

Ecological Simplification: Human Influences on Riverscape Complexity

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The rationale of most restoration strategies is that with reconstruction of natural habitats comes biodiversity, and ecosystem functioning and services will follow suit. Uncertainty and frequent failure in restoration outcomes, however, are recurrent and likely related to the complexity of ecosystem properties. Here, we propose ecological simplification as the general mechanism by which human impacts have modified cross-scale relationships among landscape complexity, integrity, and niche diversity in ecosystems. To manage and reverse the negative effects of ecological simplification, the interplay between research and management must quantify the large-scale complexity of reference to restore simplified systems and to link these measures to niche diversity quantified at finer scales. Because of their historical interaction with human societies, we use riverine floodplains as model ecosystems to review the causes and consequences of simplification and to discuss how contemporary restoration can minimize the effects of simplification on biodiversity, functioning, and services of riverine floodplains.

Keywords: ecological simplification, complexity, niche diversity, restoration, floodplains

In their natural state, landscapes exhibit two distinct characteristics: They are structurally complex and exhibit complex behavior. Structural complexity results from the interplay between climate and geomorphic processes, whereas behavioral complexity emerges from biological communities that the structure supports (Green and Sadedin 2005). Landscape *complexity* entails variation in forms and functions of distinct units manifested along dimensions of heterogeneity, connectivity, and legacy (Cadenasso et al. 2006). *Heterogeneity* results from the spatial structure of distinct landscape units and its variation over time as a shifting mosaic of patches (Borman and Likens 1979, Stanford et al. 2005), typically driven by environmental gradients or disturbances. *Connectivity* refers to the network formed by these patches and the transition areas among them through which energy and matter move (Ward et al. 1999). *Legacy* addresses those interactions among landscape units reflecting historical conditions. Multidimensional complexity, evident at landscape scales, is typically related to variation in biological form and function at finer scales. The relationship between complexity and biological diversity has been a focus of classic ecological theory (e.g., Hutchinson 1957), on the basis of the principle that complex landscapes increase niche diversity because the variation in abiotic and biotic factors allows the survival and coexistence of species with similar requirements (Croker 1967).

The concept of complexity was popularized among ecologists following its definition as *biocomplexity* (Michener et al. 2001, Cottingham 2002). However, the theoretical basis for its application relates to addressing ecosystems as *complex adaptive systems* (CAS; Levin 1998), in which macroscopic properties such as food-web structure, biodiversity–function relationships, and patterns in nutrient dynamics emerge from endogenous interactions among species, between species and the environment, and among extant subsystems. This perspective is consistent with the classic ideas of the realized niche of Hutchinson (1957) in that it predicts the occurrence of communities structured by interactions among coadapted species in particular environments (Green and Sadedin 2005). When human activities have degraded the ways in which ecosystems are organized and interact, both niche and CAS perspectives implicitly suggest that restoration should reestablish complexity and niche diversity at appropriate spatial and temporal scales. This requires, however, a comprehensive knowledge of how complexity is qualitatively and quantitatively related to niche diversity, particularly when projects address restoration at the landscape scale.

Integrity, complexity, and ecological simplification

Ecological integrity has been defined as “. . . the ability to support and maintain a balanced, integrated adaptive

