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Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology

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Abstract. A heuristic framework for understanding and predicting the distribution and categorical abundance of species in stream communities is presented. The framework requires that species be described in terms of their functional relationships to habitat selective forces or their surrogates, which constitute “filters” occurring at hierarchical landscape scales (ranging from microhabitats to watersheds or basins). Large-scale filters are viewed as causative or mechanistic agents that constrain expression of local selective forces or biotic potential at lower scales. To join a local community, species in a regional pool must possess appropriate functional attributes (species traits) to “pass” through the nested filters. Biotic interactions are also a potential filter on local community composition, and they are invoked at the lower hierarchical levels, after species have passed through the physico-chemical habitat filters. Potential landscape filters and their associated selective properties are identified, as are prospective species traits (for invertebrates and fish) that correspond with filters. A categorical niche model is used to illustrate how relative abundances of species in local communities might be predicted from habitat data collected at different scales.

The framework emphasizes a biologically based approach to understanding and predicting species distribution and abundance and local community composition by explicitly considering environmental constraints imposed at different scales. As such, it can complement non-mechanistic, correlative approaches to community prediction that often lack generality. Operationalizing the framework will require additional research to specify more clearly 1) the degree to which habitat features at different scales are linked functionally or statistically, 2) what species traits are possessed by strongly interactive species (e.g., keystones) and which habitat filters most strongly constrain the distribution of these species, and 3) the functional significance of a range of species traits and the extent to which these traits are correlated and hence respond in concert to the presence, or modification, of a particular filter. Multi-scale, mechanistic understanding of species–environment relations will likely contribute to better predictions about large scale problems, such as the establishment and spread of exotic species or alterations in community composition with changing land use or climate.

Key words: Species traits, functional groups, filters, landscape, habitat, hierarchy, community composition, community assembly, understanding, prediction.

The most general goal of science is to generate understanding.

Pickett et al. (1994)

A predictive science of community ecology will have to be based on underlying processes, but without dealing with the details of those processes.

Orians (1980)

Understanding and predicting the composition of local biological communities across the landscape is one of the main challenges confronting ecologists, including stream ecologists. Although local environmental features have long been identified as determinants of local community composition, only more recently have we recognized that population and com-

munity patterns are products of interacting multiple causes (Hilborn and Stearns 1992) generated at multiple spatial and temporal scales (Allen and Starr 1982). Local community composition thus results from an interplay of local and regional factors, both abiotic and biotic (Menge and Olson 1990, Ricklefs and Schluter 1993, Hildrew and Giller 1994). Although stream ecologists are beginning to document this interplay, especially with respect to abiotic factors (e.g., Strayer 1983, Corkum and Ciborowski 1988, Corkum 1990, Schlosser 1991, Cummins 1992, Biggs 1995, Poff and Allan 1995, Richards et al. 1996, 1997, Roth et al. 1996), the relative influence of local and regional factors over species distribution and abundance and local community composition remains largely unknown.

A fundamental goal of basic ecological re-

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search is to *understand* how observed ecological patterns are generated by specific processes or constraints, thus allowing for valid generalizations (cf. Wiens 1984). Therefore, understanding patterns of distribution and abundance of lotic species requires that we test theoretical predictions about functional relationships between species and their environments across a range of spatial and temporal scales. Applied ecological research, by contrast, generally seeks to *predict* ecological patterns, often for the purposes of resource management. Although it may be possible to predict patterns of distribution and abundance without reference to biological mechanisms or scale (Moss et al. 1987, see Peters 1991), such non-mechanistic, correlative approaches are of uncertain generality. Including biological mechanisms and multi-scale environmental constraints in correlative approaches may make their predictions more robust and generalizable.

In this paper, I present a heuristic framework for considering how habitat conditions expressed at multiple scales influence the distribution and abundance of stream species. Specifically, I suggest that species can be described in terms of their *functional* relationships to various habitat features, which can be defined at different spatial scales and organized hierarchically (from microhabitat patch to watershed or basin). Both the functional attributes and habitat characterizations are considered to hold at geographic scales and thus have potentially broad generality. I refer to scaled habitat features as “filters” that influence the probability that individual species with specified functional attributes (species traits) are able to persist as members of a local community. Thus, the kinds of attributes expected in a local community (its functional diversity or organization) can be predicted at different scales of spatial resolution of stream “habitat.” Biotic interactions also serve as a potential filter on local community composition, but only if interactive species possess attributes suited to the scaled abiotic habitat constraints.

The individual components in this approach are well established in the literature, and the perspective presented here is an attempt to integrate them. I do not claim that this framework is exhaustive or definitive, or even easily testable; I propose it not as a substitute for existing approaches to stream community prediction,

but rather as a complement. Indeed, approaches or models such as the one presented here are perhaps impossible to falsify experimentally; their usefulness derives from how well different lines of evidence “fit” model predictions (Pickett et al. 1994), as is also the case for most ecological studies that have large-scale, comparative components (Pace 1991, Ricklefs and Schluter 1993). As long as such models are constructed logically from mechanistic principles, new data and knowledge can be used to refine the conceptual framework over time, thereby increasing ecological understanding and, potentially, predictive capability (cf. Wiens 1992).

