURTIS. 2003. Temperature influences on water permeability and chlorpyrifos uptake in aquatic insects with differing respiration strategies. Environmental Toxicology and Chemistry 22:2806–2812.

CHEVENET, F., S. DOLÉDEC, AND D. CHESSEL. 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshwater Biology 31:295–309.

CHOWN, S. L. 2012. Trait-based approaches to conservation physiology: forecasting environmental change risks from the bottom up. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 367:1615–1627.

DOLÉDEC, S., D. CHESSEL, C. J. F. TER BRAAK, AND S. CHAMPELY. 1996. Matching species traits to environmental variables: a new three-table ordination method. Environmental and Ecological Statistics 3:143–166.

DOLÉDEC, S., AND B. STATZNER. 2008. Invertebrate traits for the biomonitoring of large European rivers: an assessment of specific types of human impact. Freshwater Biology 53:617–634.

DOLÉDEC, S., AND B. STATZNER. 2010. Responses of freshwater biota to human disturbances: contribution of *J-NABS* to developments in ecological integrity assessments. Journal of the North American Benthological Society 29: 286–311.

DOWNES, B. J. 2010. Back to the future: little-used tools and principles of scientific inference can help disentangle effects of multiple stressors on freshwater ecosystems. Freshwater Biology 55(Supplement 1):60–79.

DRAY, S., AND P. LEGENDRE. 2008. Testing the species traits–environment relationships: the fourth-corner problem revisited. Ecology 89:3400–3412.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

FLENNER, I., O. RICHTER, AND F. SUHLING. 2010. Rising temperature and development in dragonfly populations at different latitudes. Freshwater Biology 55:397–410.

FRIBERG, N., N. BONADA, D. C. BRADLEY, M. J. DUNBAR, F. K. EDWARDS, J. GREY, R. B. HAYES, A. G. HILDREW, N. LAMOUROUX, M. TRIMMER, AND G. WOODWARD. 2011. Biomonitoring of human impacts in natural ecosystems: the good, the bad and the ugly. Advances in Ecological Research 44:1–68.

GASTON, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, UK.

GAYRAUD, S., B. STATZNER, P. BADY, A. HAYBACHP, F. SCHÖLL, P. USSEGLIO-POLATERA, AND M. BACCHI. 2003. Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. Freshwater Biology 48:2045–2064.

GILLER, P. S., A. G. HILDREW, AND D. G. RAFFAELLI (EDITORS). 1994. Aquatic ecology: scale, pattern and process. Symposia of the British Ecological Society with the American Society of Limnology and Oceanography. Blackwell Scientific Publications, Oxford, UK.

GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proceedings of the Royal Society of London Series B: Biological Sciences 205: 581–598.

GRIME, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111: 1169–1194.

HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, UK.

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

HAWKINS, C. P., J. R. OLSON, AND R. A. HILL. 2010. The reference condition: predicting benchmarks for ecological and water-quality assessments. Journal of the North American Benthological Society 29:207–219.

HILDREW, A. G. 1986. Aquatic insects: patterns in life history, environment and community structure. Pages 35–45 *in* H. H. Velthuis (editor). Proceedings of the 3rd European Congress of Entomology. Part 1. Nederlandse Entomologische Vereniging, Amsterdam, The Netherlands.

HORRIGAN, N., AND D. J. BAIRD. 2008. Trait patterns of aquatic insects across gradients of flow- related factors: a multivariate analysis of Canadian national data. Canadian Journal of Fisheries and Aquatic Sciences 65:670–680.

ILG, C., AND E. CASTELLA. 2006. Patterns of macroinvertebrate traits along three glacial stream continuums. Freshwater Biology 51:840–853.

JOHNSON, C. G. 1969. Migration and dispersal of insects by flight. Methuen and Co., London, UK.

KEARNEY, M., AND W. PORTER. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

KEDDY, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

KUTSCHERA, U., AND P. WIRTZ. 2001. The evolution of parental care in freshwater leeches. Theory in Biosciences 120: 115–137.

LAMOUROUX, N., N. L. POFF, AND P. L. ANGERMEIER. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. Ecology 83:1792–1807.

LANCASTER, J., AND B. J. DOWNES. 2010. Ecohydraulics needs to embrace ecology and sound science, and to avoid mathematical artefacts. River Research and Application 26:921–929.

LANCASTER, J., B. J. DOWNES, AND A. GLAISTER. 2009. Interacting environmental gradients, trade-offs and reversals in the abundance–environment relationships of stream insects: when flow is unimportant. Marine and Freshwater Research 60:259–270.

LAWTON, J. H. 1999. Are there general laws in ecology? Oikos 84:177–192.

