Advanced Review

A 'behaviorscape' perspective on stream fish ecology and conservation: linking fish behavior to riverscapes

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Landscape ecology (and its application to rivers and streams: riverine landscapes or riverscapes) provides an expansive depiction of patterns of physical and biological phenomena, yet mechanisms driving those patterns are rarely identified. Behavioral ecology aims to elucidate mechanisms of organisms' response to their environment, but often lacks the context of natural conditions and the surrounding landscape or riverscape. Bringing together the relative strengths of these two fields—context in the case of riverscapes and mechanism in the case of behavioral ecology—can provide fisheries managers and conservation biologists with improved predictions of fish response to anthropogenic impacts such as habitat degradation, landscape fragmentation, and climate change. Existing research on fish behavior incorporating a riverscape perspective includes the study of fish migration and dispersal, habitat selection, and reproduction and life history strategies. The merging of these disciplines is termed 'behaviorscapes' and a program of research would adhere to four principles: (1) study fish populations or communities in a natural setting, (2) account for landscape and riverscape context, (3) incorporate a refined understanding of fish behavior, and (4) forge linkages between individual behavior and population or community demographics. Several potential directions for future research exist, including developing or improving technologies to map internal heterogeneity of rivers; making explicit links between that heterogeneity and fish behavior through observations or experiments; and employing an iterative approach to using ecological knowledge, *a priori* hypotheses, and precise spatial analysis to bridge the pattern-process divide.

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INTRODUCTION

Ecology is an interdisciplinary field integrating the study of organisms, their environment, and the interaction between organisms and environment.[1] Even so, the various sub-disciplines of ecology are often practiced separately as if in a vacuum, each having emphasis on either physical or biological processes. Landscape ecology[2] and its extension to rivers—termed 'riverscapes'[3] or 'riverine landscapes'[4]—have made strides in describing patterns, but often stop short of explaining mechanisms driving those patterns.[5] Behavioral ecology, on the other hand, has made tremendous contributions to mechanistic understanding of animal behavior, including their dispersal and migration, habitat selection, and reproductive and life history strategies[6]; but often lacks context of natural conditions and the surrounding landscape in which populations and communities

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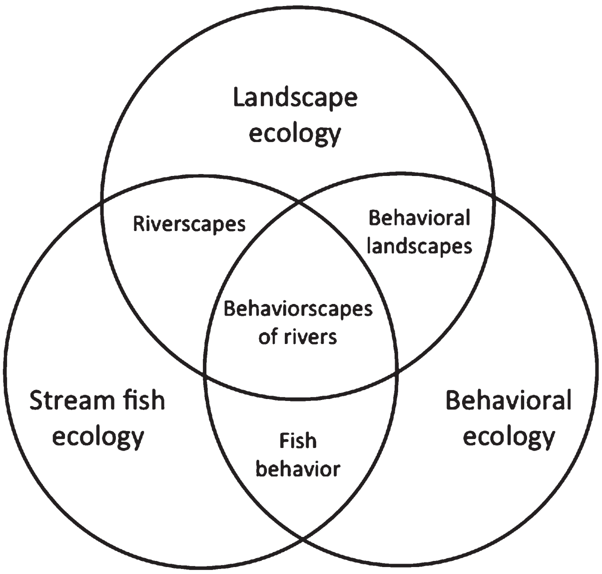

FIGURE 1 | A 'behaviorscape' approach to the study of riverine systems lies at the intersection of landscape ecology, stream fish ecology, and behavioral ecology.

live. The intersection between seemingly disparate fields is often the nexus of creativity, sparking new ideas and generating novel hypotheses.[7] We propose that the intersection among landscape ecology, stream fish ecology, and behavioral ecology (Figure 1) is one such instance of a fruitful union that can contribute to the understanding and conservation of stream fish and their habitats.

This article is not intended to be a thorough review of the discipline of landscape ecology of rivers, or of behavioral ecology as it relates to fish, but a synthesis of the disciplines as they relate to a potential union. We first outline the historical context and current direction of research on riverine landscapes; next we highlight relevant themes in behavioral ecology as they relate to stream fish; and finally we propose a 'behaviorscape' approach to stream fish ecology, starting with examples of research that partially or completely meet the expectations of the union and ending with a justification of four principles for behaviorscapes.