My goals in presenting this biologically based, mechanistic framework are primarily to 1) encourage multi-scaled understanding and prediction in stream ecology, 2) generate discussion among stream ecologists about how to do this, and 3) emphasize critical knowledge gaps and research needs. In attempting to accomplish these goals, I 1) present a rationale for using species traits as predictors of species distribution and abundance and of community composition, 2) describe environmental filters and how they can operate at multiple spatial and temporal scales in a landscape hierarchy, 3) present a simple niche model to make hypothetical predictions about community composition at different habitat scales, and 4) discuss advantages and uncertainties of this multi-scaled filtering approach.

Species traits as functional units in predictive stream ecology

Orians (1980) argued that a predictive community ecology could be constructed based on ecological aggregate variables, if 2 conditions were met: 1) Aggregate variables should be mechanistically related to evolutionary principles, i.e., species should be aggregated into functional groups according to organismal attributes that are subject to natural selection, and 2) abiotic (rather than biotic) environmental factors should provide the primary foundation for theories of community structure based on ecological aggregate variables, because abiotic factors are minimally influenced by any co-evolved relations among species. Thus, habitats with similar environmental selective forces should have species with similar attributes or “adaptations” and therefore community structure (de-

fined in terms of the aggregate variables). This general approach to assessing community composition in terms of environmental constraints (i.e., community functional organization) has been used in several systems (e.g., Grime 1977, Southwood 1977, Wiens 1984, Schoener 1986, Menge and Sutherland 1987), including streams (e.g., Vannote et al. 1980, Poff and Ward 1990, Schlosser 1990, Townsend and Hildrew 1994). The challenge with this approach is identifying and quantifying habitat features in terms of selective forces that induce mortality (cf. Stearns 1992), and aggregating species according to traits that represent adaptive responses to these selective forces.

Ecological aggregation is controversial because information about individual species must be sacrificed (Hay 1994); however, the technique provides a powerful, biologically based tool for making the study of complex multi-species assemblages more tractable. Perhaps the best known aggregation method is grouping species into guilds of similar resource use (Root 1967). But environmental factors other than food or space resources may act to limit species distribution and abundance and thus contribute to predicting community responses to changes in habitat selective forces (Orians 1980, see Hawkins and MacMahon 1989). For example, Shelford (1911, 1912) grouped freshwater fish species based on physiological, behavioral, and life history traits to predict that similar habitats should be characterized by similar types of species, irrespective of taxonomic status. Grouping species according to functional similarity has received renewed interest in basic ecology (e.g., Keddy 1992a, 1992b, Smith et al. 1997) and has important management implications for applied ecology (e.g., Lenat 1993, Austen et al. 1994). In Table 1, I provide a selective summary of the breadth of use of species traits and functional groups in ecological investigations.

In stream ecology, Cummins (1973) defined functional feeding groups for aquatic invertebrates based on their mouthpart morphology and feeding behavior. Species traits other than those associated with feeding are now relatively well-developed for a wide range of lotic taxa (Table 1). These traits presumably represent functional relationships with important environmental selective forces, such as stream flooding or drying, local shear stress, temperature extremes, and human pollution. In recent years, a

few species traits have been combined with taxonomic indicators to produce indices of biotic integrity for fish (Karr et al. 1986) and macroinvertebrates (Kerans and Karr 1994, Fore et al. 1996).

Presently, using species traits to characterize or predict lotic community composition is largely univariate in approach, i.e., restricted to analysis of single or a few traits. However, using many traits simultaneously enhances understanding how species composition will change as environmental constraints vary across the landscape. A multi-trait approach to predicting community composition under variable environmental constraints has been suggested (e.g., Verner 1984) and has been pursued to some extent in streams (e.g., Statzner et al. 1994, Poff and Allan 1995, Rader 1997, Richards et al. 1997, Townsend et al. 1997).

For the concept of species traits to be useful (i.e., predictive) in stream ecology, traits must be defined in terms of *functional significance* relative to qualitative and quantitative habitat conditions. For some traits, this may be done a priori based on biological understanding and theory. For example, energy sources influence relative success of foraging mode or trophic groups (Cummins 1973); fast generation time promotes persistence in temporally unstable environments (Gray 1981); and substrate availability constrains reproductive success of certain fishes (Balon 1975). Determining how to group species for other traits is more difficult. Correlative approaches may be justified when species distribution and abundance are examined in response to strongly selective physiological gradients, for which an unambiguous, mechanistic interpretation is available. Examples include broad-scale comparative studies that have established differences in thermal and silt tolerances of fishes (Ohio EPA 1989, Eaton et al. 1995) and pollution tolerance of invertebrates (Hilsenhoff 1987, Lenat 1993). However, using correlative studies to infer differences among species in trait expression is often questionable, because these studies do not lend themselves to mechanistic interpretation, either because many habitat factors change across sites or because traits respond to more than one habitat factor. For example, dorso-ventral flattening in macroinvertebrates may be an "adaptation" to reduce drag and allow persistence in areas of high shear stress (Statzner and Holm 1982), or to al-

TABLE 1. Selected examples of functional species traits developed for various assemblage types.