LENAT, D. R., AND V. H. RESH. 2001. Taxonomy and stream ecology—the benefits of genus- and species-level identifications. Journal of the North American Benthological Society 20:287–298.

LEVIN, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award lecture. Ecology 73:1943–1967.

LIESS, M., R. B. SCHÄFER, AND C. A. SCHRIEVER. 2008. The footprint of pesticide stress in communities—species traits reveal community effects of toxicants. Science of the Total Environment 406:484–490.

MALTBY, L. 1995. Sensitivity of the crustaceans *Gammarus pulex* (L.) and *Asellus aquaticus* (L.) to short-term exposure to hypoxia and unionized ammonia: observations and possible mechanisms. Water Research 29: 781–787.

MCGILL, B. J., B. J. ENQUIST, E. WEIHER, AND M. WESTOBY. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21:178–185.

MCLACHLAN, A. 1983. Life-history tactics of rain-pool dwellers. Journal of Animal Ecology 52:545–561.

MENEZES, S., D. J. BAIRD, AND A. M. V. M. SOARES. 2010. Beyond taxonomy: a review of macroinvertebrate trait-based community descriptors as tools for freshwater biomonitoring. Journal of Applied Ecology 47:711–719.

MOKANY, K., AND S. H. ROXBURGH. 2010. The importance of spatial scale for trait–abundance relations. Oikos 119: 1504–1514.

OLDEN, J. D., N. L. POFF, AND K. R. BESTGEN. 2006. Life history strategies predict fish invasions and extirpations in the Colorado River basin. Ecological Monographs 76:25–40.

PIANKA, E. R. 1970. On r- and K-selection. American Naturalist 104:592–597.

POFF, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16:391–409.

POFF, N. L., J. D. OLDEN, N. K. M. VIEIRA, D. S. FINN, M. P. SIMMONS, AND B. C. KONDRATIEFF. 2006. Functional trait niches of North American lotic insects: trait-based ecological applications in light of phylogenetic relationships. Journal of the North American Benthological Society 25:730–755.

POFF, N. L., M. I. PYNE, B. P. BLEDSOE, C. C. CUHACIYAN, AND D. M. CARLISLE. 2010. Developing linkages between species traits and multiscaled environmental variation to explore vulnerability of stream benthic communities to climate change. Journal of the North American Benthological Society 29:1441–1458.

POLLARD, A. I., AND L. L. YUAN. 2010. Assessing the consistency of response metrics of the invertebrate benthos: a comparison of trait- and identity-based measures. Freshwater Biology 55:1420–1429.

POWELL, F. L. 2010. Studying biological responses to global change in atmospheric oxygen. Respiratory Physiology and Neurobiology 173S:S6–S12.

RESH, V. H., A. G. HILDREW, B. STATZNER, AND C. R. TOWNSEND. 1994. Theoretical habitat templets, species traits, and species richness – a synthesis of long-term ecological research on the upper Rhône River in the context of currently developed ecological theory. Freshwater Biology 31:539–554.

RESH, V. H., AND D. M. ROSENBERG. 2010. Recent trends in life-history research on benthic macroinvertebrates. Journal of the North American Benthological Society 29: 207–219.

ROMBOUGH, P. 2007. The functional ontogeny of the teleost gill: which comes first, gas or ion exchange? Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 148:732–742.

SAINTE-MARIE, B. 1991. Review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223:189–227.

SCHMIDT-KLOIBER, A., AND R. C. NIJBOER. 2004. The effect of taxonomic resolution on the assessment of ecological water quality classes. Hydrobiologia 516:269–283.

SHIPLEY, B., D. VILE, AND E. GARNIER. 2006. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. Science 314:812–814.

SIEPEL, H. 1994. Life-history tactics of soil microarthropods. Biology and Fertility of Soils 18:263–278.

SIEPEL, H. 1995. Applications of microarthropod life-history tactics in nature management and ecotoxicology. Biology and Fertility of Soils 19:75–83.

SOUTHWOOD, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46:337–365.

SPICER, J. I., AND B. R. MCMAHON. 1994. Gill function in the amphipod *Megalorchestia* (Orchestoidea) *californiana* (Brandt, 1851) (Crustacea). Canadian Journal of Zoology 72:1155–1158.

STATZNER, B., AND L. A. BÊCHE. 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? Freshwater Biology 55(supplement 1):80–119.

STATZNER, B., B. BIS, S. DOLÉDEC, AND P. USSEGLIO-POLATERA. 2001. Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition on invertebrate communities in European running waters. Basic and Applied Ecology 2:73–85.

STATZNER, B., N. BONADA, AND S. DOLÉDEC. 2008. Predicting the abundance of European stream macroinvertebrates using biological attributes. Oecologia (Berlin) 156:65–73.

