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Applications of Genetic Management and Conservation and Their Habitats

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Data to Improve ervation of River Fishes



Environmental variation and landscape features affect ecological processes in fluvial systems; however, assessing effects at management-relevant temporal and spatial scales is challenging. Genetic data can be used with landscape models and traditional ecological assessment data to identify biodiversity hotspots, predict ecosystem responses to anthropogenic effects, and detect impairments to underlying processes. We show that by combining taxonomic, demographic, and genetic data of species in complex riverscapes, managers can better understand the spatial and temporal scales over which environmental processes and disturbance influence biodiversity. We describe how population genetic models using empirical or simulated genetic data quantify effects of environmental processes affecting species diversity and distribution. Our summary shows that aquatic assessment initiatives that use standardized data sets to direct management actions can benefit from integration of genetic data to improve the predictability of disturbance–response relationships of river fishes and their habitats over a broad range of spatial and temporal scales.

Aplicaciones de datos genéticos para mejorar el manejo y la conservación de peces de río y sus hábitats

La variación ambiental y los rasgos paisajísticos afectan los procesos ecológicos en los sistemas fluviales; sin embargo, evaluar dichos efectos en escalas espaciales y temporales que sean relevantes para el manejo, constituye un reto importante. Los datos derivados de estudios genéticos pueden ser usados en conjunto con modelos paisajísticos y con evaluaciones ecológicas tradicionales para identificar puntos calientes de la biodiversidad, para predecir la respuesta de los ecosistemas ante impactos antropogénicos y para detectar amenazas a los procesos subyacentes. Aquí se muestra que la combinación de datos taxonómicos, demográficos y genéticos de las especies en paisajes fluviales complejos, permite a los manejadores comprender mejor las escalas temporales y espaciales sobre las cuales los procesos ambientales y las perturbaciones tienen influencia sobre la biodiversidad. Se describe cómo los modelos de genética de poblaciones que se valen de datos reales o simulados, sirven para cuantificar los efectos de los procesos ambientales en la diversidad y distribución de las especies. Se muestra que las iniciativas de evaluación del ambiente acuático basadas en sets de datos estandarizados y encaminadas a dirigir acciones de manejo, pueden beneficiarse de la integración de datos genéticos para mejorar la predicción de la relación perturbación–respuesta de los peces de río y de sus hábitats a lo largo de una amplia escala de tiempo y espacio.

Applications de données génétiques pour améliorer la gestion et la conservation des poissons de rivière et de leurs habitats

Les variations environnementales et les paysages caractéristiques affectent les processus écologiques dans les systèmes fluviaux. Toutefois, l'évaluation des effets à des échelles de gestion temporelles et spatiales relève du défi. Les données génétiques peuvent être utilisées avec les modèles de paysages et les données traditionnelles d'évaluation écologique pour identifier les points chauds de biodiversité, prédire les réponses de l'écosystème aux effets anthropiques, et détecter les déficiences des processus sous-jacents. Nous montrons que, en combinant les données taxonomiques, démographiques et génétiques des espèces de paysages fluviaux complexes, les gestionnaires peuvent mieux comprendre les échelles spatiales et temporelles sur lesquelles les perturbations et processus environnementaux influencent la biodiversité. Nous décrivons comment les modèles génétiques de la population issues de données génétiques empiriques ou simulées peuvent quantifier les effets des processus environnementaux sur la diversité et la distribution des espèces. Notre résumé montre que les initiatives d'évaluation aquatiques faisant appel à un ensemble de données normalisées pour mener des actions de gestion directes peuvent bénéficier de l'intégration des données génétiques pour améliorer la prévisibilité des relations perturbation–réponse des poissons de rivière et de leurs habitats sur une large gamme d'échelles spatiales et temporelles.

INTRODUCTION

Fisheries managers are increasingly interested in understanding how river habitats affect biological diversity in space and time and how habitats are affected by landscape features associated with disturbance at local (reach) and network (watershed) spatial scales. Over the last decade, numerous efforts have been initiated to measure the status of aquatic habitats at spatial scales ranging from individual stream reaches and estuaries to river networks and hydrogeographic regions (e.g., Paulsen et al. 2008; Stoddard et al. 2008; Carlisle et al. 2009). The goal of aquatic habitat assessments as stated by Esselman et al. (2011) is to “provide a scientific basis for objective comparisons of habitat conditions in diverse aquatic systems and across large regions to facilitate prioritization of conservation activities and to help measure progress” (p. 134). Here, we show how genetic data can complement existing databases to advance the broader management goals of assessing the condition of system processes, including the degree of disturbance of these processes, as well as the cumulative effects of these processes on resulting patterns of aquatic biodiversity.

Traditionally, aquatic habitat assessments involve collection of geographically extensive surrogate landscape variables

that serve as proxies for local habitat and process condition (Esselman et al. 2013). These proxy data are then used to model disturbance–response relationships, characterize system condition, and predict responses (e.g., abundance, distribution, and species diversity) of fish and other aquatic organisms (Allan 2004). Though this approach may provide valuable information, the coarse spatial resolution and lack of process-driven indices of biotic response constrain our ability to forecast resulting patterns of biodiversity. Consequently, managers are faced with incomplete and often difficult decisions on how to use assessment results to forecast future levels of diversity or abundance at specific sites and how to affect process change at scales and rates that are consistent with management needs or time horizons.

In order for management to be successful, managers must be provided with the tools to identify key mechanisms affecting system processes, as well as the scale over which such mechanisms operate. Specifically, it is critical that new data sets become available to address current data shortfalls in spatial and temporal resolution to allow managers to accurately determine how to conserve intact systems and effectively diagnose and restore impaired ecosystem processes. Our goal is to assist fisheries managers and groups involved in aquatic assessment

to conceptually link landscape-scale genetic data, traditional biodiversity measures, and aquatic assessment methodologies. Fisheries managers can benefit from advances in genetic technology and quantitative techniques to answer complex questions (see Table 1). By clarifying terminology regarding operational units, driving forces, and estimated parameters in traditional aquatic biodiversity assessments and population genetic analyses, we hope to help managers understand the complementarity of these approaches and the advantages of adding genetic data to traditional assessment approaches.

Genetic data can serve as an alternative biodiversity measure to be used with aquatic habitat data (Table 2). Molecular markers provide fundamental measures of biodiversity (e.g., genetic diversity measured as the number alleles, proportion of loci heterozygous, or population allele frequencies) that serve as a starting point to understand effects of landscape processes on aquatic systems. Indeed, a large body of literature has reported parallels between biodiversity measured in terms of genetic diversity and species diversity (see review by Vellend and Geber 2005), often in response to environmental features (e.g., Lamy et al. 2013). However, within the fisheries literature, disciplines such as population genetics have largely focused on quantifying genetic diversity and effects of underlying microevolutionary processes (e.g., migration, genetic drift, mating system, selection), within and among fish populations, but have remained largely separate from disciplines focused on ecological responses to environmental disturbance.