LANDSCAPE ECOLOGY OF STREAMS AND RIVERS

Landscapes and Riverscapes

In an earlier edition of the widely used undergraduate textbook *Ecology*,[8] the reader is introduced to the discipline of landscape ecology by way of the ancient Japanese tradition of climbing a nearby hill each spring. The tradition, called *kunimi*—meaning to see (*mi*) the domain (*kuni*)—was likely meant to assess the interior and boundaries of community property from a perspective not afforded in the lowland valleys, but only from the surrounding heights. The discipline of landscape ecology interprets landscapes from a similar broad perspective (see Box 1) and has recently been defined as 'the science of studying and improving the relationship between spatial pattern and ecological processes in a landscape at multiple scales'.[9] This includes the investigation of spatial relationships among ecosystems or 'landscape elements', the functional interactions among those landscape elements such as flows of energy or species, and the alterations in the structure and function of the landscape mosaic over time.[2] Inherent in this perspective

BOX 1

THE LANDSCAPE METAPHOR

The preeminent 11th century landscape painter Guo Xi from Henan Province, China, proclaimed, 'Landscapes are large objects and he who looks at them must do so from a distance if he is to grasp the form, the position, the spirit, and the image of mountains and streams'.[11] Later, in Europe, the painting *Landscape with Charon Crossing the Styx* by Patinir[12] portrays Charon rowing souls of the dead across the river at its central focus. To the left and right are tributaries flowing from Heaven and Hell with headwaters emerging from the fountain of Paradise and from Hades. The river's two banks are rendered with expert use of perspective, color schemes, and brush texture to impart scale and mood of the expansive scene. The term landscape derives from the Dutch *landschap* and was first used to describe the method of painting fantastical interpretations of natural scenery, typically infused with religious themes.

Ecologists have co-opted the landscape metaphor through the exploration of fitness landscapes,[13] landscape genetics,[14,15] behavioral landscapes,[16] landscapes of fear,[17] landscapes of food,[18,19] seascape ecology,[20] and even underwater soundscapes.[21,22] Metaphors are useful vehicles form communicating complex concepts,[23] and the landscape metaphor appears to be a particularly useful concept accounting for the simultaneous local and expansive perspectives required to understand how individuals, populations, and communities interact in their environment.

is the importance of scale of observation—both spatial and temporal—on interpretations made by the researcher or land manager, a phenomenon that is not unique to landscapes but general to all of ecology.[10]

Landscape ecology provides many important insights for conservation of populations and communities, such as managing protected areas in context of the surrounding landscape, aligning scales of management and administration to those of populations or ecological processes, and incorporating human values into restoration design. A landscape perspective also provides direction on what spatial and temporal scales to designate reference conditions and in setting restoration priorities.[24] For all these benefits, stream ecologists and fisheries biologists have been slow to adopt principles of landscape ecology.[3]

Studies of terrestrial ecosystems have primarily driven the development of landscape theory, for example: quantification of size and shape of forested patches in Ohio landscapes,[25] mapping fractal geometry of Great Britain's coastline[26] and the consequences for biota of coastline geometry in Alaska,[27] or the dispersal of small mammals in experimentally manipulated prairie landscapes of Kansas representing various levels of fragmentation.[28] Drivers of fragmentation of European landscapes (especially transportation networks and developing areas) have received special attention in both research and policy arenas because of their pervasiveness throughout the continent and documented negative impacts on migrating wildlife.[29] Work in terrestrial systems contributed to the important concept of metapopulations,[30] which implicates the spatial and temporal environmental heterogeneity and arrangement of habitats in the local extinction and colonization of multiple, interdependent populations. Prior to the formal integration of rivers and landscapes, landscape ecologists typically treated rivers as simplistic elements of a broader landscape mosaic, sometimes as linked with their surrounding terrestrial environments through material and energy flows, and only occasionally as internally heterogeneous landscapes in their own right.[4]

Freshwater scientists, although informally incorporating a landscape perspective for decades, have more recently formalized landscape ecological thinking into a 'riverine landscape'[4] or 'riverscape'[3] perspective (see Figure 2). These schools of thought have three major themes in common. First, streams and rivers are strongly influenced by surrounding riparian and terrestrial conditions[31–35]; second, the hierarchical nature of streams and the importance of

FIGURE 2 | The Willamette River in Oregon, USA, displays a diversity of surrounding landscape elements (foothills, forests, and fields) and riverscape features (meanders, islands, bars, and floodplain pools). (Courtesy of Eric Buist, Freshwaters Illustrated).

spatial and temporal scale[36–38]; and third, variability of riverine processes in space and time as the object of study versus statistical noise. Examples of the latter theme include the 'serial discontinuity concept'[39–41] describing departures from a predictable gradient of riverine properties such as water temperature or primary productivity, the 'flood pulse concept'[42] describing the temporal variability in river flow and its impact on biological communities, or the influence of the spatial arrangement of resource patches on biota.[43–46] Basin shape, network geometry, and confluence effects (e.g., increased flow, fans, bars, and terraces) affect sediment distribution size,[47] which in turn affect the response of riverine biota. The branching network pattern and flow-dependency of streams and rivers has implications for how genes, individuals, and populations move through riverine systems.[48] The differential response of organisms to these characteristics of the landscape depends on their ecological, morphological, life history, and behavioral traits.[4]