STATZNER, B., S. DOLÉDEC, AND B. HUGUENY. 2004. Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. Ecography 27:470–488.

STATZNER, B., K. HOPPENHAUS, M. F. ARENS, AND P. RICHOUX. 1997. Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. Freshwater Biology 38:109–135.

STATZNER, B., V. H. RESH, AND S. DOLÉDEC. 1994. Ecology of the upper Rhône River: a test of habitat templet theories. Freshwater Biology 31:253–554.

STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51:3–47.

STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

STENECK, R. S., AND M. N. DETHIER. 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69:476–498.

TOWNSEND, C. R., S. DOLÉDEC, AND M. R. SCARSBROOK. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. Freshwater Biology 37:367–387.

TOWNSEND, C. R., AND A. G. HILDREW. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31:265–275.

USSEGLIO-POLATERA, P., M. BOURNAUD, P. RICHOUX, AND H. TACHET. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. Freshwater Biology 43:175–205.

VANDEWALLE, M., F. DE BELLO, M. P. BERG, T. BOLGER, S. DOLÉDEC, F. DUBS, C. K. FELD, R. HARRINGTON, P. A. HARRISON, S. LAVOREL, P. MARTINS DA SILVA, M. MORETTI, J. NIEMELA, P. SANTOS, T. SATTLER, J. P. SOUSA, M. T. SYKES, A. J. VANBERGEN, AND B. A. WOODCOCK. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodiversity Conservation 19:2921–2947.

VAN KLEEF, H. H., W. C. E. P. VERBERK, R. S. E. W. LEUVEN, H. ESSELINK, G. VAN DER VELDE, AND G. A. VAN DUINEN. 2006. Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes. Hydrobiologia 565:201–216.

VAN NOORDWIJK, C. G. E., P. BOER, A. A. MABELIS, W. C. E. P. VERBERK, AND H. SIEPEL. 2012. Life-history strategies as a tool to identify conservation constraints: a case-study on ants in chalk grasslands. Ecological Indicators 13: 303–313.

VERBERK, W. C. E. P., AND D. T. BILTON. 2011. Can oxygen set thermal limits and drive gigantism? PLoS One 6: e22610.

VERBERK, W. C. E. P., R. S. E. W. LEUVEN, G. A. VAN DUINEN, AND H. ESSELINK. 2010a. Loss of environmental heterogeneity and aquatic macroinvertebrate diversity following large-scale restoration management. Basic and Applied Ecology 11:440–449.

VERBERK, W. C. E. P., H. SIEPEL, AND H. ESSELINK. 2008a. Applying life-history strategies for freshwater macroinvertebrates to lentic waters. Freshwater Biology 53: 1739–1753.

VERBERK, W. C. E. P., H. SIEPEL, AND H. ESSELINK. 2008b. Life-history strategies in freshwater macroinvertebrates. Freshwater Biology 53:1722–1738.

VERBERK, W. C. E. P., G. VAN DER VELDE, AND H. ESSELINK. 2010b. Explaining abundance-occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. Journal of Animal Ecology 79:589–601.

VIOLLE, C., M.-L. NAVAS, D. VILE, E. KAZAKOU, C. FORTUNEL, I. HUMMEL, AND E. GARNIER. 2007. Let the concept of trait be functional! Oikos 116:882–892.

WEBB, C. T., J. A. HOETING, G. M. AMES, M. I. PYNE, AND N. L. POFF. 2010. A structured and dynamic framework to advance trait-based theory and prediction in ecology. Ecology Letters 13:267–283.

WEINER, J. 1995. On the practice of ecology. Journal of Ecology 83:153–158.

WESTOBY, M., M. R. LEISHMAN, AND J. M. LORD. 1995. On misinterpreting the 'phylogenetic correction'. Journal of Ecology 83:531–534.

WINEMILLER, K., AND K. ROSE. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196–2218.

WRIGHT, I. J., P. B. REICH, M. WESTOBY, D. D. ACKERLY, Z. BARUCH, F. BONGERS, J. CAVENDER-BARES, F. S. CHAPIN, J. H. C.

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

CORNELISSEN, M. DIEMER, J. FLEXAS, E. GARNIER, P. K. GROOM, J. GULIAS, K. HIKOSAKA, B. B. LAMONT, T. LEE, W. LEE, C. LUSK, J. J. MIDGLEY, M.-L. NAVAS, Ü. NIINEMETS, J. OLEKSYN, N. OSADA, H. POORTER, P. POOT, L. PRIOR, V. I. PYANKOV, C. ROUMET, S. C. THOMAS, M. G. TJOELKER, E. VENEKLAAS, AND R. VILLAR. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Received: 13 June 2012
Accepted: 4 February 2013

Downloaded From: https://complete.bioone.org/journals/Freshwater-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use