Genetic data can supplement traditional fish and habitat assessment methods to provide an integrated, multidisciplinary approach for assessment of aquatic diversity (e.g., Selkoe et al. 2015). Measures of genetic diversity within (e.g., heterozygosity) and among populations (e.g., variance in allele frequency; F_{ST} ; Weir and Cockerham 1984) integrate multiple components of demography that influence population growth and viability, dispersal, and effective population size (i.e., the number of individuals in a population that contribute offspring to the next generation). Accordingly, genetic data and emerging computational tools have enormous potential to improve conservation efforts and fish habitat and climate planning, in terms of both conserving genetic variation per se (and thus evolutionary potential and resiliency to environmental change; Hoffmann and Sgro 2011) and understanding ecological attributes of aquatic species and communities (e.g., to estimate abundance, dispersal, hybridization; Allendorf et al. 2013; Table 1 in the present article). In particular, genetic techniques can link spatial and temporal variation in landscape features to physiological processes, survival, and reproduction (Allendorf et al. 2013). Furthermore, recent methodological advances in the genetics arena provide the foundation to characterize and interpret genetic diversity measured at multiple spatial scales throughout river networks, including advances in genetic marker availability (e.g., Hohenlohe et al. 2013; Narum et al. 2013a), population genetic monitoring and computational approaches (e.g., Landguth et al. 2010; Waples et al. 2013), and empirical evaluations of population genetic theory developed for river systems (e.g., Morrissey and de Kerckhove 2009).

The objective of this article is to outline the potential of landscape-scale genetic data and analyses to fill information gaps in aquatic biodiversity monitoring and assessment efforts. We hope that this synthesis will stimulate further discussion of how to best use these data to rehabilitate, conserve, and protect aquatic habitats and freshwater species. A primary goal of landscape genetic studies is linking ecological processes

and landscape features to measures of genetic diversity within populations and levels of spatial genetic structure (SGS) among populations (Manel and Holderegger 2013). Here, we illustrate the usefulness of genetic data and landscape genetic approaches for assessing population vulnerability and the effects of landscape features on levels of diversity at population, community, and species levels. We further highlight the growing potential of population genomics (Hohenlohe et al. 2013) to identify genes and genome regions associated with fitness (i.e., differential survival or reproductive success of individuals of different genotype), phenotypic variation, and associations with environmental features (e.g., Dammerman et al. 2015). Using published data (Landguth et al. 2014; Muhlfeld et al. 2014), we provide an example simulation that demonstrates how aquatic landscape genetic analyses can be integrated with existing environmental and climate data (Figure 1; Cooter et al. 2010) and applied in the context of aquatic assessment efforts such as those being conducted by the National Fish Habitat Partnership (NFHP).

THE TERMINOLOGY AND PURVIEW OF GENETIC ANALYSES

Genetic data provide useful information on the compositional, structural, and functional attributes of plant and animal biodiversity (after Franklin 1980; see Figure 1). Groups diverge genetically (typically quantified by changes in allele frequency) as a function of the length of time they have been isolated, the amount of movement and gene flow, local population size, and mutation rate of the marker employed. Additionally, current patterns of genetic divergence among populations are affected by the history of disturbances (natural and anthropogenic) and selection in response to specific features of the local environment (Garcia de Leaniz et al. 2007). Just as the identity and variety of species quantified in traditional stream assessments provide measures of compositional diversity, genetic data (e.g., measures of genetic diversity within populations including heterozygosity and allelic diversity) provide measures of diversity that can be apportioned at species, population, and individual levels (examples in Table 1).

Genetic diversity within a locale or collection site provide a measure of α -genetic diversity that can be used as a response variable with predictor variables such as landscape features and disturbance measures. Estimates of variance in allele frequency among locales (e.g., quantified using F_{ST} or G'_{ST}) provide a measure of β -genetic diversity among populations or collection locations. These estimates of genetic diversity can be used as response variables to assess how landscape features and disturbance influence persistence of aquatic species (e.g., Kovach et al. 2015). Genetic data can also be used to estimate traditional ecological metrics (population size, movement, dispersal, etc.), as in the field of molecular ecology and demographic monitoring (Freeland et al. 2011). Further, noninvasive genetic techniques can be applied to stream assessments over multiple spatial scales. For example, environmental DNA (eDNA) can provide a means of quantifying taxonomic diversity over large areas without the need to handle individuals (e.g., Jerde et al. 2011; see Table 1).

Conservation actions for species will not automatically protect the underlying genetic diversity at other scales of ecological organization (e.g., among populations or individuals within populations). Genetically distinct but continuously distributed populations often exist within short distances.

Table 1. Examples of questions addressed or types of information available from genetic data for river population and ecosystem management with supporting references.

Question or kind of information	Example	References
Estimation of species diversity	Environmental DNA allows geographic expansive sampling to identify species presence/absence and species diversity	Takahara et al. (2012); Kelly et al. (2014)
Documentation of effects of barriers to movements and gene flow	Provides insights into effects of dams on gene flow Describes effects of land use on gene flow and levels of genetic diversity	Wofford et al. (2005); Raeymaekers et al. (2008) Blum et al. (2012)
Genetic diversity, inbreeding, and genetic rescue: Does genetic variation effect individual and population performance?	Restoration of genetic variation reversed inbreeding depression and increased fitness in a stream populations Genetic and evolutionary rescue	Vrijenhoek (1989); Leberg (1990) Tallmon et al. (2004); VanderWal et al. (2013)
Census, effective population size, and number of breeders (past and present)	Migration barriers, isolation, and effective population size	Whiteley et al. (2010); Waples et al. (2013)
Population structure and conservation units or management units	Genes with important function have higher genetic differentiation between populations than do neutral genes Functional gene markers might help identify cryptic conservation units	Vasemagi and Primmer (2005); Narum et al. (2010, 2013a) Funk et al. (2012); Limborg et al. (2012)
Gene flow, connectivity, and dispersal (past and present)	Restoration and maintenance of migratory connectivity (transporting fish above barriers) Effects of stream habitat, hierarchical dendritic structure	Wofford et al. (2005); Raeymaekers et al. (2008) Hughes et al. (2009); Morrissey and de Kerckhove (2009)
Riverscape structure or variation (or environmental change) affects population connectivity (gene flow)	Population divergence and life history variation Population divergence and stream temperature Effects of natural physical barriers to gene flow Genetic variation by local abundance of quality habitat	Neville et al. (2006) Kanno et al. (2011); Narum et al. (2013b) Costello et al. (2003); Whitley et al. (2006) Ozerov et al. (2010)
Local adaptation, selection, and unnatural selection	Phenotypic and genomic adaptation to freshwater by colonizing stickleback fish Thermal adaptation Unnatural selection associated with harvest	Hohenlohe et al. (2010) Narum et al. (2013b); Hemmer-Hansen et al. (2007) Allendorf and Hard (2009)
Phylogenetics, systematics, and hybridization	Anthropogenic fish introductions lead to hybridization and reduced fitness Superinvasive alleles spread via natural selection, providing markers for early detection of nonnative introgression	Muhlfeld et al. (2009) Hohenlohe et al. (2013)
Forensics, genetic identification, and law enforcement	Illegal harvest and marketing fraud is detected. Geographic regions or streams or lakes involved (suffering) can be identified by genetic assignment tests	Stokstad (2010)
Disease ecology and transmission	Pathogens explain reduced population abundance (using gene expression tools) Microbial colonization of fish eggs and stream flow	K. M. Miller et al. (2011) Fujimoto et al. (2013)
Community genomics	Evolution in stream phenotypes significantly affects ecosystem structure and function	Bassar et al. (2010)
Disentangling the effects of contemporary and historical landscape features on aquatic diversity	Importance of historical hydrological structure predicted based on geomorphological and biogeographic models are more predictive than current landscape structure	Poissant et al. (2005); Bernatchez and Wilson (1998)
Estimating reproductive success and the number of adults recruiting offspring to the population	Pedigree reconstruction identifies recruitment from individual nests Parentage analysis estimates number of parents contributing to offspring produced and reproductive success	Hessenauer et al. (2012) E. C. Anderson and Garza (2006); Duong et al. (2013)