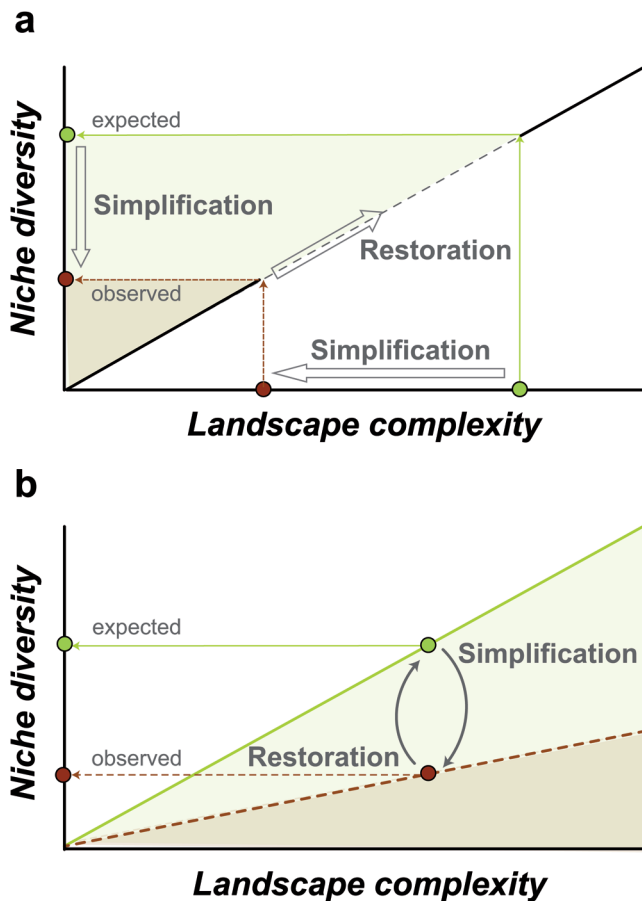


Figure 1. The predicted effects of ecological simplification due to loss of (a) landscape complexity and (b) ecological integrity on the relationship between landscape complexity and niche diversity for an ecosystem of a given size.

assemblage of organisms having species composition, diversity, and functional organization comparable to that of natural habitat of the region” (Karr and Dudley 1981). By definition, *integrity* is a comparative term and generally declines with increasing anthropogenic alterations. Landscapes with their integrity intact should express all the potential niche diversity associated with a given complexity. Ecological integrity therefore depends on how well mechanisms controlling complexity–diversity relationships are operating at appropriate spatial and temporal scales. For this article, we address *ecological integrity* as the degree to which niche diversity expected for a given complexity is actually observed under existing conditions. Integrity is expected to be maximal in relatively pristine settings and reduced in those where particular human influences have disrupted how existing complexity is expressed as niche diversity.

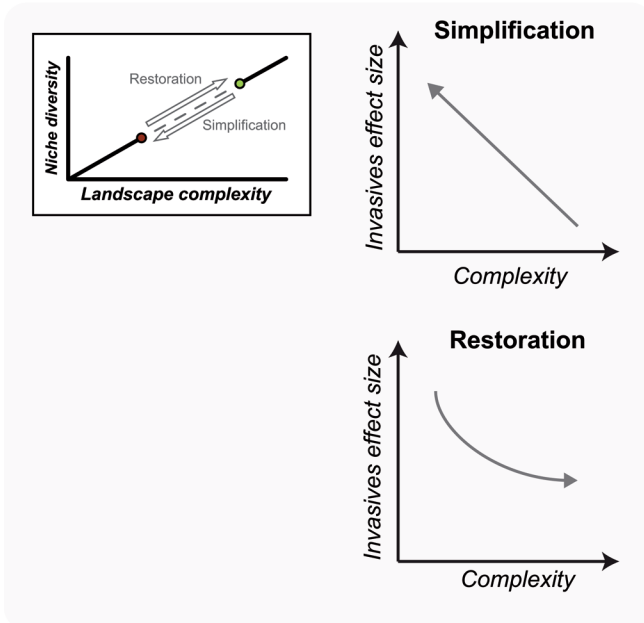
The human reduction of complexity and integrity results in ecological simplification. Here, we define *ecological simplification* as the reduction in niche diversity due to the loss of landscape complexity and ecological integrity, generally resulting from human activities. Simplification can result

from either of these processes alone or in combination (figure 1). Simplification is caused by decreased complexity when structural changes to landscapes result in loss of niche diversity (figure 1a). In these cases, reduced niche diversity alters local interactions controlling biodiversity and ecosystem function. Simplification of this type transforms highly complex landscapes into more homogenous, less complex entities, reflecting exogenous control (i.e., human influences) over endogenous properties such as complex behavior. Although this type of simplification is typically associated with loss of heterogeneity (Tockner et al. 2010), it may occur along any of the three axes of complexity (Cadenasso et al. 2006). For instance, habitat fragmentation results in reduced connectivity and has negative consequences for biodiversity, population genetics, and ecological interactions (e.g., Fahrig 2003). Simplification along the legacy axis is illustrated by homogenization of historical flow regimes caused by impoundments and its influence on biodiversity of fluvial ecosystems (e.g., Poff et al. 2007).

Alternatively, human–environment interactions may not reduce the complexity of a landscape but instead alter how it is translated into niche diversity (figure 1b). These types of human influences undermine ecological integrity, causing a decline in niche diversity not directly related to reduced landscape complexity. Chemical pollution is probably the most common example of this type of simplification, because it reduces diversity, not through loss of structural variance in the landscape but by causing stress and mortality to species that would otherwise occupy available niches. For example, the loss of diversity through acidification is well documented in freshwater environments without accompanying structural loss (Vinebrooke et al. 2004). Similarly, metals and pesticides residing in sediments of aquatic systems are notorious for causing diversity loss (Lake et al. 2000). Even elements essential for growth can prove to impair biodiversity depending on form and concentration. For instance, nitrogen (N) pollution generates high levels of ammonia, nitrite, and nitrate that may impair survival, growth, and reproduction in aquatic species, reflecting the direct toxicity of these inorganic compounds (Camargo and Alonso 2006). Pollution that increases phosphorus (P) availability may also indirectly promote toxicity and the loss of biodiversity by enhancing the abundance of toxic cyanobacterial species (Christoffersen 1996). In addition to changes in the abiotic template, invasive species have the potential to alter habitat suitability for an array of species, especially in aquatic ecosystems (Sala et al. 2000).