System	Traits	Reference(s)
Stream hyphomycete fungi	Life history, dispersal, morphology	Pattee and Chergin (1995)
Stream bryophytes	Growth form, reproduction, flood resistance	Muotka and Virtanen (1995), A.M. Suren (NIWA, Christchurch, New Zealand; unpublished data)
Stream algae	Substratum preference Desiccation tolerance	Round (1964) Peterson (1987)
Marine algae	Growth morphology, resistance to grazing	Dring (1982), Steneck and Dethier (1994)
Riverine plants	Reproduction, dispersal, competitive ability Flood scour resistance, regeneration after disturbance	Barrat-Segretain (1996) Henry et al. (1996)
Wetland plants	Desiccation tolerance	van der Valk (1981), Day et al. (1988), Bouton and Keddy (1993), Hills et al. (1994)
Riparian plants	Competitive ability, height Water/salinity stress tolerance	Menges and Waller (1983) Busch and Smith (1995)
Terrestrial plants	Stress, disturbance, competition, life history, life form, dispersal, morphology, reproduction	Grime (1977), Grubb (1985), Montalvo et al. (1991), Leishman and Westoby (1992), Wilson and Roxburgh (1994), McIntyre et al. (1995), Smith et al. (1997)
Marine invertebrates	Trophic group	Menge et al. (1986), Bosman et al. (1987)
Terrestrial invertebrates	Trophic group	Crossley et al. (1976), Otto and Svensson (1982), Moore et al. (1988)
Zooplankton	Life history Body size	Allan (1976), Romanovsky (1985) Sheldon et al. (1972)
Stream invertebrates	Trophic group Pollution tolerance Flow exposure group Rheophily Morpho-behavioral group Body size Mobility, life history, flood resistance Drift "Drought" traits (e.g., flexible life cycle, protected egg, high vagility)	Cummins (1973) Hilsenhoff (1987), Lenat (1993) Gowns and Davis (1994) Merritt and Cummins (1996) Corkum and Ciborowski (1988), Merritt and Cummins (1996) Poff et al. (1993) Hawkins (1990), Cobb et al. (1992), Flannagan et al. (1992), Scarsbrook and Townsend (1993), Usseglio-Polatera (1994), Merritt and Cummins (1996), Richards et al. (1996), N. L. Poff (unpublished data), C. R. Robinson (EAWAG, Zurich; unpublished data), Statzner et al. (1997) Wilzbach et al. (1988), Rader (1997) Williams (1996)
Marine fish	Life history	Winemiller and Rose (1992)
Freshwater fish	Life history Trophic group	Shelford (1911, 1912), Winemiller and Rose (1992) Kushlan (1976), Horwitz (1978), Grossman et al. (1982), Schlosser (1982), Berkman and Rabeni (1987), Bayley (1988), Poff and Allan (1995)

TABLE 1. Continued.

System	Traits	Reference(s)
Small mammals	Habitat preference	Schlosser (1982), Leonard and Orth (1988), Lobb and Orth (1991), Kingsolving and Bain (1930), Poff and Allan (1995)
	Reproductive mode	Balon (1975)
	Body morphology	Gatz (1979), Bain et al. (1988), Scarnecchia (1988), Poff and Allan (1995)
	Pollution tolerance	Karr et al. (1986), Ohio EPA (1989)
	Turbidity tolerance	Brazner (1994)
	Thermal tolerance	Brazner (1994), Eaton et al. (1995), Smale and Rabeni (1995a)
	Hypoxia tolerance	Smale and Rabeni (1995a)
	Flood resistance	Detenbeck et al. (1992)
	Trophic group	Fox and Brown (1993), Kelt et al. (1995)
	Trophic group	Alerstam and Högstedt (1982), Verner (1984)
Birds	Trophic, breeding, and migratory strategies	Dolédéc et al. (1996)

low access to small crevices away from fast flow (Nielsen 1951), or both. Experimental investigations of the functional significance of traits in a given environmental regime can help determine the usefulness of such traits (see Keddy 1992a). In this vein, Wilzbach et al. (1988) experimentally demonstrated that macroinvertebrate species with non-streamlined body shapes are more easily eroded from areas of high shear. Thus, high flow areas may tend to select against non-streamlined species (but such species may nonetheless occur in sheltered habitats in high flow areas). Similarly, Smale and Rabeni (1995a, 1995b) experimentally determined hypoxia and hyperthermia tolerances in the laboratory for headwater stream fishes to predict community composition among streams varying in dissolved oxygen and thermal characteristics.

Multi-scale habitat filters and functional organization in streams

Environmental conditions can be viewed as constituting “filters” through which species in the regional species pool must “pass” to potentially be present at a given locale (Tonn et al. 1990). The species pool includes all species in a region (summed over all microhabitats). Given long time periods, all species are assumed capable of dispersing to all locales in the region; therefore, the absence or low abundance of a species at a locale reflects the action of selective

filters, which are essentially habitat features that can be defined at any scale (see Tonn 1990, Tonn et al. 1990). To pass through a filter, a species requires organismal traits that match the selective characteristics of the filter(s). Keddy (1991, 1992a, 1992b, 1994) has argued that a filters framework can facilitate understanding about how communities are assembled and how they respond to environmental change. Empirical examples of this approach exist, at least for wetland plants at the local scale (van der Valk 1981, Weiher and Keddy 1995). In principle, it should be possible to make scaled predictions about local community composition in streams (and other systems) by considering *multiple* landscape filters.