A common misconception about integrating a landscape perspective into stream fish ecology is that sampling a large number of river reaches across very broad areas, then relating attributes of biota (e.g., fish occurrence or density) to basin-scale variables (e.g., ecoregions or geology) will substitute for mapping variability and complexity. On the contrary, current thinking is that in order to describe heterogeneity inherent in rivers, researchers must make observations in a spatially continuous fashion and over long time periods to match scales relevant to management, rather than studying typical reach lengths of 50–500 m and time periods of 2–4 years.[3] One way to account for physical heterogeneity of rivers over larger scales is to incorporate novel technologies[49] such as remote sensing of water temperature,[50,51] channel bathymetry,[52] or stream discharge.[53] Sampling biota over extensive regions and in a spatially continuous fashion often employs less novel technology but is nonetheless physically demanding and time consuming; however, approaches such as single-pass electrofishing,[54,55] streamside visual counts,[56] and snorkelling[50,57–60] have been employed to map spatially continuous distributions of stream fish. These approaches are complimented by recent developments in spatial analysis using accessible tools for geographic information systems (GIS) that account for the unique features of riverine environments, such as streamflow directionality and spatial autocorrelation along linear networks.[61]

What Is Missing? Mechanistic Understanding

In a chapter on fish community composition in *Methods in Stream Ecology*,[62] the authors state that 'conclusions drawn from descriptive studies are subject to the same problems as inferring the plot of a mystery novel by reading only the last paragraph'. In a similar vein, one critique of landscape ecology is that it fails to elucidate mechanisms behind observed patterns, threatening to turn the discipline into an obsolete endeavor with little relevance to real world management problems.[5] Specifically regarding landscape-scale riverine research, a recent review of the discipline's progress[49] suggests that a renewed focus on mechanisms—discerning the causal relationships behind observed patterns—will better facilitate contributions to conservation.

Recent advances in river classification based on land use history and fluvial geomorphology use a combination of remotely sensed information and ground-based 'reading' of the landscape, and may help researchers select sites in which to measure any number of variables of interest including fish occurrence or abundance.[63,64] However, while this and similar approaches increase our understanding of heterogeneity in the physical landscape, fish and other biota are still typically sampled for presence or abundance in a few disparate sites and averaged across categories of a river classification,[65] leaving the researcher to infer the distributions of biota across broad areas. When spatially continuous surveys of fish are coupled with detailed knowledge of the landscape, their distribution is not inferred but known.[50,59,66] However, the mechanisms driving their distribution are still inferred and can only be discovered through careful observation, experimentation, or application of ecological theory. Fortunately, an entire discipline is organized around the discovery of mechanisms that drive patterns and can provide insights and heuristic tools: behavioral ecology.[6,67] The next section summarizes relevant ideas of behavioral ecology related to riverine fish research and conservation.

BEHAVIORAL ECOLOGY OF STREAM FISHES

Applications of Behavioral Ecology

Behavioral ecology emerged from ethology as a means to 'understand how [animal] behavior evolves in relation to ecological conditions, including both the physical environment and the social environment (e.g., competitors, predators, and parasites)'.[6] The discipline is focused on four major questions about the causative factors, developmental explanations, functional consequences, and evolutionary history of the behavior of individuals and groups[68] (see Box 2). Each behavior expressed by individuals can be explained in terms of either its 'proximate' or 'ultimate' cause. Proximate explanations refer to the causal and developmental factors describing why and how behaviors are expressed, while ultimate causes explain why and how the behavior evolved. The range of topics within behavioral ecology is immense, but prominent areas of study include individual decision making, predator–prey interactions, competition for resources, group living and social behaviors, communication, and reproductive strategies (e.g., sexual selection, parental care, and mating systems).[6]

Two primary methods for describing the functional aspects of behaviors include comparative and experimental approaches. The comparative approach, Darwin's[69] method of choice but still a mainstay of the field, involves comparison of behaviors across species and seeking environmental correlates that explain their adaptive value. Previously, a major conceptual flaw in this approach was the relatedness of species and the resulting nonindependence of their behaviors, which made comparisons across closely related species problematic. However, since the 1980s, the explicit incorporation of phylogenies—the evolutionary relationships among species—has been used to control for these relationships, and it describes the order in which behavioral traits arise in a lineage.[70] The experimental approach—field applications advocated by Tinbergen—involves manipulating behaviors and observing the corresponding change in survival or fitness.[71]