Even though our conceptual model presents complexity and niche diversity as linearly related (figure 1), the relationship might well be nonlinear in specific cases (Wu and David 2002). Nonlinear relationships raise concern over the potential to exceed ecological thresholds (Groffman et al. 2006), such as the establishment of nonnative species. Invasive species can be both a cause and consequence of simplification (Didham et al. 2005). On one hand, they may alter complexity via ecosystem engineering and exclude native species

a. Invasive species and landscape complexity



b. Invasive species and ecological integrity

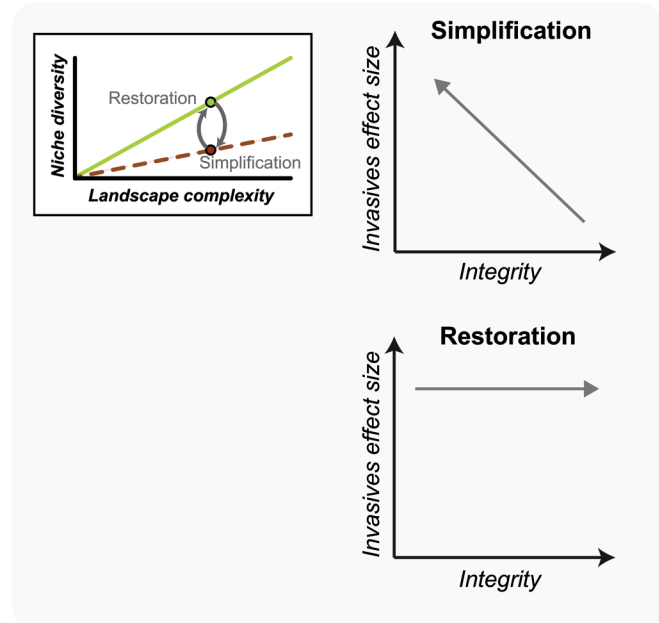


Figure 2. The expected responses of invasive effect size to diversity, biomass, productivity, and nutrient uptake in riverine floodplains as a result of (a) decreased complexity and (b) the loss of integrity.

(Crooks 2002) or result in integrity loss via species displacement (Wilson 1992), causing ecological homogenization (Olden et al. 2004). On the other hand, invasive species may access the system as a result of simplification. Reductions in niche diversity due to the loss of landscape complexity enhance the relative contribution of nonnative species to ecosystem form and function (i.e., effect size; figure 2a). This is particularly true if human-derived structures provide habitat appropriate for invasive species that then aggressively displace native species. Under these conditions, habitat restoration may restore complexity but may not stimulate the expected reduction of invasive effect size. Instead, the effect size may approach an asymptotic decrease because of the competitive superiority of invasive species not eliminated by the structural changes bestowed by restoration (figure 2a). Similarly, simplification via loss of integrity is predicted to promote invasive effect size (figure 2b), reflecting a reduced contribution from native species with specialized niche tolerance compared with that of the more generalist invaders (Snyder et al. 2006). Broad niche tolerance by invasive species is also expected to make effect size relatively immune to the influences of restored integrity; tolerance by resident invasive species should allow them to occupy crucial native niches even after appropriate physical and chemical conditions are restored (figure 2b). Even though invasive species are argued to promote simplification and influence the efficacy of restoration, there is a general lack of knowledge regarding the environmental drivers dictating the establishment of many nonnative communities.

Although the focus of most restoration plans has been the reconstruction of habitat heterogeneity (Bernhardt et al. 2005), it is likely that this step is necessary but not sufficient to reestablish natural complexity. In the case of running water ecosystems, Palmer and colleagues (2010) demonstrated that very few restoration projects targeting increased habitat heterogeneity, such as channel reconfiguration and in-stream habitat improvement, actually resulted in biodiversity recovery. They emphasized the need for the targeted amelioration of multiple stressors at a time. We contend that the relationships among complexity, integrity, and niche diversity (figure 1) can be used to guide restoration approaches to multiple stressors and that most simplified ecosystems will require multidimensional restoration of this type.