The hierarchical, landscape-scale view of stream habitat proposed by Frissell et al. (1986) provides a useful conceptual context for many aspects of both basic and applied stream ecology (e.g., Poff and Ward 1990, Gregory et al. 1991, Bayley and Li 1992, Naiman et al. 1992, Hawkins et al. 1993, Maxwell et al. 1995, Imhof et al. 1996, Jensen et al. 1996, Rabeni and Sowa 1996, Townsend 1996). These authors have described slightly different numbers of levels and diversity of elements within levels in their habitat hierarchies, reflecting various research interests. I specify a set of only 4 habitat levels, a minimum number that span the relevant scales for a wide range of lotic species, both inverte-

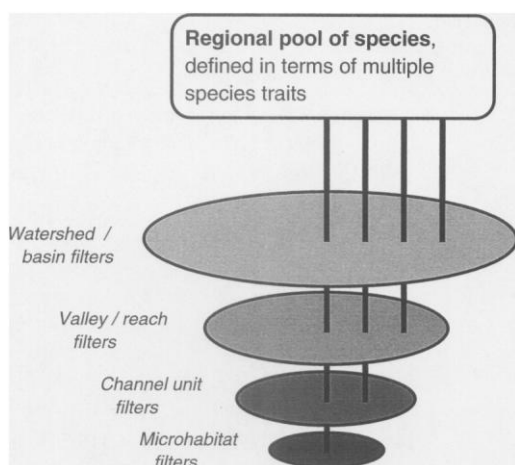


FIG. 1. Distribution and abundance of species reflects their possessing traits that allow them to “pass” through multiple habitat filters (abiotic + biotic) at hierarchical spatial scales (see Table 2). Species that lack traits suitable for passing through a large scale filter are limited in abundance at all lower scales (indicated by truncation of vertical lines). For example, occurrence of species in a particular type of microhabitat means they possess traits suitable for prevailing watershed/basin, valley bottom/stream reach, and channel unit habitat conditions that make up the set of multiple hierarchical filters in which that particular microhabitat is nested.

brates and vertebrates. The levels are, from coarsest to finest: basin or watershed, stream valley bottom or stream reach, channel unit (e.g., riffle/pool), and microhabitat (e.g., sediment patch). These levels provide a useful first approximation for identifying habitat filters that may operate to influence species distribution and abundance across the landscape (Fig. 1). Because environmental factors associated with different spatial and temporal scales can influence species distribution and abundance, considering the selective action of habitat filters at multiple scales can increase understanding and predictive ability in ecology (see Duarte 1991). Accordingly, identifying species traits that are sensitive to habitat characteristics at different levels will likely enhance our ability to predict how species distribution is regulated across the landscape. For example, riparian vegetation can directly constrain the distribution of shredding invertebrates (Molles 1982), so that even when microhabitat conditions are otherwise ideal, species requiring coarse leaf litter will vary in their

local distribution within or among basins, depending on the presence of suitable riparian conditions (a constraint imposed at a scale above the local microhabitat).

The concept of multi-scale filters could be viewed as an analogy, because environmental selective forces operate on individuals in local habitats. However, in a hierarchical context, large-scale constraints (filters) are causative or mechanistic agents (Pickett et al. 1994), precisely because they can constrain expression of local selective forces or biotic potential by influencing vital rates, such as mortality and reproduction (see Rabeni and Sowa 1996). Further, as mechanistic integrators of small-scale habitat selective forces, they have predictive potential as statistical surrogates. For example, hydrologic variability measured at the basin scale may serve as a coarse filter on community composition, not because it imposes mortality directly on species having inappropriate traits, but because it influences aspects of local habitat stability (Poff and Allan 1995, Richards et al. 1997), which can select directly against traits. Coarse landscape filters cannot and should not be expected to explain all local variation in biotic composition, because they represent an averaging of *variability* in finer scale habitat features that are relevant to the biota (Allen and Starr 1982). In the disturbance example, if local habitat provides refugia from extremely high or low flows, then the ability of the basin filter to predict community composition based on “flood” or “drought” traits would be reduced (see Townsend et al. 1997).