BOX 2

TINBERGEN'S FOUR QUESTIONS OF BEHAVIORAL ECOLOGY

Imagine snorkelling a clear stream (see Figure 3(a)) and observing a school of fish. A juvenile bull trout, *Salvelinus confluentus* approaches and flashes its white underbelly in a seemingly aggressive manner. The trout reestablishes its position at the head of the pool in front of other fish and resumes foraging. One at a time, small drifting bits are picked out and rejected by the trout, but eventually it rises to the surface to capture an adult mayfly. What cues signalled the trout to your presence as a potential threat? When in its lifespan did the trout develop the ability or impetus to display aggression—was this a learned or inherited trait? The aggressive display caused the trout to momentarily lose its position in the hierarchy of foraging fish, so the behavior was potentially costly. What adaptive advantage was provided by the trout's risky display, and what was the trade-off in terms of lost feeding opportunity? And how did both these behaviors evolve from primitive precursors to more complex responses?

The Dutch Ornithologist Nikolaas Tinbergen is considered as the founder of behavioral ecology, a discipline aimed at answering these very questions about why given behaviors are observed in nature:[68] (1) what are proximate stimuli or mechanisms that *cause* a behavior? (2) how did the behavior *develop* ontologically? (3) what is the behavior's *adaptive advantage* or *function*? and (4) what is the *evolutionary history* or *phylogeny* of the behavior? These four questions still form the foundation of behavioral ecology.[6]

At first glance, much of behavioral ecology can be perceived as an ivory tower pursuit with questionable value as an applied science. However, potential contributions to conservation[72–75] and ecological theory[76,77] abound. Behavioral ecology can provide more accurate depictions of key demographic parameters used to understand population viability. The behavioral responses of wildlife to habitat degradation, landscape fragmentation, and road networks, for instance, affect population size (N), growth rate (r), and reproductive skew, which in turn affect effective population size (N_e).[78] Knowledge of individual behavior can provide understanding of how populations will respond to habitat fragmentation or degradation, disease, and reintroduction efforts, as well as provide useful information for population monitoring and modeling.[79] In fact, behavioral diversity has been posed as an equally important target for conservation alongside taxonomic and genetic diversity.[80]

What Is Missing? Natural Conditions and the Broader Context

Early behavioral ecology of terrestrial fauna—specifically insects,[81] birds,[68,82,83] and primates[83]—stemmed from influential ethologists that advocated observing subjects in the wild. These creatures could often be observed quite easily in nature—sometimes in one's own backyard—whereas fish are more obscure, living beneath the water's surface and less visible to scientists and the general public.[84] Perhaps for these reasons, even the most applied behavioral ecology research on fishes may be carried out while paying little attention to natural conditions.

The mismatch between the local spatial scales, where it is more efficient to observe animal behavior, and the broader landscape context has real implications: local-scale studies often point toward density dependence as a controlling factor for populations, yet at the population-scale density dependence rarely emerges as an important control.[85] Behavioral ecology has historically focused on individuals (especially model organisms[86]) that are easy to observe and experiment upon, whereas conservation biologists focus on populations and communities that face anthropogenic impacts such as habitat loss and degradation, and may be scarce and difficult to observe.[87] To make behavioral ecology relevant to real world fish management and conservation problems, it is critical to conduct research under the natural conditions and landscape contexts to which fish are exposed.

TOWARD A BEHAVIORSCAPE APPROACH

A behaviorscape approach builds from the strengths of landscape ecology, stream fish ecology, and behavioral ecology (Figure 1). While gaps have already been successfully bridged between the disciplines of landscape ecology and stream fish ecology[3,4] and between landscape ecology and behavioral ecology,[16] we argue that a formal integration between all three fields has not been achieved except in a few notable cases. To predict and mitigate animal responses to habitat degradation and climate change, a more refined understanding of animal behavior is required within a landscape context, specifically regarding movement, habitat selection, and reproductive strategies as they might occur in changing or novel environments.[77]

FIGURE 3 | (a) Snorkelling is an efficient method of surveying fish distributions and observing fish behavior in clear streams. (b) Male Chinook salmon (*Oncorhynchus tshawytscha*) migrating upstream to spawning grounds. (c) A school of foraging speckled dace (*Rhinichthys osculus*). (d) A male river chub (*Nocomis micropogon*), surrounded by Tennessee shiners (*Notropis leuciodus*), carries a stone to its nest. (Courtesy of Freshwaters Illustrated).

We therefore outline these broad categories of fish behavior[88–90] as they relate to riverine landscapes.