For example, Fraser and Bernatchez (2005) demonstrated that genetic data can reveal multiple evolutionary lineages of Brook Trout *Salvelinus fontinalis* in a single drainage. Cryptic species can also go undetected based on morphological data but become apparent with genetic data (Bickford et al. 2007; see Table 1). Furthermore, there is often disagreement over existing taxonomies and key pathways of connectivity among populations or management units, both of which can be addressed with genetic data (McRae and Beier 2007). Likewise, analyses that incorporate spatially explicit data on genetic diversity can be used in regional assessments of biodiversity to

prioritize areas for conservation (Funk et al. 2012).

Figure 2 illustrates the information contained in genetic data at multiple spatial scales within a river network. A hypothetical scenario is provided that includes data for a single biparentally inherited locus with two alleles and three genotypes for each of five populations (1–5) collected from each of three stream tributaries. A species may be present in equal abundance in each stream location (e.g., Figure 2, populations 1–4) and thus may contribute equally to measures of species diversity within (α -diversity) and between (β -diversity) locations. However, genetic diversity (e.g., the frequency

Table 2. Comparison of terminology used in population and landscape genetics and stream ecology and management.

Categories		Population genetics/landscape genetics	Stream ecology and fisheries
Operational units			
	Subdivision Focal unit Observed data	Population Gene/locus Allele frequency	Local community Species Species relative abundance
Major forces			
		Genetic drift Gene flow Selection	Dispersal Disturbance
Spatial structure			
		Population genetic structure	Species distribution, composition, and abundance variation
	Model	Island model Stepping stone model Isolation by distance Isolation by resistance Isolation by barrier	Landscape disturbance
Measurement			
	Within population or locale	Heterozygosity or genetic α -diversity	Species relative abundance and diversity within a site or ecological α diversity
	Between population or locales	Variance in allele frequency (Fst) or genetic β -diversity	Variation in species composition and abundance among sites or ecological β -diversity
Parameters			
		Average number of migrants Effective population size Distribution in allele frequency	Average number of migrants Effective community size Distributions of species abundances and composition
Community assembly rules			
		Genetic drift/gene flow Selection/drift	Ecological drift/migration Selection/migration Diversity/area relationships Ecological drift/disturbance relationships

of heterozygous Aa genotypes) can provide an informative measure of abundance. Specifically, levels of genetic diversity, as measured by the number of alleles and heterozygosity, are typically lower in populations of smaller size. Similarly, population differences in allele frequency (and genealogy) can be used to infer directionality of gene flow (e.g., upstream to downstream; Figure 2). The lack of strong associations between interpopulation differences in allele frequency and geographic distance (isolation by distance) could indicate the presence of barriers (Wofford et al. 2005; Table 1 in the present article; e.g., comparisons of allele frequencies in populations 2 and 5; Figure 3). Finally, intermediate allele frequencies in reach 4 and deviations between observed genotypic ratios and those expected under Hardy Weinberg equilibrium (example here showing a lower frequency of heterozygotes than expected; see Figure 2 caption) indicate admixture between members of differentiated populations.

Laboratory and Analytical Tools for Genetic Data

Methods for analyzing variation in DNA sequences from natural populations are rapidly advancing. Tried and tested markers, such as microsatellites and single nucleotide polymorphisms, have been the workhorses of empirical fisheries genetics for nearly two decades. Currently, applications of DNA sequence data are expanding because of the declining cost and increasing availability of next-generation sequencing technologies and methods that use sequence variation among individuals obtained by next-generation sequencing for

genotyping (e.g., Narum and Alex 2013). The availability of sequence data will continue to expand because it provides whole genome resolution and because new methods for sequencing portions of genomes have been developed (e.g., M. R. Miller et al. 2007) and are being widely applied with fish species (Table 1). Computational tools and approaches for genotype and sequence data now include a range of options for quantifying ecological processes, population demography, and genetic responses in dendritic ecological networks (e.g., Neuenschwander 2006; Kalinowski et al. 2008; Landguth et al. 2012). Further, genetic data play an important role in quantifying causal relationships between changes in biodiversity with human disturbance and can characterize the response of aquatic organisms to habitat perturbations in terms of adaption or dispersal through river networks (Allendorf et al. 2010; Blum et al. 2012).

SPATIAL SCALES, UNDERLYING PROCESSES, AND VALIDATION OF TRADITIONAL BIODIVERSITY DATA

Understanding current and future levels of species diversity, population abundance, and movements within stream networks is critical for effective management in the face of climate change and other human stressors to aquatic ecosystems (Allan 2004). In this context, genetic data can be used to address three fundamental management needs. First, managers need to understand how landscape processes affect habitat conditions,