Although the need for multi-scaled environmental predictors of species distribution or community composition has often been identified by stream community ecologists (e.g., Strayer 1983, 1993, Corkum and Ciborowski 1988, Schlosser 1991, Cummins 1992, Richards and Host 1994, Poff and Allan 1995, Rabeni and Sowa 1996, Richards et al. 1996, 1997, Suren 1996), general organizational frameworks are rare (but see Imhof et al. 1996 for an example). In Table 2, I use a hierarchical habitat classification to identify landscape features that can be expressed in terms of habitat filters that *potentially* select against particular traits of aquatic species. Much of the information in Table 2 is based not on empirical data, but on potential landscape filters and species traits suggested by the literature (see Table 1). (Thus, this informa-

tion should be viewed as a starting point for discussion.) These filters range from broad-scale constraints to the local microhabitat filters familiar to most ecologists. Biotic filters, which can be very important, are most easily invoked at local scales, after the tolerances of species to local abiotic factors have been established (Tonn et al. 1990, Keddy 1992a). I restrict consideration of species traits to macroinvertebrates and fish, mainly because these groups are well studied. Although taxonomic uncertainties associated with species-level identification of aquatic insects may complicate species trait assignments, traits for invertebrate genera may be adequate given the frequently overlapping ecological roles played by conspecifics (Wiggins and Mackay 1978). Most multi-scale work on other groups, such as algae, has focused on taxonomic diversity or components of production rather than species traits per se (e.g., Biggs 1995, Stevenson 1997). These alternative response variables might be placed in a multi-scale framework; however I do not pursue that here.

In principle, associating species traits with landscape filters allows us to predict which species are likely to be removed from the regional species pool at a particular scale. A challenge, however, is specifying at what scale (or scales) a filter operates. For some filters, this is not difficult because they are associated with only 1 habitat scale. Shear stress, for example, is inherently local. By contrast, other filters may be assigned to more than 1 habitat scale. Temperature conditions, which greatly influence species distribution and abundance (Vannote and Sweeney 1980) vary at many scales in response to climate, elevation, land use, riparian shading, and groundwater. Consequently, species traits associated with thermal tolerance may potentially be selected against at any of several habitat scales.

Knowing the coarsest scale at which a filter can be applied will depend on defining the degree of hierarchical constraint among filters, i.e., how strongly habitat features at one scale regulate habitat features at the lower scale(s). Returning to the disturbance example, if basin hydrologic regime is used as a surrogate for the various components constituting a disturbance filter, its utility as a predictor of "disturbance traits" will probably depend on how strongly it correlates with channel morphology (valley-reach scale), sediment size distribution (channel

unit scale), and hence microhabitat stability. The high relative abundance of multi-voltine macroinvertebrate taxa has been associated with such a coarse-grained filter in certain tributaries to the Great Lakes which are flashy due to clay soils (Richards et al. 1997, N. L. Poff, unpublished data). In other geologic settings, tight linkages among habitat levels may not occur, and a disturbance filter might not be as predictive at a coarse scale.

Given these caveats (e.g., functional significance of species traits, scale of filter action, hierarchical constraint among filters), the initial attempt to identify filters and associated species traits in Table 2 should be viewed as preliminary and speculative. The purpose of the table is to stimulate critical evaluation, modification, and additional research.

A niche model to filter species traits at different habitat scales

A useful guide to operationalize the proposed filtering framework is provided by Brown et al. (1995), who used a simple model to explain geographic patterns in local abundance of bird species based on abiotic niche requirements. The Brown et al. model assumes that species performance is continuously distributed along several limiting environmental axes, to define each species' fundamental niche (*sensu* Hutchinson 1957). I simplify this approach by defining both environmental axes and species performances along environmental axes as categorical variables. This allows us to postulate a finite number of trait combinations (categorical "niches") and provides a basis on which to predict how categorical change in environmental conditions (at different scales) will select against combinations of species traits (functional groups) and thus modify community composition.

As an example of how this approach might work, consider the strength of a filter to fall into 1 of 3 categories: 1.0 (strong), 0.5 (intermediate), and 0.0 (weak or absent). Similarly, consider that the resistance of a species trait to being filtered to have 1 of 3 states: 1.0 (unaffected by filter), 0.5 (moderate resistance), and 0.0 (weak resistance). Assume that species with highly resistant traits (i.e., trait strength = 1.0) are not removed by any filter; species with moderate resistance (trait = 0.5) are affected only by the strongest filter, which is arbitrarily defined as

TABLE 2. Speculative generalized relationships between hierarchical landscape features, system attributes, landscape filters, and associated species traits (see Table 1). Particular filters may be associated with more than one landscape level depending on particular biophysical settings.

Spatial scale	Landscape feature(s)	System attribute(s)	Constraint or filter	Traits	
				Macro-invertebrates	Fish
Basin/watershed	History	Species evolution and dispersal	Biogeography	Taxonomic, distribution range	Taxonomic, distribution range
	Climate	Hydroclimatology	Seasonality of flow	Life history	Life history
			Intermittency/permanence	Life history, tolerance, behavioral avoidance	Life history, tolerance, behavioral avoidance
	Climate and geology	Biome	Vegetation	Trophic group	?
		Hydrologic regime	Flow variability	Generalization	Generalization
			Flood frequency	Life history, body size	Life history, body size
			Drought frequency	Drought traits	Life history, body size, mobility, tolerance
		Thermal regime	Temperature extremes	Thermal tolerance	Thermal tolerance
		Water chemistry	pH, Inorganic nutrients	pH sensitivity	pH sensitivity?
	Human activity	Land use pattern	Human impact	Pollution tolerance	Pollution tolerance
			Enrichment	Pollution tolerance	Pollution tolerance
		Urbanization	Siltation	Silt tolerance	Silt tolerance
			Increased flashiness	Flood resistance ^a	Flood resistance ^b
		Channelization	Increased flashiness	Flood resistance ^a	Flood resistance ^b
		Barriers	Barrier to movement	Migration traits	Migration traits
Valley/reach	Confinement, slope	Flood stream power	Flood intensity	Flood resistance ^a	Flood resistance ^b
	Lithology	Sediment size range	Litho-habitat	Sediment preference	Reproductive mode
	Stream size	Width/depth	Habitat volume	?	Body size
	Valley width	Riparian influence	Food resource base	Trophic group	Trophic group
	Land use	Riparian conditions	Wood, cover	?	Habitat group
			OM inputs, cover	Trophic, habitat groups	Trophic, habitat groups
	Channel morphology	Bankfull geometry	Flood intensity	Flood resistance ^a	Flood resistance ^b
		Thermal regime	Temperature extremes	Thermal tolerance	Thermal tolerance
Channel unit	Morphometry	Channel hydraulics	Water velocity	Rheophilic	Current preference