Behavioral Ecology with Applications to Riverine Landscapes

Movement

Schlosser and colleagues introduced a ‘dynamic landscape model of stream life history’[91–94] where fish move among often distant patches in the landscape to accommodate different life history stages (see Figure 3(b)). In a study of fish dispersal in beaver-influenced landscapes, migrations of young age classes of large lake species (e.g., black crappie, *Pomoxis nigromaculatus*; smallmouth bass, *Micropertus dolomieui*; yellow perch, *Perca flavescens*; and burbot, *Lota lota*) to smaller stream and pond complexes were inferred through sampling community structure and fish size classes at individual sites.[95] In a wilderness stream network, the more direct approach of using radio tags was employed to evaluate long-distance migrations of mountain whitefish (*Prosopium williamsoni*), bull trout (*S. confluentus*), and large-scale suckers (*Catostomus macrocheilus*), coupled with nested hierarchical observations of fish distribution patterns and habitat conditions to describe how dispersal affected fish community structure on a seasonal basis.[96] Torgersen et al., also using radio tags, found that spring Chinook salmon (*Oncorhynchus tshawytscha*) migrated to pre-spawning ‘holding’ habitats in spring based on pool availability, but when water temperatures warmed in summer moved to adjacent cool patches or ‘thermal refugia’, an observation only possible through continuous spatial mapping of the riverscape coupled with radio tagging across seasons.[50]

Movement and dispersal are perhaps the most difficult behaviors to observe directly, as they often occur in short time periods over vast distances (e.g., Atlantic salmon, *Salmo salar*, were recently observed straying extreme distances, from Great Britain to the Iberian Peninsula[97]) couple with the difficulties of tagging small and/or cryptic individuals. While some studies use inference about the behavioral mechanisms of dispersal—such as analysis of community structure at point-in-time sample locations[95]—other approaches can be employed such as models accounting for an organism's behavior, movement rules, and searching strategies;[98] incorporating the cognitive spatial maps of organisms;[99] or through direct experimentation.[77] An analysis of the state of movement ecology suggested a unifying framework based on first principles is lacking.[100] Advances in our understanding of the behavioral aspects of movement and dispersal of fishes will likely involve a more refined comprehension of their perceptual range and homing ability, which affects how fish respond to opening or closing of corridors or colonization from source to sink areas.

Habitat Selection

Fish, like most animals, select habitat based on the most suitable combination of biotic, abiotic, and spatial factors available to them[101,102] (see Figure 3(c)). Many stream fish are ideal organisms for testing habitat selection theories because they are mobile enough to assess patch quality on a regular basis,[103] which allows them to perceive and respond to differences in their potential food intake rates and other factors. Ideal free distribution (IFD)[104,105] is one prevailing theory of habitat selection that attempts to explain how organisms select habitat based on the combination of patch quality and competitors. IFD improved upon previous theories of habitat optimization[106] by accounting for the negative effect of competitors on patch quality. Over time, IFD theory has been enriched by a succession of models that have included additional factors such as predation risk,[107] refuge or cover for foragers, [108] asymmetric competition,[109] physiological demands,[110] and multiple species.[111–114] Since its origins more than 40 years ago, IFD theory has incorporated more realistic patch selection scenarios and has been repeatedly tested in several systems, yet the complex relationships among habitat, competition, and behavior are still poorly understood for fish—partly because many studies have not applied this theory in natural field settings.[115]

Notable exceptions where IFD was tested in natural settings include a study of grazing, armoured catfish (Loricariidae) in a Panamanian stream where habitat quality was defined by high rates of algal production, but even shady locations provided the same 'habitat quality' in terms of food production because of the higher competitor densities—and subsequently higher total grazing intensity—in so-called rich patches.[116] Using broad-scale surveys of fish distribution in Japanese streams invaded by brown trout, *S. trutta* and rainbow trout, *O. mykiss*, regression and isodar methods from community ecology revealed that endemic Asian white-spotted charr, *S. leucomaenis,* was negatively affected by invading trout.[117]

IFD is not the only theory of habitat selection but other approaches[118] also have implications for a riverscape perspective of fish ecology. For example, net rate of energy intake and resulting habitat selection by brown trout, *S. trutta,* were modeled based on hydraulic sheer zones, invertebrate drift, and fish bioenergetics and later verified in a New Zealand stream.[119] Other relevant research areas for habitat selection in riverine landscapes include the behavioral response of individuals to novel environments;[120] assessment of predation risk using chemosensory cues under varying environmental conditions;[121] positive interactions among individuals including behavioral refuges,[122] conspecific attraction,[123] and the benefits of aggregation[124]; and determining the appropriate spatial scale at which habitat selection occurs.[125]

Reproductive Strategies and Life Histories

Studies of reproductive strategies in fishes typically involve mating systems and sex allocation, sexual selection, and parental care[90] (see Figure 3(d)). Life history theory has served as an organizing concept explaining different reproductive strategies in environments with varying predictability in conditions. Building on the simplified *r* versus *K*-selected paradigm,[126] reproductive guilds of fishes were described[127] and later incorporated into a framework of life history theory for North American marine and freshwater fishes.[128] In the latter framework, fish life history strategies were described as opportunistic, periodic, or equilibrium corresponding to environments having stochastic, seasonally variable, or constant conditions, respectively.