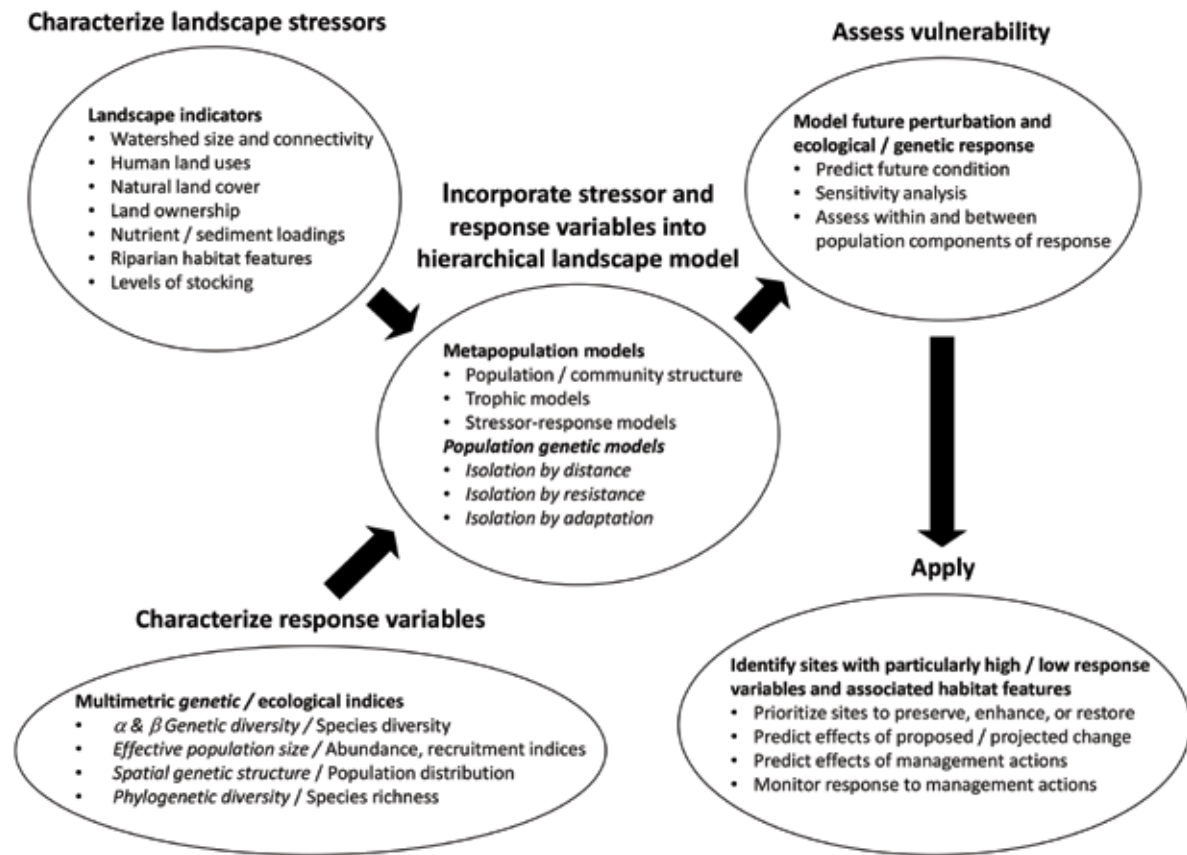


Figure 1. Landscape approach integrating genetic (in italics) and traditional aquatic assessment data to establish associations between measures of genetic and ecological diversity at each of several hierarchical spatial scales involving natural environmental and anthropogenic stressors or surrogates.

including the distribution and abundance of fish species across space and time. Second, managers require information on the scales over which landscape processes exert influence and over which proposed management actions are likely to be successful. Finally, managers would benefit from independent data to validate disturbance–response relationships that have been defined based on traditional stream assessment methods.

Identification of the Scales over Which Processes Exert Influence

Issues of scale are a central challenge in ecology (Dungan et al. 2002), genetics (C. Anderson et al. 2010), and fisheries management (Fausch et al. 2002). To effectively protect or rehabilitate aquatic systems, managers often need to know the spatial extent of sampling and analysis, the scale at which phenomena exert effects on biodiversity, and the scale at which responses to management actions will be realized. Managers often lack information concerning whether fish populations respond environmental conditions at local scales (e.g., stream reach scale; Figure 2) or to variables at larger (e.g., watershed or network) scales (Durance et al. 2006; Figure 2; Table 1). Likewise, it is difficult to assess whether populations recover via local recruitment or dispersal and gene flow from a broader network area (Fagan 2002), whether recovery will occur within acceptable time horizons, or whether recovery will require assistance from translocations (i.e., genetic rescue to offset inbreeding effects [Tallmon et al. 2004] or evolutionary rescue

by translocating locally adapted genotypes [VanderWal et al. 2013]).

Genetic data can help address scale-related questions (C. Anderson et al. 2010), including identification of the spatial scale over which disturbance exerts influence and over which the benefits of proposed management actions are expected to be realized (Table 1). For example, Kanno et al. (2011) documented population structure in Brook Trout using individual-level genetic data and riverscape features as predictor variables at multiple spatial scales. Below we discuss how genetic data can be used to assess the influence of dispersal and gene flow on population recovery.

Identification of Underlying Processes

Management actions to reduce loss of biological diversity necessitate preserving the ecological and evolutionary processes that sustain that diversity (Moritz 2002). However, conservation actions are often implemented based on inferences drawn from indirect data or symptoms of process impairment, as opposed to mechanistic understanding of underlying cause. The coarse resolution of existing landscape and disturbance data sets limits their utility for identifying processes underlying diversity at local, network, or regional spatial scales. Physical, chemical, and biotic processes affect biodiversity, the spatial and temporal scales of process effects (e.g., Perkin and Gido 2012), and scales of resource responses to management actions (Poff and LeRoy 2009). Yet, current data sets are not sufficient to elucidate effects