Riverine floodplains and ecological simplification

Riverine floodplains are excellent laboratories for the development and testing of ecological theory because of their rapid habitat turnover, high complexity, and long history of human–environment interaction (Tockner et al. 2010). Although the concepts presented here are applicable to any threatened ecosystem, we use rivers and their floodplains as model landscapes in which to address the character and consequences of ecological simplification.

Floodplain inundation occurs naturally during the flood pulse (Bayley 1995), a process that has been shown to influence ground- and surface-water connectivity, biodiversity, and bioproduction in riverine landscapes worldwide.

Naturally functioning floodplains also provide important ecosystem services, such as the amelioration of flood damage (Shankman and Smith 2004), the consumption and storage of energy and materials (Valett et al. 2005), and the maintenance of shallow aquifers that provide base flow to rivers as well as irrigation and potable water. These properties are derived from complex and dynamic terrestrial and aquatic habitats (Ward et al. 1999) resident on intact floodplains. Their complexity reflects environmental heterogeneity and connectivity produced by “cut-and-fill alluviation” and the shifting habitat mosaic it creates (Stanford et al. 2005).

Globally, riverine floodplains have been pivotal for the evolution of ancient civilizations into modern societies as significant locations for social, agricultural, and industrial development. The growing complexity of human societies has resulted in increasingly simplified floodplains. River flow is harnessed by dams, effectively stranding many river floodplains. Reduction in flood flows and the establishment of revetments for transportation along river corridors, gravel mining, harvesting, channelization, and agricultural and urban expansion all substantially reduced the natural complexity and integrity of floodplain networks (Decamps et al. 1988, Hauer et al. 2003). This pattern of human colonization along floodplains has occurred worldwide to a greater or lesser extent (Tockner and Stanford 2002).

The natural flow regime is crucial for biodiversity production and maintenance for rivers and their floodplains. A recent synthesis focusing on how to link human needs and natural processes in river landscapes (Arthington et al. 2010, Poff et al. 2010) emphasized that flow variability is the “master variable” and that historical flow influences on river and floodplain biodiversity are robust and widespread (Poff et al. 1997). The consequences of dam construction are easily observed in the decreased flood occurrence documented over the last century for the Columbia River in the United States (figure 3a), a complex river system with salmon species that have been the staple of life for Native Americans since before European settlement.

These findings emphasize how simplification along the legacy axis (i.e., flow regime) can reduce complexity even if riverscape heterogeneity and connectivity remain the same. Simplification of the flow regime results in the loss of historical niches (Poff et al. 1997) and promotes conditions that favor the spread of more generalist species, potentially enhancing invasive-species effect size (figure 2a). Olden and colleagues (2004) and Poff and colleagues (2007) elegantly addressed this phenomenon by linking the gradual replacement of native biota by locally expanding nonnatives to convergence in riverine flow regimes across 186 midsize river systems. In the United States, widespread flow simplification during the sixties and seventies has had a contemporary influence on salmon migration and on the prevalence of and adaptation among other invasive animal species (Quinn and Adams 1996).

River channelization is another cause of floodplain simplification, and the practice is expected to increase in the

future. Both the dredging and constriction of large river systems to achieve more navigable and confined channels impose new geomorphic domains in which hydrologic and geomorphic processes are no longer capable of maintaining habitat heterogeneity and connectivity within the historically flooded area. This is primarily attributed to the construction of training structures along the main channel shore that includes rip raps, groynes, or other revetment structures designed to decrease erosion along the river shoreline (Henning and Hentschel 2013). Training structures stabilize river banks, reduce flooding effects, and maintain depths and widths required for navigation (McCartney et al. 2012); however, they also lead to the isolation of permanently and seasonally inundated floodplain habitats, such as side channels, springbrooks, ponds, wetlands, and sloughs.

Therefore, river channelization causes simplification along all three axes of complexity primarily because of the loss of off-channel contributions historically maintained by river dynamics (Lorang and Hauer 2006). In a survey of ten different floodplains across Montana, in the United States, we found that most spatial variations in nutrient concentrations and other features of niche diversity were associated with off-channel environments (figure 3b, supplemental table S1). Greater habitat variance suggests that biological form and function influencing energy flow and nutrient cycling in off-channel environments differ from those in the main channel. Enhanced variation and biodiversity in off-channel components of the landscape rely on dynamic connections with the main channel that contribute to complexity. This is in agreement with previous studies showing that channel confinement can cause drastic decreases in the richness of aquatic invertebrate communities (Bellmore and Baxter 2014) and result in the loss of fish production and the biodiversity associated with off-channel environments (Bayley 1995).