The life history strategies described above can be generalized as behavioral and ecological traits, a strong focus of study in community ecology.[129] In the field of stream ecology, the concept of landscape filters[130] provided a formal approach for explaining which organism's traits are observed in which environments. Since then, the field of trait ecology has flourished due to analytical[131] and conceptual[129,132,133] advances, in addition to applications to studies of riverine landscapes.[134–138]

While life history theory and trait ecology provide conceptual grounding for combinations of strategies fishes may employ, studies of isolated behaviors are also prevalent and have applications for riverine landscapes. Spawning behavior of salmonids is a topic of much research and conservation. Especially in the Pacific Northwest, USA.[139] In an Alaskan stream with a long time record (1972–2005) of water temperature and biological data, researchers demonstrated a

TABLE 1 | Principles, Rationale, and Examples of the Behaviorscape Approach

Behaviorscape Principle	Rationale	Example
1. Study fish populations or communities in natural conditions	Provides external validity to study; informs scientists about genuine interactions in nature	Observations of birds preying on emerging aquatic insects in Japanese streams led to important research on stream-forest energy flows (reciprocal subsidies)[142]
2. Account for landscape and riverscape context	Recognizes influence of surrounding landscape and internal heterogeneity of rivers on fish habitat conditions	Spawning salmon in Oregon streams chose habitat based on physical habitat (pools) in spring, but moved to holding positions in spatially adjacent thermal refugia in summer; pattern only discovered via spatially continuous surveys[50]
3. Incorporate refined understanding of fish behavior	Brings realism and mechanistic understanding to observed patterns	Fish behaviors (foraging and competitive bouts) in an Oregon stream were risk-prone in structurally complex habitats, and these behaviors mediated selection of habitats across a gradient of competitor densities[143]
4. Forge linkages between individual behavior to population or community demographics	Ensures the usefulness of the study for management and conservation	Behavioral strategies of brown trout in Sweden (exploration tendency, behavioral flexibility, and aggressiveness) were linked to growth rate, survival, and movement[144]

shift in pink salmon (*O. gorbuscha*) behavior toward premature spawning due to earlier than normal water warming as a result of climatic changes.[140] When coupled with warmer incubation temperatures and earlier migration of fry, these results point toward the increased risk of these fish becoming mismatched in timing with the foraging resources they evolved to rely upon during their early marine life stage.

While reproductive behavior can be observed in a laboratory or in controlled field settings, the short duration and limited spatial extent of its occurrence make it a notoriously difficult phenomenon to observe in nature. Fortunately, reproductive success (or failure) can also be inferred from landscape genetics. In the case of three-spined sticklebacks, *Gasterosteus aculeatus*, in a Belgian stream, geographical determinants of genetic connectivity included natural factors, but severed longitudinal corridors by anthropogenic structures had a stronger effect, with the potential to disrupt population structure.[141] The effect of landscape features (e.g., elevation, upstream distance, precipitation, and temperature) on heterozygosity of 21 rainbow/steelhead trout (*O. mykiss*) populations in the Pacific Northwest, USA, was tested against a null model of fluvial distance and found to be significant in explaining gene exchange across populations. Future directions for landscape genetics-riverscape research would be to incorporate the internal heterogeneity of riverine landscapes into these types of analyses, rather than relying on environmental correlates at broad scales.

Principles of a Behaviorscape Approach to Stream Fish Ecology

The above sections highlight a subset of historical and current thinking in the fields of riverine landscapes and fish behavioral ecology. The combination of the disciplines gives origin to a new study framework we call the 'behaviorscape' approach, having the potential to elucidate behavioral mechanisms driving fish distributions across the landscape and contribute significantly to the conservation and ecology theory of stream fish. Principles common to behaviorscape studies would include (1) studying of fish populations or communities in natural conditions, (2) accounting for landscape and riverscape context, (3) incorporating a refined understanding of fish behavior, and (4) forging links between individual behavior and fish population or community demographics. The list presented in Table 1 outlines the rationale for these four principles.