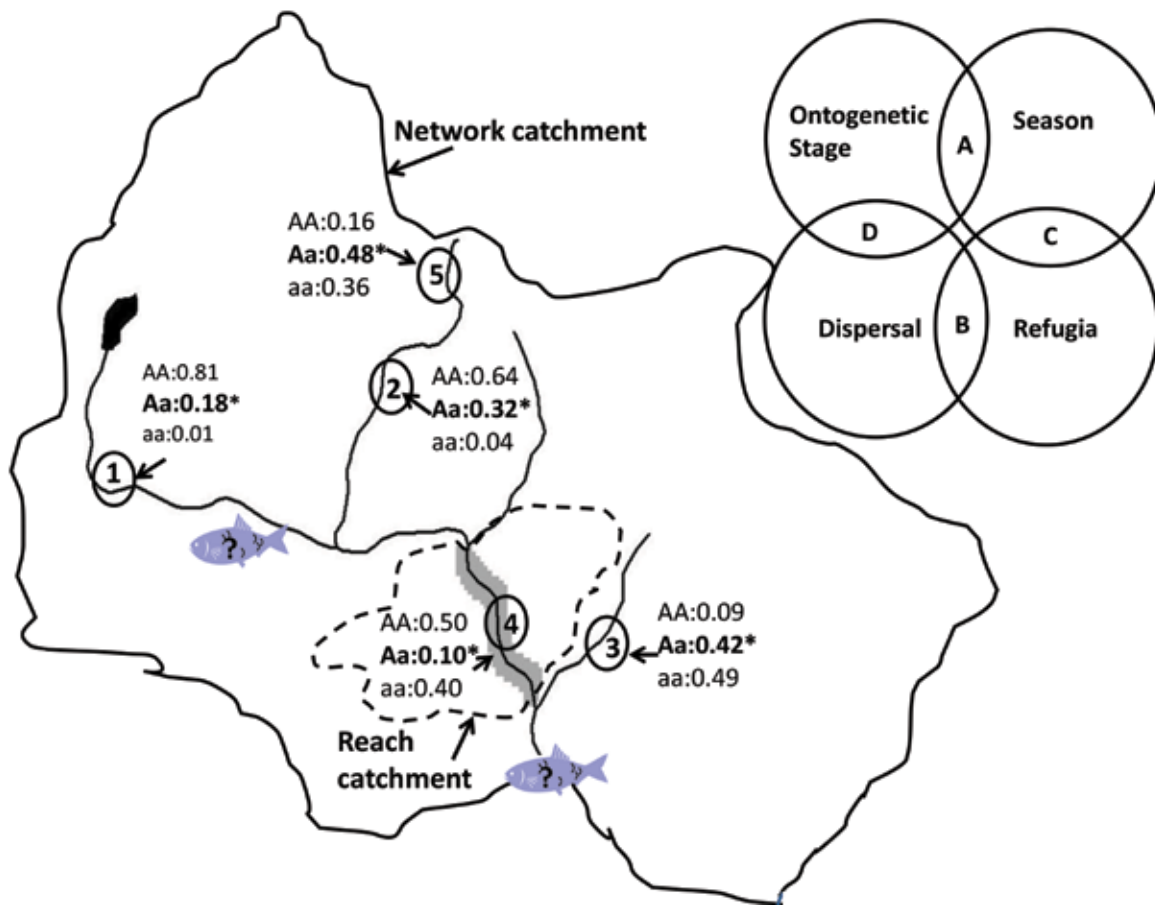


Figure 2. Importance of connectivity at local (reach) and larger (network) spatial scales. Broader landscape (catchment) features interact directly or indirectly with stream habitats. Effects are reflected in levels of genetic diversity within and degree of genetic differentiation among local populations (e.g., 1–5) and affect biological processes of stream organisms (intersections A–D). Hypothetical examples of interpretations of genotypic data collected from stream reaches are provided. Genotypes in populations 1–3 and 5 are in Hardy Weinberg proportions (i.e., if the frequency of allele A is p , then the expected frequency of the AA genotype is p^2 and the expected frequency of the Aa heterozygote (H_e) is $2p(1 - p)$, where $p = 0.9, 0.8,$ and 0.3 in reaches 1–3, respectively. Reach 4 contains a mixture of individuals from multiple populations with $p = 0.55$ and the observed fraction of heterozygotes (0.1) is lower than the expected (0.495), which is typical of admixed populations.

of basic processes that affect recruitment and levels of diversity, such as material transport, disturbance, and connectivity.

With the addition of genetic data, managers can be better informed about processes underlying observed relationships between biodiversity response variables (local recruitment, local abundance, and connectivity) and measured disturbance variables (Table 1). For example, Blum et al. (2012) showed that point source pollution affecting water quality along specific stream reaches was associated with low population levels of genetic diversity and high interpopulation differences in allele frequency in Central Stoneroller *Campostoma anomalum*, suggesting that pollution was reducing local abundances and connectivity among populations.

Validation of Traditional Measures of Biodiversity

Fisheries managers would benefit from independent means of validating current disturbance–response associations. Two specific points are of particular note. First, standard measures of species diversity and/or relative abundance may be attributed to historical processes or disturbance that genetic data can help to resolve (i.e., ghosts of landscapes past [Harding et al. 1998] or ghosts of past introductions [Neville and Bernatchez 2013]). Second, species diversity and relative abundance as estimated via standard monitoring efforts will likely fail to detect

substructuring at fine or large spatial scales, which determines the scale of inference (e.g., reach vs. watershed).

By revealing the spatial structure of populations, genetic data can serve as a means of validating the scale of inference of national standardized data layers (e.g., habitat condition scores determined from U.S. rivers as part of NFHP) as well as serving as an independent means of evaluating the efficacy of commonly used measures of vulnerability in fisheries management (Table 2). For example, studies of Brook Trout in eastern maritime regions of Canada by Poissant et al. (2005) found that SGS was predicted by historical geomorphological and biogeographic connectivity associated with past hydrological regimes. Gomez-Uchida et al. (2009) characterized the degree of SGS for three codistributed salmonid species in eastern maritime Canada. Due to species-specific difference in life history, the degree of SGS and relative influences of landscape features on SGS varied greatly among species, though all species were present in all systems studied.

APPLICATIONS OF GENETIC DATA IN RIVER NETWORKS

At large spatial scales (e.g., landscape or network), fluvial systems exhibit a fractal-like network structure (Figure 2), where smaller, lower-order reaches join to form larger, higher-order

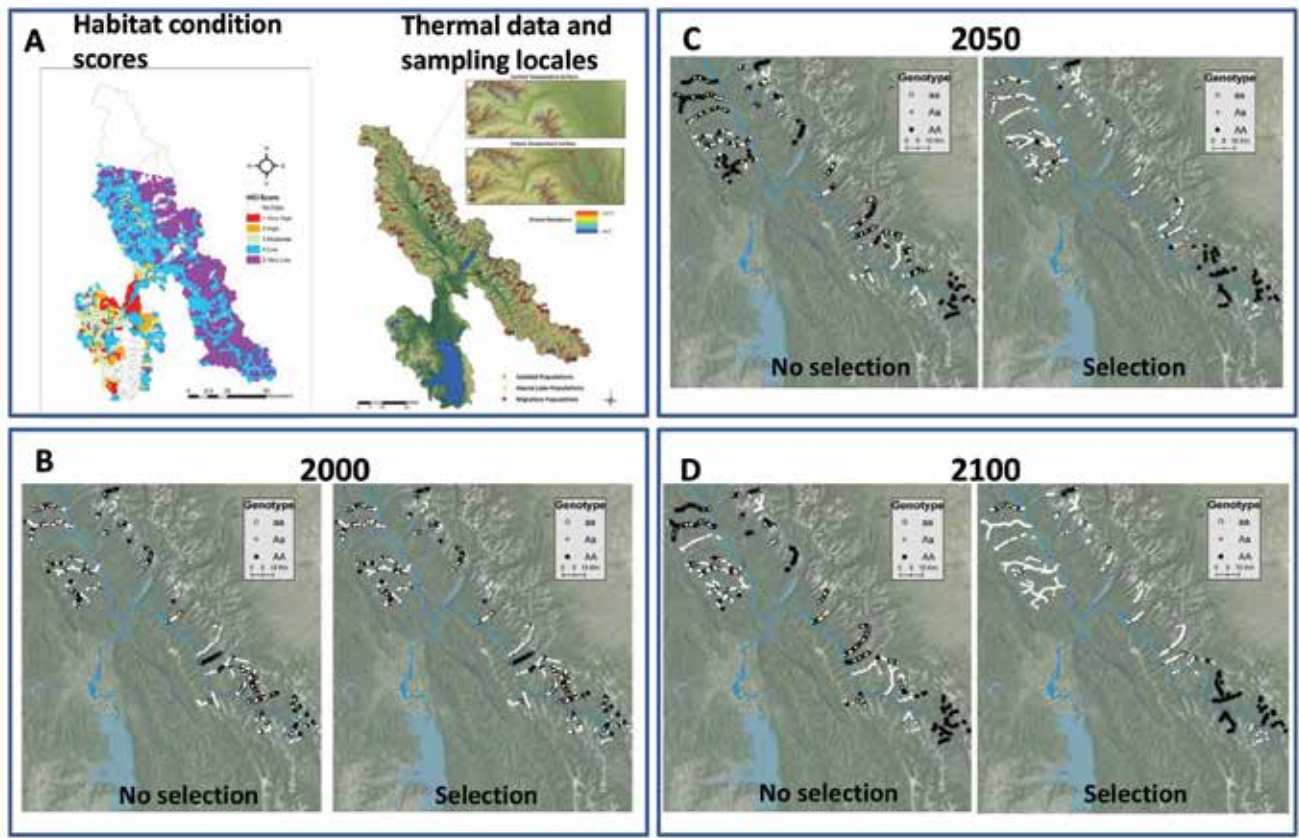


Figure 3. Synthesis of results from a spatially explicit, individual-based, riverscape demo-genetic program (CDFISH v0.52; Landguth et al. 2012) assessing how increasing stream resistance influences genotype distributions and indices of measures of variability (heterozygosity; H_s) and intersample genetic differentiation (G'_{ST}). Analyses are conducted for a network of threatened migratory and resident Bull Trout populations in the upper Flathead River, Montana, using neutral and adaptive loci (background in Lundguth et al. 2014; Muhlfeld et al. 2014). (A) Habitat condition scores from the 2010 assessment of fluvial habitats for the National Fish Habitat Partnership and stream temperature for the Flathead system (Jones et al. 2013), and probabilities of Bull Trout occurrence in response to temperature. Scenario 1 (current temperature + habitat condition without spatial selection operating) at year 2100 and scenario 2 (future temperature + habitat condition with spatial selection operating) at year 2100. Projected distributions of genotypes at a neutral and selected locus under the two disturbance regimes are shown in 50-year increments (B)–(D). Figure continues on next page.