A range of riverscape complexity: Comparing temperate floodplains in Europe and North America

The magnitude and extent of floodplain simplification reflect worldwide patterns of human development and migration. As a result, the average European floodplain is more simplified than those in North America, reflecting the fact that human expansion, and particularly the practicing of agriculture on river floodplains, started much earlier. Precocious simplification by European countries resulted in revetment construction as early as the seventeenth century. In the United States, the Army Corps of Engineers developed the inland waterway system in 1820 (McCartney et al. 2012). Cross-continent comparisons between river systems of similar size, therefore, should be considered relevant for management and restoration purposes, especially if the alternative is inconsistent historical data or reliance on ecological theory developed from unaltered tropical floodplains (Bayley 1995).

To illustrate the usefulness of such an approach, we compared representative sections of two well-known river

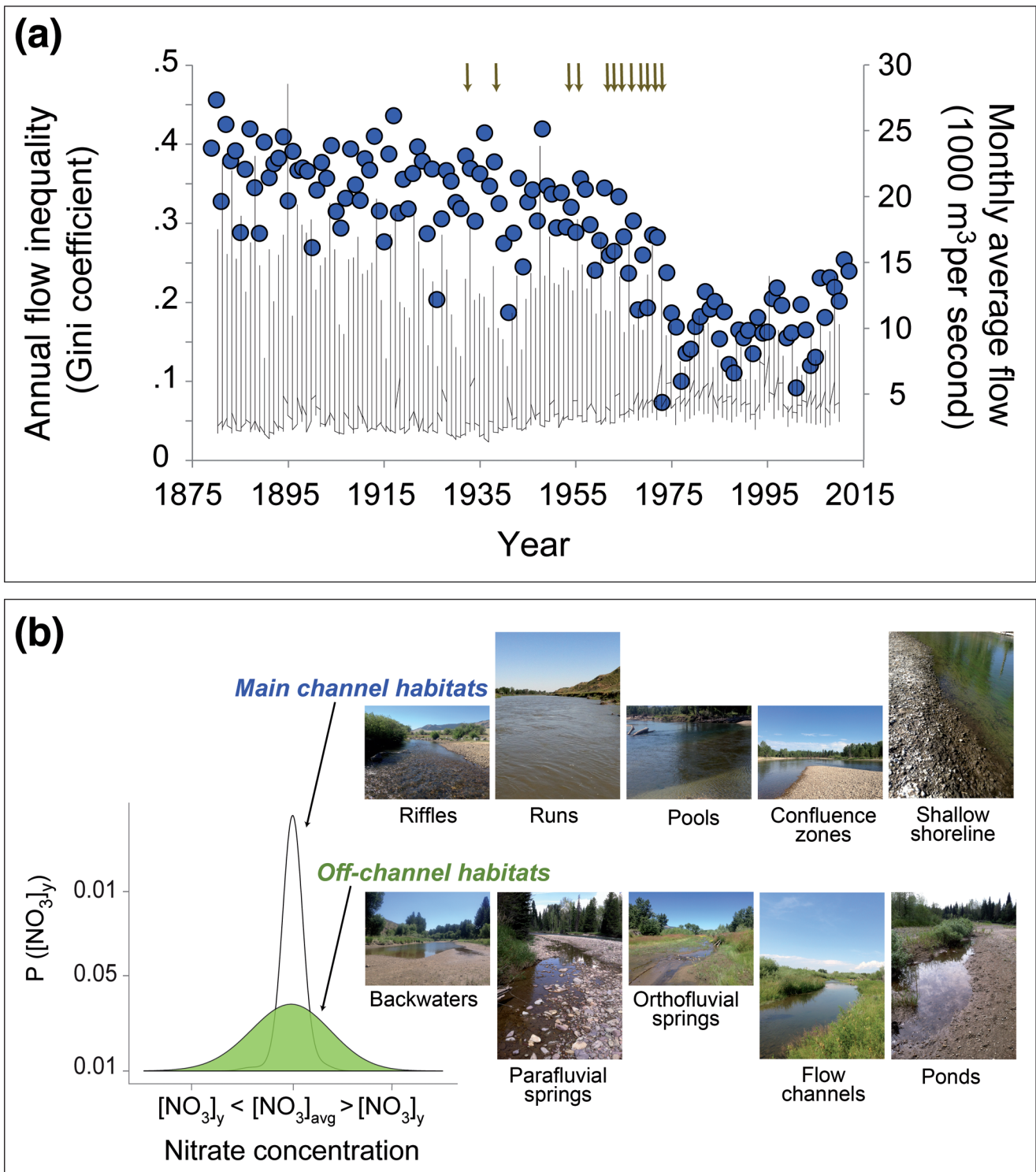


Figure 3. (a) River flow variability for the Columbia River (upstream of Portland, Oregon) over the last 135 years represented by monthly average flow and annual Gini coefficients (G). Gini coefficients represent flood occurrence, with $G = 0$ indicating absence of significant floods and $G = 1$ indicating a scenario in which a single day accounted for 100% of the total annual river discharge. The arrows indicate the year of construction of 13 major dams in the main stem of the Columbia River. (b) The probability of observing average, high, and low nitrate (NO_3) concentrations in aquatic habitats located in the main channel and within the floodplain area (i.e., off-channel habitats). The probability distributions correspond to data collected from ten river floodplains across Montana, during base flow conditions. Abbreviation: m^3 , cubic meters.