Study Fish Populations or Communities in Natural Conditions

Ignoring whether experimental fish came from identical populations in the wild, or how closely aquaria represent natural conditions, for example, yields conclusions that may be meaningless in the riverine landscape in which the organism lives.[83] In a similar vein, mathematical theories have great value but to be of use, need testing in field settings.[115] Fortunately, a variety of observational and experimental approaches are at hand for applying animal behavior to landscapes.[77] An iterative approach to observation and experiment in using ecological theory and *a priori* hypotheses can be used to uncover mechanisms that drive patterns on the landscapes.[145] The 'natural conditions' to which fish are exposed include other species, which can have profound effects on their distribution and performance.[102] Furthermore, studies in natural systems reconnect researchers with the natural history they ultimately hope to understand[146] (see Figure 3(a)), and may spark hypotheses based on real behaviors and interactions observed in the wild.

Account for Landscape and Riverscape Context

Natural and cultural landscapes surrounding rivers and streams affect dynamics within the stream channel,[35] and so does the internal heterogeneity within the channel and floodplain[3,4] (see Figure 2). Studies that account for the context of the surrounding landscape and make explicit examinations of longitudinal, lateral, and temporal variation[147]—rather than treat the variation as statistical noise—have a better chance of elucidating mechanisms linking organisms to the complex environments in which they actually live. A landscape perspective means more than studying large spatial extents and averaging across similar land units; rather, spatially continuous sampling may be required to uncover the variation in patterns at intermediate scales relevant to managers[3,66] in addition to the influence on basin geometry, network pattern, and flow directionality of freshwater systems. Classification schemes that group rivers according to geomorphic behavior, potential for change, and other characteristics[64,148,149] can and should be incorporated, but care should be taken not to lose sight of local but important exceptions to average conditions across a classification unit.

Incorporate a Refined Understanding of Fish Behavior

The assumptions made about animal behavior from the early 20th century to the present progressed from viewing animals as robot-like automatons following invariant, fixed action pattern responses to external stimuli; then as overly efficient decision makers accounting for simultaneous optimal solutions; and more recently (and more reasonably) somewhere in between.[6] A true understanding of how animals might respond to changes in the landscape—either to degradation or restoration—can only help reduce (or mitigate the impacts of) encroaching land use and climate change.[16,77,150] Most current examples of this approach are based on the response of terrestrial fauna to anthropogenic change,[151–156] but a similar approach could be applied more consistently to stream fish ecology.

Forge Linkages between Individual Behavior and Population or Community Demographics

The value of any research into behavioral ecology is exponentially increased if an implicit or explicit link is made to population or community demographics, which can inform whether populations or communities thrive or go extinct. Habitat degradation and fragmentation, among other anthropogenic disturbances, influence wildlife mating systems, social plasticity, dispersal, mate choice, reproductive performances, infanticide, and conspecific attraction; all of which affect parameters linked to effective population size.[78] It is likely that this framework works in a similar manner for fish, for example, a genetic basis for behavioral diversity of salmonids may equate to evolutionary responses to climate change.[157] Researchers have recently demonstrated that animals[158] including fish[159] have unique personalities, which at first glance may seem irrelevant to demographics. However, the shyness of trout *does* relate to fitness-linked traits, as in the case of brown trout (*S. trutta*) whose exploration tendency, behavioral flexibility, and aggressiveness were linked to growth rates, survival, and movement in a natural stream in western Sweden.[144] This implies the existence of a 'landscape' of social behavior that is under-explored in stream fish ecology, another potential area for future research.

A true behaviorscape approach would incorporate interactions among individual behavior and a broader definition of the biotic environment to include fish assemblage dynamics, food webs, and the entire biotic community to which a focal species is exposed. The breadth of an individual's foraging behavior and subsequent food web links, for example, is often related to coexisting species that constrains its niche space;[160] however, the identity of species forming those links may be interchangeable, accommodating multiple pathways to ecosystem resistance and resilience.[161] Understanding patterns of habitat selection of three *Cottus* species in a western Oregon stream underlined the importance of the combined effects of physical gradients, predation, and interference and exploitation competition.[162] The response of one species to another may manifest in the form of an altered phenotype for the first species (e.g., change in foraging behavior), which in turn can affect the population density or the fitness of the second species in a different manner than before the phenotypic change.[163] Including multiple species, diverse food webs, and the broader biotic community into study designs can be complex; however, these factors cannot be simply ignored in pursuit of an uncluttered study design.