reaches (Frissel et al. 1986; Grant et al. 2007). This physical network structure can influence local community composition through mechanisms acting at multiple scales through (1) the movement of individuals among network branches (e.g., Lowe and Bolger 2002); (2) the concentrative transfer of disturbances from diffuse, upstream branches to downstream reaches (e.g., Gomi et al. 2002); and (3) the propagation of localized downstream impacts to extensive upstream networks (Morrissey and de Kerckhove 2009). Measures of genetic diversity within populations (e.g., heterozygosity) and among populations (e.g., F_{ST} or G'_{ST}) can be applied to resolve these network or riverscape effects on community composition and diversity.

The great benefit of genetic data is in assessing the spatial dimensions of putative impacts on local community composition, including both the scale of impact (e.g., local vs. network level) and the directionality of impact (e.g., upstream vs. downstream propagation). Organisms inhabiting stream environments generally carry out important aspects of their life histories at intermediate and large spatial scales (Angermeier et al. 2002; Figure 2) and respond to habitat changes that frequently occur at intermediate temporal scales (Fausch et al. 2002). For example, aquatic organisms must have access to resources to meet life requirements during all times of the

year and across all ontogenetic stages (Figure 2, intersection A; e.g., during spawning migration: Schlosser 1991). Disturbance events, such as flood, wildfire, or drought, mean that organisms must be able to recolonize habitats (Figure 2, intersection B). Thus, processes at the metapopulation level are important for persistence. Aquatic species also exhibit seasonal shifts in habitat use (Figure 2, intersection C; e.g., in response to changing thermal regimes) and ontogenetic habitat shifts to meet forage needs (e.g., Figure 2, intersection D; Schlosser 1991).

These metapopulation and life history dynamics, combined with stochastic events and spatiotemporal variability in effects of landscape features on local habitat, mean that measures of species abundance and diversity will vary greatly within a locale over time (Knouft et al. 2011). Information provided by genetic markers can help to resolve the source of this variability by revealing the magnitude and direction of movements, spatiotemporal changes in relative abundance, and degree of population admixture (Figure 2). For example, Hänfling and Weetman (2006) used multi-locus genotypic data to quantify asymmetric gene flow at small scales (<0.5 km) in Bullhead *Cottus gobio*. Using genetic data, the authors documented high rates of net immigration from small upstream populations into larger downstream populations.

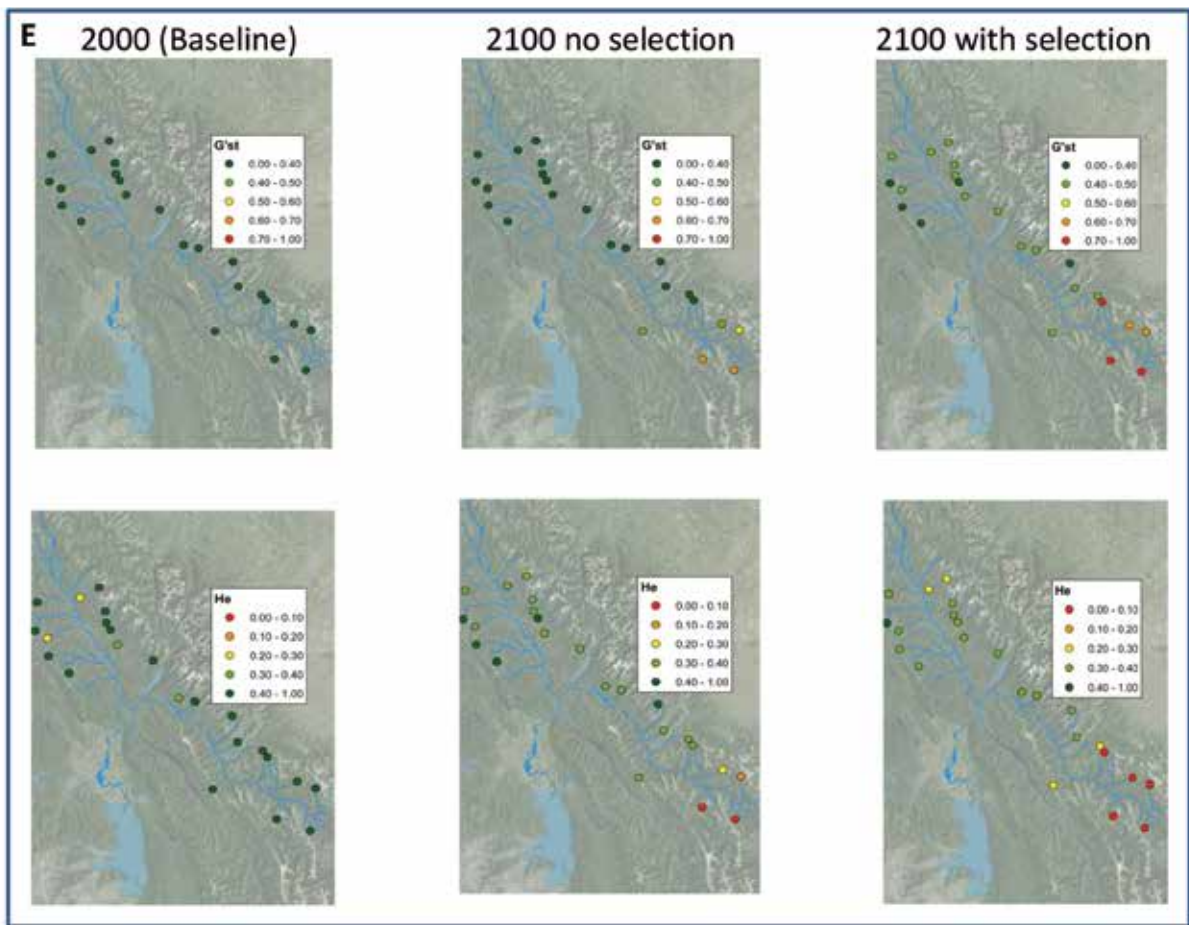


Figure 3 (continued). Estimated measures of heterozygosity within populations (H_e) and variance in allele frequency among populations (G'_{st}) at the initial generation, under both scenarios are shown in caption E.

Dendritic Ecological Network Structure Influences Community Composition

Habitat quality within dendritic stream networks typically varies spatially, and habitat occupancy of stream species varies seasonally and among individuals of different ontogenetic life stages. Source–sink ecological theory predicts that individuals will typically occur in areas of high habitat quality and that immigration from “source” populations can stabilize recipient populations (Pulliam 1988), thereby buffering aquatic communities from disturbance events. In stream networks, immigration from source reaches can occur longitudinally, along individual channels (Macneale et al. 2005), or laterally, between adjacent, hydrologically independent channels (Brown and Swan 2010). Applications of genetic data to detect sources and sinks in aquatic systems is well established (e.g., Gaggiotti 1996) and is critical for understanding recolonization processes that affect populations inhabiting spatially and temporally dynamic river systems.