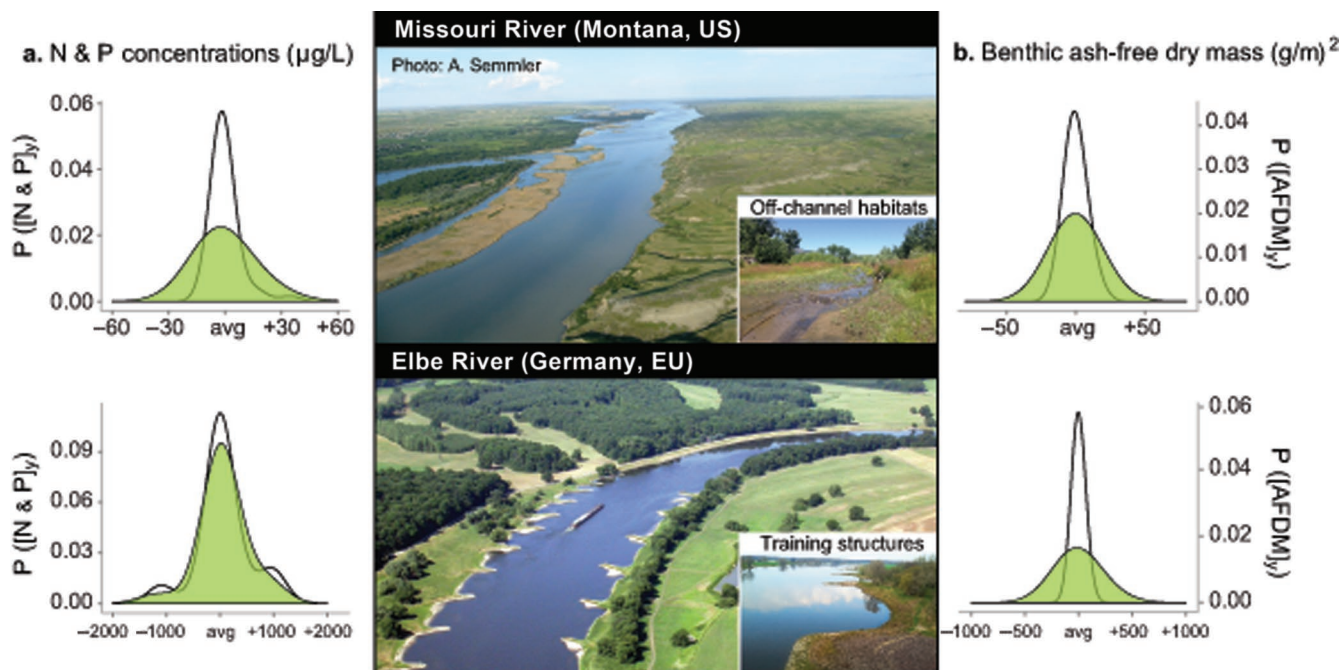


Figure 4. Contributions of naturally created habitats along the shore of the Missouri River (Montana) and shoreline training structures (rip-rap, standard groynes, and off-line revetments) of the Elbe River (Germany) to observed niche diversity in each river system. Probability distributions of (a) the sum of nitrogen (N) and (P) concentrations and (b) ash-free dry mass in the river benthos are represented for both the main channel (white) and shoreline habitats or training structures (green). Abbreviations: AFDM, ash-free dry mass; avg, average; L, liter; m, meter; μg , micrograms.

systems: the Missouri River in eastern Montana, United States, and the Elbe River in Saxony-Anhalt, Germany. Fort Peck Dam impounds the Missouri River (mean annual discharge, 280 cubic meters [m^3] per second) as it traverses eastern Montana, and forms the fifth largest reservoir in the United States. Although the Missouri River is far from pristine, a relative lack of human constraint has allowed for continuing floodplain connectivity and heterogeneity below the dam (figure 4). In contrast, the Elbe River (mean annual discharge of 368 m^3 per second), while not the most impacted large river in Central Europe, has a long history of channel training structures, mostly groynes, along the main channel shoreline (figure 4) resulting in a constricted channel embedded in an agricultural and highly developed urban landscape. Groynes in the Elbe River have altered many floodplain habitats, disconnected floodplain wetlands from channel flow, and led to erosion of previous sand and gravel banks promoting artificial stabilization through revetment construction (Scholten et al. 2005).