TABLE 2. Continued.

Spatial scale	Landscape feature(s)	System attribute(s)	Constraint or filter	Traits	
				Macro-invertebrates	Fish
Microhabitat		Pool depth	Habitat volume	N/A	Body size, depth preference
	Substrate size distribution	Substrate availability	Substrate requirement	Body size	Spawning group
		OM retention	CPOM export	Trophic group	—
		Embeddedness	Lack of interstitial space	Morpho-behavioral, body size?	Spawning group
	Vertical hydraulic exchange	Interstitial flow	Oxygen or temperature requirement	?	Spawning
	Maximum sediment size, wood	Flood refugia	Substrate mobility	Flood resistance ^a	Flood resistance ^b
	Water depth, velocity	Nearbed hydraulics	Hydraulic stress	Flow exposure group, morpho-behavioral group	Body morphology
	Particle size/-wood	Substrate type	Substrate requirement	Substrate preference	Substrate preference
		Flood refugia	Substrate mobility	Body morphology, behavioral avoidance	?

^a High mobility, resistance to crushing, fast population turnover time, high fecundity, etc

^b Body shape, mobility

having a 50% chance of removing them; and species having weak resistance (trait = 0.0) have a 50% chance of removal by intermediate filters, but a 100% chance of removal by strong filters. The choice of 3 filter and 3 trait strengths, though arbitrary, represents the simplest expansion beyond a binary ("on/off") condition.

A hypothetical example is presented in Table 3, which illustrates how predictions about species filtering can be made at multiple spatial scales using the categorical niche model and making several assumptions. For each landscape level, the associated filters are identified and contrasted with the potential species traits influenced by those filters. Each trait-filter combination receives a numerical score (the *probability* that species possessing specific traits will pass through the filter), as defined above. The joint probability associated with the suite of trait-filter combinations results from multiplying the individual probabilities together. This

multiplicative function emphasizes the importance of environmental factors that limit species distribution and abundance (see Brown et al. 1995). In this way, the model can be used to predict either the *categorical abundance* or the *relative likelihood* of occurrence of particular species at some specified scale of resolution, i.e., species that score highest would be expected to be the most abundant or to have the highest probability of occurrence, while those with low scores would not be abundant because of some limiting environmental factor(s) (see Table 3). Note that for cases where the lowest joint probability score is 0.0, the associated categorical abundance is "rare". This model should not be used to predict species *absence*, because it does not incorporate spatial factors (e.g., distance to refugia) and temporal factors (e.g., time lags) that can potentially influence species presence and absence (e.g., by regulating the effectiveness of dispersal).

TABLE 3. Hypothetical example of using a niche model to predict categorical abundance for 6 hypothetical species at 4 landscape scales. For each landscape scale, 2–3 filters are listed (cf. Table 2) along with species trait strengths for each filter. High values for trait strength indicate “tolerance” for landscape filter. Each filter is assigned a hypothetical strength, which determines the likelihood that a species with a given trait strength relative to the filter will pass through the filter (see text for clarification of numerical system). The categorical abundance for each species at each landscape level is calculated by multiplying the conditional trait strengths within a landscape scale. The potential status of categorical abundance (or likelihood of occurrence) for each species at each landscape scale is characterized as abundant (A), common (C), uncommon (U), or rare (R). The landscape scale characterized by the lowest categorical abundance is indicated as “limiting”.

A. Strength of filters relative to traits

Landscape filter	Trait strength for species						Hypothetical filter strengths	Likelihood of passing through filter for species					
	1	2	3	4	5	6		1	2	3	4	5	6
Basin/watershed													
High temperature	1	0.5	0	0	0.5	0	Interm. (0.5)	1	1	0.5	0.5	1	0.5
Nutrient enrichment	1	0.5	0	0.5	0	0.5	Strong (1.0)	1	0.5	0	0.5	0	0.5
Stream acidity	1	0.5	0	1	0.5	0.5	Weak (0.0)	1	1	1	1	1	0.5
Valley/reach													
Flood intensity	1	0.5	0	0.5	1	0	Strong (1.0)	1	0.5	0	0.5	1	0
Fine sediments	1	0.5	0	0.5	0.5	0	Interm. (0.5)	1	1	0.5	1	1	0.5
Lack of CPOM input	1	0.5	1	0.5	0.5	1	Interm. (0.5)	1	1	1	1	1	1
Channel unit													
Water velocity	0	0.5	0.5	0.5	1	0	Interm. (0.5)	0.5	1	1	1	1	0.5
CPOM export	1	0.5	0	0.5	0.5	1	Weak (0.0)	1	1	1	1	1	1
Embeddedness	1	0.5	0.5	0	1	0.5	Strong (1.0)	1	0.5	0.5	0	1	0.5
Microhabitat													
Hydraulic stress	0	0.5	0.5	0	1	0	Interm. (0.5)	0.5	1	1	0.5	1	0.5
Substrate mobility	0	0.5	0.5	0.5	1	0	Interm. (0.5)	0.5	1	1	1	1	0.5