Assessing and maintaining immigration within stream networks is especially valuable for management and conservation of aquatic species and ecosystems. Genetic data have been used in aquatic species to estimate degree of connectivity as a function of (1) geographic distance (isolation by distance), (2) degree of riverscape resistance or disturbance (isolation by resistance; Neville et al. 2006), (3) barriers to dispersal (isolation by barriers; Wofford et al. 2005), or (4)

localized adaptation (isolation by adaptation; Bradbury et al. 2013; Table 1). Genetic data have also been used to quantify rates of movements among stream branches (e.g., Morrissey and de Kerckhove 2009). Occurrence of such lateral subsidies shifts the scale of management from individual channels to the network of hydrologically independent but connected branches, allowing for more flexible mitigation strategies. In cases where restoration of a focal reach is too costly, species diversity (or genetic diversity; Figure 2) in that reach can be bolstered by maintaining habitat quality and immigrant subsidies from hydrologically independent but connected branches.

A second important consequence of the dendritic structure of stream networks is the potential for concentrative impacts in downstream communities originating from disturbances or changes in connected upstream networks (Frissell et al. 1986). The high sensitivity of ecological processes in headwater streams to human disturbances leads to low thresholds of impact (Lowe and Likens 2005). Consequently, human-induced disturbances (e.g., roads, atmospheric pollution, logging, or urbanization) spread across multiple headwater regions and are likely to manifest in strong effects on downstream communities. This can result in perplexing patterns where downstream communities exhibit significant reductions in diversity, have high proportions of tolerant individuals, and/or have degraded habitat conditions but with no clear environmental driver at the local scale (Esselman et al. 2011; Daniel et al. 2015). Population

genetic data allow assessment of such concentrative impacts and are crucial to making sense of these apparent mismatches to develop mitigation strategies.

Finally, the dendritic structure of stream networks can cause apparently minor, spatially discrete disturbances in downstream reaches to have disproportionately large and spatially extensive effects in upstream reaches (Fagan 2002). In the community context, these effects are most likely to result from blocking dispersal or migration between downstream and upstream reaches, causing a reduction in diversity in upstream reaches. This process impairment is exemplified by the effects of dams on communities in upstream tributaries (Fausch et al. 2009). However, this is an extreme example, and similar effects can result from downstream impairments that are far less obvious, such as habitat degradation, water withdrawals, or poorly designed road crossings in a single downstream reach. Similar to the concentrative effects discussed above, these propagative upstream effects will tend to decouple local patterns of community composition in upstream reaches from both local and landscape-level habitat conditions in and around those reaches. Here again, managers would greatly benefit from genetic tools to identify these propagative effects, thereby allowing mitigation actions to be directed to the true source of alteration.

Genetic data are valuable for assessing network-level effects on local fish community composition because they can provide information on both the scale and directionality of impact and sources of immigrant subsidies from source populations (examples in Table 1). For example, in cases where immigrant subsidies are thought to boost local diversity in impaired reaches, estimates of gene flow in a focal species can be compared between longitudinal populations (i.e., along a continuous channel) and populations in adjacent, hydrologically independent channels. Using gene flow as an index of dispersal (e.g., as inferred from population differences in allele frequency described in Figure 2), this analysis would reveal both overall levels of population isolation and relative levels of exchange between populations.

Comparisons of rates and spatial patterns of gene flow and spatial patterns in genetic diversity in a focal species will be informative in cases where reduced species diversity in upstream communities is thought to result from the propagation of downstream effects. Specifically, gene flow between downstream and upstream populations and genetic diversity in upstream populations should be reduced relative to networks without a putative downstream barrier. For example, human disturbances that fragment river networks, such as dams or water withdrawals, may impede species from accessing critical habitats, and changes in land use or climate may alter habitats, changing their suitability for select species or assemblages. Genetic data are amenable to use with standard methods of barrier detection (e.g., Wombling: Crida and Manel 2007; Monmonier algorithms: Manni et al. 2004), as well as spatial Bayesian clustering methods (e.g., Corander et al. 2004), aspatial analyses, principle coordinates analysis, and other non-Bayesian methods (reviewed in Blair et al. 2012). Further, genetic data allow quantification of the lag time (in generations) to detect the effects of barriers to gene flow based on the magnitude of differences in allele frequency (Landguth et al. 2010). Genetic data may also provide measures of genetic diversity within and among populations (e.g., Figure 2) as a means of inferring effects of landscape processes occurring throughout river networks that may differentially affect each species. In situations where quantitative assessments of

abundance are not feasible except in a relative sense among locales (e.g., catch per unit effort), genetic data can provide measures of effective population size and number of breeding adults (Waples et al. 2013; Table 1).

INTEGRATING EVOLUTIONARY CONCEPTS IN AQUATIC ASSESSMENT PROGRAMS

Human activities continue to fragment and degrade fluvial systems, underscoring the importance of maintaining the capacity of aquatic organisms to adapt to changing environmental conditions. Analyses of thousands of loci mapped across the genome make possible the identification of loci that might be under selection, associated with environmental variables, and potentially adaptive (Allendorf et al. 2010). These analyses can be achieved by generating a distribution of population genetic statistics that characterize how genetic variation is apportioned among populations and individuals (Vasemägi and Primmer 2005). Analyses identify “outlier” loci that show unusually high or low population differentiation (Hohenlohe et al. 2013). Such outlier loci and environmentally associated variation in the frequency of alleles at these loci can help identify potentially adaptive genes and source habitats of origin (including hatchery and wild populations).

Genetic data can help manage for evolvability or adaptive potential of natural populations in several ways. First, having management goals that maintain high genome-wide variation and a large local effective population size (N_e) would be beneficial to fisheries managers because variation (and N_e) are proportional to the ability of a population to respond to selection and adapt (Allendorf et al. 2013). Second, fisheries managers would benefit by maintaining high variation at functional gene loci important for fitness in current (and ideally future) environments, such as genes for disease resistance and thermal tolerance, which may include planning for assisted gene flow (Aitken and Whitlock 2013). Third, fisheries managers can exploit genetic data to monitor and maintain a large population size and numbers of spawners (Waples et al. 2013), which is important to avoid extirpation, demographic bottlenecks, and loss of ecosystem services that depend on large fish population sizes. The use of many genetic markers (including markers in adaptive genes) can help to monitor and manage for maintenance of gene flow and to maintain demographic connectivity—both of which are crucial for long-term population persistence. In addition, genomics data can aid in identification of conservation units (Funk et al. 2012) by identifying genetically unique or locally adapted alleles.