AN APPLICATION OF THE BEHAVIORSCAPE APPROACH: LINKING FISH BEHAVIOR TO HABITAT SELECTION IN A HIGH DESERT STREAM

In this section, we provide an example of how the behaviorscape approach can be applied to provide managers with important information for conservation of a fish population. The declining abundance of a threatened population of steelhead trout (*O. mykiss gairdneri*) tributaries of in the South Fork John Day River of eastern Oregon was attributed to warm water temperature, migration barriers, lack of structural complexity as refuge habitat, and competition. However, the relative importance of these factors and their cumulative effect on the population was unknown. Extensive mapping of fish abundance and stream conditions via spatially continuous snorkeling, rapid habitat assessment, and remotely sensed thermal imagery of surface water revealed that at the basin scale, water temperature explained most of the distribution of steelhead, with strong selection for upstream coldwater reaches. However at smaller (segment and tributary) scales, steelhead trout were clustered in areas of abundant pools, suggesting the importance of channel morphology, i.e., refuge habitat for juvenile salmonids. When the entire fish assemblage was considered, longitudinal position within the stream network had a large impact on whether 'coolwater' and 'coldwater' guilds coexisted or exhibited resource partitioning.[143]

Evaluation of patterns of steelhead trout growth and migration of individually marked fish revealed that regions of high growth potential shifted up and downstream seasonally, underlying the importance of seasonal as well as spatial context.[164] Individual fish, however, did not appear to track these regions of high growth potential in a warmer-water tributary, based on low rates of movement during summer months, even though apparent survival rates were consistently higher in cooler upstream reaches[164] and fish were exposed to temperatures linked to physiological stress as indicated by expression of heat shock proteins.[165,166] Timing of emigration to downstream reaches in fall was related to growth rate during summer and body size in fall, with larger and faster-growing fish migrating earlier and subsequently rewarded with more optimal winter growth conditions; these early migrants also initiated smolting sooner than late migrants.[164]

To address the role of fish behavior more directly, observational studies and experimental manipulations were conducted concurrently and following the above studies.[143] Underwater video throughout the stream network revealed that steelhead trout exhibited risk-prone behaviors, with theoretically higher energetic payoff (i.e., foraging near the surface and frequent aggressive bouts) in habitats with ample refuge; whereas fish displayed risk-averse behavior, with lower potential energetic gain (i.e., foraging near the benthic zone and fewer aggressive bouts) in simplified habitats lacking structural refugia. Foraging and aggressive behaviors were observed while food availability and densities of steelhead and a potential competitor, juvenile Chinook salmon, were being manipulated. Principles of IFD theory [104,105] and isoleg theory[111,112] were used in the interpretation of results to reveal that given homogenous habitat complexity and water temperature, trout selected local habitats based primarily on the intensity of intraspecific competition, with higher densities of conspecifics equating to stronger selection of poor quality patches. Additionally, the relative abundance of steelhead trout versus Chinook salmon also affected the risk-prone versus risk-averse trout behaviors described above; thereby, implicating the social context of a fish's environment in factors theoretically linked to fitness and population viability.

In summary, multiple methodological approaches in the same study system synergistically accounted for landscape context at a broad scale, fish migration at intermediate scales, and fish behavior and physiological responses at finer scales. The results of each approach informed the others; each study provided either contextual background or mechanistic understanding that helped resolve the 'behaviorscape' of this particular steelhead trout population.

CONCLUSION

Structural heterogeneity describes the spatial or temporal complexity of a system property regardless of functional effects, whereas functional heterogeneity describes variability in properties that affect ecological processes such as population density, nesting, foraging behavior, growth rate.[167] It is this latter category of functional heterogeneity where behavioral ecology has the most potential to provide mechanistic understanding—a chance to elucidate the causal pathways leading to current patterns on the landscape. The intersection between landscape ecology, stream fish ecology, and behavioral ecology (Figure 1) can provide insights into both structural and functional heterogeneity, and their interaction.

Potential future research areas will likely involve continued development of methods and technologies for assessing heterogeneity of riverine landscapes[49] while simultaneously resolving understanding of behavioral responses to heterogeneity.[77] How can this be achieved? By employing large numbers of technicians conducting experimental manipulations and observing fish behavior at every pool and riffle in the stream network? While it is easy to recommend doing behavioral ecology across extensive landscapes, it is much more difficult to execute owing to logistical constraints on time, personnel, or ethical considerations. One solution to this problem is to start with a broad-scale approach to mapping heterogeneity of fish distributions, followed by testing hypotheses about the mechanisms driving pattern at local scales.[143] Another promising method to bridging the pattern-process divide is the 'space as surrogate' approach,[145] where the combination of *a priori* hypotheses, ecological theory, precise spatial analysis of residuals to model fits, and *in situ* experiments are employed to arrive at in-depth ecological understanding. The proposed principles of the behaviorscape approach (Table 1) have already been employed in a few notable cases, but more work along these lines is needed.

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