It is well understood that restoration of the natural flow regime and flood pulse has great potential for enhanced biodiversity (Poff et al. 1997). Restoring natural flow variability regenerates the capacity of the river to do geomorphic work necessary to create and maintain a patchwork of habitats with different physical structure, age, and successional state. Similarly, reconnection between river channels and their floodplains increases nutrient-processing rates (Valett et al.

2005, Kaushal et al. 2008), whereas re-meandering can significantly enhance stream–subsurface hydrologic exchange in floodplain sediments (Kasahara and Hill 2008). However, current human constraints in many landscapes make restoration of natural hydrologic regime and connectivity unviable. Therefore, efforts to enhance diversity are frequently restricted by cultural priorities and geographic constraints. Paradoxically then, introduction of different types of training structures is now considered to provide some complexity to the main channel of the Elbe River by enhancing topographic heterogeneity and generating variation in near-structure flow conditions (Henning and Hentschel 2013).

If flow variability is the “master variable” to generate floodplain complexity (Poff et al. 1997), heterogeneity is the most important dimension of complexity to generate resilience in natural systems (Levin 1998), which in turn promotes adaptive responses to stress and perturbations such as pollutants, pests, or invasions. Therefore, increasing heterogeneity within the confined channel may at least reduce losses of integrity that are more likely to occur in riverine floodplains with simplified complexity. Although restoration efforts to increase complexity in the main channel will never fully compensate for the niche loss due to floodplain isolation and simplification, the restoration of large rivers is currently based on knowing which type of training structures can maintain the river navigable while contributing to restore part of the floodplain’s niche diversity (Kotenko

2003). In this perspective, many studies highlight the value of groyne fields as biotopes that increase diversity in the absence of intact and interactive floodplains. For instance, groyne fields generate greater fluctuations in temperature, dissolved oxygen, and pH than those observed in bulk flow of the Elbe River (Boehme 2006). Further, groynes promote deposition of nutrients in particulate form (Schwartz and Kozerski 2003) and generate spawning, nursery, and feeding habitats for many fish species (Eick and Thiel 2013). Recent additions of more advanced off-bankline revetments result in enhanced biodiversity and benthic secondary production compared with those of standard groynes (Brabender 2015).

To what extent does niche diversity associated with the variety of training structures in the Elbe River compare with the niche diversity resulting from natural complexity provided by off-channel habitats of the Missouri River? Our data show that in terms of dissolved N and P, training structures do not expand variation in nutrient concentrations as happens among naturally created habitats (figure 4, supplemental table S2). However, despite homogeneity in nutrient concentrations among Elbe River habitats, groyne fields do generate a much wider distribution of benthic organic matter resources than that observed in the main channel, representing patterns of heterogeneity very similar to those observed in the Missouri River and its more natural floodplain habitats (figure 4, table S2). Overall, simplification associated with the confinement of the Elbe River results in the reduction in niche diversity relevant to primary producers due to enriched and homogeneous nutrient availability (figure 4). In contrast, benthic consumers inhabiting training structures in the Elbe River who rely on particulate organic materials derived from allochthonous or autochthonous materials seem to have similar resource niches to those in the shoreline of the Missouri River (figure 4).

Although more structurally diverse groyne fields may contribute to greater variation in organic matter resources and enhanced diversity and abundance of aquatic invertebrates in large, simplified rivers, the original simplification of shoreline complexity and loss of ecological integrity provides optimal conditions for establishment of invasive invertebrate species (figure 2). This is especially true for large rivers given the role of navigable waterways in propagation and spread of aquatic invasive species (Leuven et al. 2009). Novel physicochemical environments associated with training structures can alter the quality of shoreline habitats and provide ecological niches suitable for the establishment of exotic species (Frueh et al. 2012). For instance, substituting rip rap for sandy shores introduces allochthonous habitat types (i.e., boulders, cobbles) that further invasive species over native counterparts more adapted to sandy shores (Brabender 2015).