B. Species categorical abundances

Species	Basin/watershed		Valley/reach		Channel unit		Microhabitat		“Limiting” landscape scale
	Score	Status	Score	Status	Score	Status	Score	Status	
1	1.0	A	1.0	A	1.0	A	0.25	U	Microhabitat
2	0.5	C	0.5	C	0.5	C	1.0	A	“none”
3	0	R	0.0	R	0.5	C	1.0	A	Basin/watershed, valley/reach
4	0.25	U	0.5	C	0.0	R	0.5	C	Channel unit
5	0.0	R	1.0	A	1.0	A	1.0	A	Basin/watershed
6	0.125	U	0.0	R	0.25	U	0.25	U	Valley/reach

In the example, predictions about species distribution and categorical abundance in communities differ depending on the level of habitat information used to make the prediction. For example, species 3 is predicted to be “rare” at both the basin/watershed and the valley/reach scales (because of intolerance to nutrient enrichment and flood intensity) but “common” to “abundant” at the channel unit and microhabitat scales. By contrast, species 1 is “limited” in

categorical abundance at the microhabitat scale. Changing filter strengths (i.e., defining a new set of habitat conditions) could alter the abundance predictions. For example, if the nutrient enrichment filter were weak, then species 3 and 5 would no longer be “limited” at the basin/watershed scale. The example provided in Table 3 illustrates the desirability of considering multiple scales of habitat constraint on species distribution and community composition.

Critical uncertainties and research needs in developing a multi-scale filtering framework

Using the filtering framework to understand variation in community composition across the landscape will clearly require additional research. Critical uncertainties exist with respect to characterizing and quantifying the components of the filtering framework (i.e., abiotic filters, biotic filters, and species traits) and with respect to assessing the usefulness of a niche-based approach (versus alternative biologically based approaches) to predicting species distribution and abundance and community composition.

Abiotic filters

The degree of hierarchical constraint that large-scale habitat descriptors impose on small-scale habitat features is not well understood. Although there are some examples—e.g., basin agricultural land use may predict local habitat quality (Roth et al. 1996) or water quality (Hunsaker and Levene 1995)—there is a need for better understanding of how tightly linked habitat features are at different hierarchical levels. For example, how the quantity and distribution of particular categories of smaller-scale habitat elements (e.g., refugia) vary as a function of large-scale features (e.g., hydrologic regime, geologic heterogeneity) is not known. Similarly, the degree to which local thermal conditions are regulated by basin features (e.g., elevation) vs. valley/reach scale variables (e.g., channel morphology) is poorly understood, as is how these relations may change geographically (C. P. Hawkins, Utah State University, unpublished data). GIS-based research that incorporates multiple scales of habitat description could be used to establish these linkages (e.g., Meixler et al. 1996, Richards et al. 1996, Roth et al. 1996). Knowledge of functional (or statistical) habitat linkages across hierarchical levels (as well as correlations among filters within levels) not only will help to provide a basis for predicting species distribution and abundance at different scales, but also will contribute to many other areas of stream ecology.

Biotic interactions

Biotic interactions serve as filters that influence species distribution and abundance, and

they are generally viewed as operating at the local scale, after species elimination by limiting abiotic conditions (Torn et al. 1990, Keddy 1992a). Quantifying the nature of biotic filters is important, but is likely to be difficult. For example, it is not presently feasible (and may never be) to construct a matrix of pairwise species interaction coefficients for all species in the regional species pool to assess how combinations of species potentially present at a locale could modify each other's abundance or likelihood of occurrence. One promising avenue, however, may be to focus on key taxa that are strong interactors—e.g., keystone or dominant species (Power et al. 1996) or ecosystem engineers (Jones et al. 1994)—and to identify their particular environmental limits. If such strong interactors can occur in a community based on abiotic conditions, then we could adjust our predictions of community organization based on the impact(s) of these taxa. However, generalizations about the role of strong interactors (and biotic interactions in general) present special challenges (see Power et al. 1996), because interactive strength itself may vary with abiotic context at a local scale (Dunson and Travis 1991), as has been illustrated experimentally in streams with crayfish (Crowl 1990, Hart 1992), cased caddisflies (Poff and Ward 1995, Power 1995, Wootton et al. 1996), and fish (Baltz et al. 1982, Flecker 1997). Large scale habitat features, however, may also influence the distribution and abundance of strong interactors, as by creating barriers to movement (e.g., Townsend and Crowl 1991), or possibly by constraining the availability of refugia. Examining species interactions in a multi-scale context (Cooper et al. 1997, Crowl et al. 1997, Kohler and Wiley 1997, Peckarsky et al. 1997) should facilitate understanding of the scales at which biotic filters operate.