Signatures of genetic adaptation of fish inhabiting different climates, flow regimes, or thermal environments are well documented (e.g., Kovach et al. 2012). Climate change can effectively isolate populations by changing thermal or hydrologic regimes in different regions of rivers used by fish during different seasons and by different ontogenetic stages. Given overwhelming evidence for climate change and the likelihood that the scope of climate effects to fish populations will continue to expand, genetic data and analyses would help fisheries managers anticipate and mitigate these impacts (Landguth et al. 2014; Kovach et al. 2015). Genetic data will inform fisheries managers of population response to cryptic thermal barriers that decrease connectivity (i.e., reducing gene flow and thereby increasing genetic β -diversity, while also reducing effective population size and genetic α -diversity) and potentially identify the locations of these barriers to allow for management action. Given current technologies that allow

whole genomes to be interrogated, samples collected across variable environmental conditions can readily identify key genes associated with response to important stressors and will reveal linkages between gene expression and physiological conditions (e.g., Allendorf et al. 2010).

Empirical landscape genetics and spatial simulation studies can help managers monitor and predict rates of both neutral and adaptive gene flow across stream networks, once adaptive alleles have been identified (Lowe and Allendorf 2010). For example, as high elevation or high latitude streams warm, alleles for thermal tolerance are expected to “invade” higher elevation streams. Similarly, alleles for earlier spawning or migration might increase frequency in high elevation/latitude streams with changes in thermal and hydrologic regimes (Kovach et al. 2012). If empirical genetic monitoring (or simulation modeling) were to suggest that adaptive alleles will not spread fast enough to keep up with warming (or disease spread), managers could translocate fish carrying the adaptive alleles into the populations suffering high temperatures (or disease), as is being conducted in other species (Aitkin et al. 2008). The monitoring of genes influencing fitness can also be used to detect stress events, such as disease, temperature-induced die-offs, or population declines (see review in Hansen et al. 2012).

DNA markers in genes can provide early detection of hybridization, which is commonly associated with habitat alteration or management actions that introduce nonresident species to waters inhabited by native species (Scribner et al. 2001), including the spread of alleles from nonnative fish into native populations through introgression (Hohenlohe et al. 2013). Evidence of admixture (e.g., matings among individuals from genetically different populations or species) or differences in the frequencies of alleles at adaptive gene markers can be tested for correlations with environmental features to understand whether certain landscape or environmental variables (e.g., temperature) drive introgression between native and nonnative fishes (Muhlfeld et al. 2009, 2014). Hybridization driven by human activities, such as translocation of species and habitat disturbance, tends to occur quickly and reduces fitness (Muhlfeld et al. 2009), genetic integrity (Allendorf et al. 2001), and native species diversity. For example, a recent study by Muhlfeld et al. (2014) found that climate change accelerated hybridization between native Westslope Cutthroat Trout *Oncorhynchus clarki lewisi* and nonnative Rainbow Trout *O. mykiss*. Long-term genetic monitoring data, coupled with high-resolution climate and stream temperature predictions, showed that hybridization was historically prevalent in only one source population, but that during a recent 30-year period of accelerated warming, hybridization spread rapidly upstream through the river system. Decreases in spring precipitation and increases in summer stream temperature were identified as the major drivers of accelerated hybridization. Protecting genetic integrity and diversity, which is critical for long-term resiliency in the face of environmental and anthropogenic change, will be challenging when native species are threatened with invasive hybridization, underscoring the importance of genetic monitoring in native species conservation and management programs.

APPLICATIONS OF NEUTRAL AND ADAPTIVE GENETIC MARKERS: CASE STUDY OF BULL TROUT IN THE UPPER FLATHEAD RIVER

In this section, we present results from simulations conducted using data from Landguth et al. (2014) and Muhlfeld et al. (2014) on threatened Bull Trout *Salvelinus confluentus*

populations in the upper Flathead drainage (Figure 3). This example uses genotypes over a 100-year time series (2000–2100) for a neutral locus to illustrate the effects of variation in population size and connectivity (gene flow) and for an adaptive locus to illustrate the effects of selection associated with stream temperature (Figures 3B–3D). Simulations project spatially explicit measures of variability (heterozygosity; H_e) and intersample genetic differentiation (G'_{ST} ; Figure 3E).

We modeled two types of landscape disturbance using the program CDFISH (Landguth et al. 2012). The first case considers estimates of habitat condition as quantified from the 2010 assessment of fluvial habitats conducted in support of NFHP (Figure 2A). In western Montana, the disturbance features most influential to fish habitat condition included human population density and proportion of impervious surfaces in watersheds. The second case considers time series projections developed by Landguth et al. (2014) that predict changes in river thermal regimes that affect movements during upstream spawning migrations due to thermally unsuitable sections of the river. These thermal effects can influence gene flow and individual fitness if certain alleles have propensities for greater survival in higher temperature environments.

In this illustrative example, we first used an island model of migration (i.e., equal probability of migration and straying for each subpopulation) for 25 generations to establish a genetic burn-in pattern of genotype distributions (Figure 3B) before our simulations started with the given selection and resistance surfaces. The riverscape selection and resistance surfaces were then used for an additional 100 years (year 50 shown in Figure 3C and year 100 in Figure 3D) to determine increasing or decreasing population size and changes in levels of genetic variation (H_e and G'_{ST}) resulting from a combination of individual migratory behaviors and the dynamics of population vital rates. We modeled a single locus under viability selection favoring individuals with one or two copies of the “A” allele. Selection was controlled via fitness landscape surfaces (i.e., temperature) for each genotype. Then, selection was implemented through differential survival of an individual as a function of the relative fitness of the individual’s genotype at the location on the temperature surface where the dispersing individual settled.

Results differ in terms of the temporal changes in genotype frequency in the system based on the two cases. Figure 3E shows both H_e and G'_{ST} for each population at the initial generation under scenario 1 (current temperature + habitat condition without spatial thermal selection operating) at year 2100 and under scenario 2 (future temperature + habitat condition with spatial thermal selection operating) at year 2100. Increasing stream resistance influences spatial genetic structure (red populations in Figure 3E). However, to further illustrate how spatial selection can influence population structure, we plotted each individual within each population color-coded for the locus under selection. Thus, individuals with AA (black dots) disappear more quickly under scenario 2 (future temperature and spatial thermal selection operating; Figures 3B–3D). By combining spatial genetic variability (H_e and G'_{ST}) with plausible adaptive thermal responses of populations, it is possible to achieve a more comprehensive vulnerability assessment than using traditional ecological assessment data alone.

CONCLUSIONS

Genetic data and landscape genetic approaches provide a powerful and complementary tool for monitoring and predicting

population vulnerability and effects of landscape features on diversity at population, community, and species levels in river networks. We have shown that assessments of the current status and future condition of riverine fish populations and habitats can be enhanced by incorporation of genetic data. Furthermore, we suggest that the sensitivity of α - and β -genetic diversity to disturbance and variation in the scale and directionality of landscape effects dictates that ecological assessment tool kits should be expanded to include genetic data. The application of empirical and simulated genetic data and analyses, particularly as we know more about gene expression and physiological condition, will greatly expand our understanding of the effects of habitat alteration and impairment on fish communities, the proximal demographic mechanisms underlying these effects, and the scale of necessary mitigation efforts. Greater interactions among fisheries managers, biologists, and geneticists and joint efforts to collect, synthesize, and interpret multiple data sources will be especially valuable for monitoring and assessing aquatic ecosystems and for implementing effective conservation and management strategies to improve resiliency and adaptive capacity of freshwater species. Such interdisciplinary efforts can therefore help avoid impairment of intact systems and further promote rehabilitation of those systems with currently impaired processes.

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