Research agenda and strategies to restore complexity in simplified floodplains

Landscape complexity assessed at scales relevant to river restoration can and should be linked to biological assessments

that guide management decisions. In particular, remote-sensing tools can provide perspectives sufficiently scaled to build the quantitative relationships between landscape complexity and niche diversity proposed in this article (e.g., Lorang et al. 2013). Although floodplains are repeatedly touted as diverse and productive, most studies typically fail to assess complexity in a quantitative way. Luck and colleagues (2010), however, is a pioneering effort that provides quantitative assessment of complexity for over 1500 catchments around the Pacific Rim using multi-Landsat TM satellite imagery (30-meter [m] cell size). However, developing a better understanding of how networks of interactions among distinct ecological units influence biodiversity, functioning, and services associated with individual floodplains will necessarily entail assessment across spatial scales (Hauer et al. 2003). Complexity within and among floodplains requires distinguishing numerous intermediate scale characteristics such as the distribution of shallow shoreline, channel nodes, and floodplain springbrooks. To this end, Whited and colleagues (2013) generated a statistical protocol to link large-scale (i.e., Landsat TM) imagery and finer-scale remote-sensing data (i.e., 2.4-m Quikbird IKONOS) to predict the abundance of springbrooks and shallow shoreline as potential habitat for salmon reproduction. Multispectral remote sensing and/or airborne imagery can provide the detail required to measure the extent or quality of niche diversity within aquatic habitats, whereas links across scales remain a necessary but tractable goal with great potential for application to restoration and river management.

Research and management approaches that include both complexity assessment at large scales and fine-scale assessment of habitat heterogeneity are necessary to understand how human–environment interactions reduce niche diversity through simplification of complexity and integrity. Ultimately, understanding of these relationships may be used to guide management decisions by providing predicted values of complexity, integrity, and niche diversity for floodplains of a given size in a specified geographic domain. When “observed” complexity is documented to be lower than “expected” for a floodplain of a given size, or when lower niche diversity is measured for a floodplain of given complexity, simplification can be quantified at scales to commensurate with management priorities. With this approach, managers may disentangle the causes of floodplain simplification along the two axes of complexity and integrity (figure 5). Armed with this understanding of a floodplain’s status, managers may better proceed to decisions regarding the most appropriate fates for the interfaces between the world’s rivers and the land on which human communities depend.

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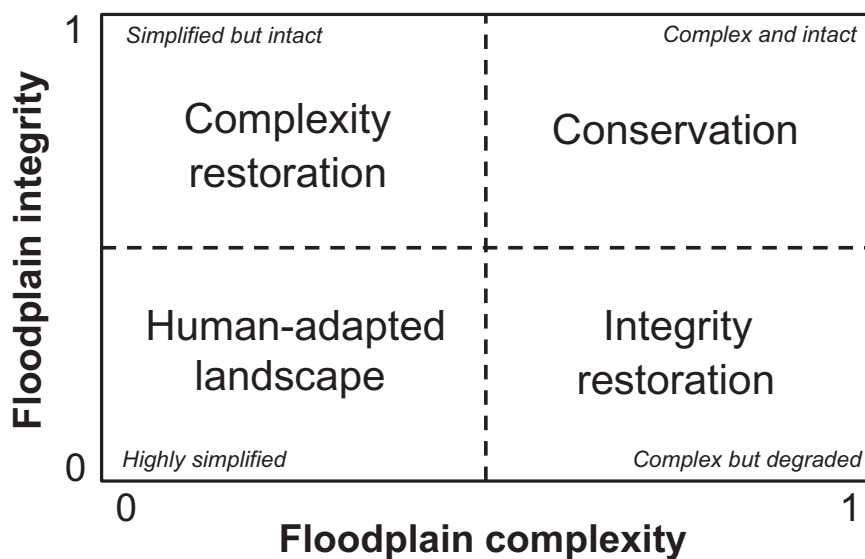


Figure 5. The four quadrants of landscape condition, as was assessed through landscape complexity and integrity, and logical managerial fates. Complex systems with high integrity (quadrant 1) should be considered for conservation and may be used as “reference” systems for restoration efforts. Most systems simplified to some extent through loss of complexity retain high integrity (quadrant 2) and are candidates for traditional complexity restoration. Other systems influenced by toxic spills, excessive nutrient enrichment, or simplification by some invasive species may retain complexity, but their diversity is reduced because of loss of integrity (quadrant 4). Management priorities for these systems should address issues of remediation to regain habitat quality for the extirpation of nonnatives. Finally, landscapes that have experienced a severe loss of complexity and integrity (quadrant 3) should be dedicated to human-adapted forms and functions.

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Supplemental material

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