Species traits

Ecologists have characterized species traits for a limited number of taxa (Table 1), yet additional research is needed to test predictions about changes in community composition across the landscape (see Keddy 1991, 1992a, 1992b). Clearly, more research is needed to quantify species traits in stream organisms (especially invertebrates), using both a priori biological understanding and experimental methods, as dis-

cussed previously. Collecting additional information on traits should result in important biological insights and further our understanding of species–environment relations. For example, although I conveniently presented species traits as independent of one another, they are, in fact, correlated to various degrees (Statzner et al. 1994, Poff and Allan 1995, Rader 1997, Townsend et al. 1997, N. L. Poff, unpublished data). Understanding these correlations is important, because they may define “syndromes” of traits that respond in concert to the presence, or modification, of a particular filter. Thus, specifying among-trait correlations may help us predict which filters are most likely to broadly influence species distribution and the functional organization of communities.

Biologically based models of community prediction

The categorical niche model presented here is only 1 example of how species trait information can be combined with environmental information to predict species distribution and community composition across the landscape. Its heuristic value is that the relevant components can be easily illustrated (e.g., filters at multiple scales, species responses to filters) and they provide a *biological basis for expectation* of species distribution and categorical abundance. The framework therefore provides a formal structure to organize or outline (but not limit) thinking about species–environment relations at multiple scales.

Alternative mechanistic approaches to community prediction can also be pursued. For example, regression techniques that predict community composition based on species traits and environmental factors have been proposed and tested using large scale habitat filters (Poff and Allan 1995, Richards et al. 1997, N. L. Poff, unpublished data) and local habitat filters (e.g., Scarsbrook and Townsend 1993, Statzner et al. 1994, Townsend et al. 1997). The regression approach does not require explicit, quantitative assumptions about how species are filtered by environmental features, in contrast to the categorical niche model, which specifies a multiplicative function (and probability levels) to emphasize the role of filters that limit species distribution (see Brown et al. 1995). Indeed, the regression technique may be very valuable in terms of specifying statistical correlations

among filters and among traits that can obviate the need for detailed understanding and thus provide “shortcuts” to mechanistic predictions. Ultimately, stream ecologists need good biological information before they can predict how multi-scale environmental factors constrain community composition. Selecting the particular model(s) to accomplish this goal is less important than recognizing that we currently require much more basic information on the relations between species traits and landscape filters.

Utility of the multi-scale filtering framework

Biological and ecological systems are complex and variable in space and time. Attempts to characterize these dynamic and variable systems in a rather static fashion with the aim of generalization (e.g., the filtering framework and niche model presented here, see also Schoener 1986) imply that only coarse-grained predictions can be made. Qualitative predictions (i.e., categorical abundance, relative likelihood of occurrence) may be supported while quantitative predictions (e.g., absolute abundance) are unrealistic. Qualitative predictions allow “noise” from natural variability to be minimized. For example, sites having presumably different habitat filters may share the same species and have similar species richness, perhaps as a result of non-selective dispersal, while the *relative success* (i.e., categorical abundance) of constituent species can vary in accordance with environmental conditions (e.g., Death 1995, Feminella 1996). A filtering framework contributes to a mechanistic understanding of those differences in relative success; it cannot be invoked to explain the presence of “unexpected” species.

Progress in population and community ecology requires that we consider constraints operating at variety of spatial and temporal scales (Ricklefs and Schluter 1993), and that we be able to generalize across biogeographic domains. This framework addresses those challenges; therefore, it may be able to contribute to greater ecological *understanding*, an important, general scientific goal (Pickett et al. 1994). Further, by focusing on species traits and environmental limiting factors, the framework may contribute to increased *prediction* in stream ecology by substituting simple mechanistic relations for complex, detailed processes (cf. Orians 1980). I do

not advocate that the multi-scale filtering framework replace existing approaches to community prediction (e.g., Moss et al. 1987, Wright 1995), but I do suggest that such non-mechanistic approaches can be strengthened by incorporating additional biological understanding (as has been *partially* done by developing biocriteria—e.g., Karr et al. 1986, Fore et al. 1996) and by explicitly considering environmental constraints imposed at different scales.

Determining the degree of predictability of community composition associated with different levels of habitat description would represent an important advance in stream ecology and have obvious management applications. For example, how much additional variation in community organization (proportional representation of species traits or of particular species) is explained by characterizing environmental filters exhaustively at the local vs. basin level using readily available GIS data? At what scale(s) does habitat need to be manipulated to enhance or restore functional organization of degraded stream communities? Can we better predict the likelihood of local establishment (and spread) of exotic species by focusing on their functional attributes relative to prevailing landscape filters? Similarly, can we predict how species composition in communities might change in response to modification of environmental filters at a variety of scales ranging from local habitat to regional climate change? These and other broad questions can be adequately addressed only when we have gained a better understanding of how scaled environmental factors constrain species performance and distribution across the landscape.

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