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Issue: *The Year in Ecology and Conservation Biology***Causes and consequences of habitat fragmentation in river networks**Matthew R. Fuller,<sup>1</sup> Martin W. Doyle,<sup>1</sup> and David L. Strayer<sup>2</sup><sup>1</sup>Nicholas School of the Environment, Duke University, Durham, North Carolina. <sup>2</sup>Cary Institute of Ecosystem Studies, Millbrook, New York

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Increases in river fragmentation globally threaten freshwater biodiversity. Rivers are fragmented by many agents, both natural and anthropogenic. We review the distribution and frequency of these major agents, along with their effects on connectivity and habitat quality. Most fragmentation research has focused on terrestrial habitats, but theories and generalizations developed in terrestrial habitats do not always apply well to river networks. For example, terrestrial habitats are usually conceptualized as two-dimensional, whereas rivers often are conceptualized as one-dimensional or dendritic. In addition, river flow often leads to highly asymmetric effects of barriers on habitat and permeability. New approaches tailored to river networks can be applied to describe the network-wide effects of multiple barriers on both connectivity and habitat quality. The net effects of anthropogenic fragmentation on freshwater biodiversity are likely underestimated, because of time lags in effects and the difficulty of generating a single, simple signal of fragmentation that applies to all aquatic species. We conclude by presenting a decision tree for managing freshwater fragmentation, as well as some research horizons for evaluating fragmented riverscapes.

**Keywords:** barrier; biodiversity; connectivity; defragmentation; edge effect; matrix permeability

**Introduction**

Fragmentation of river systems is pervasive and growing, and is a large but underappreciated threat to freshwater biodiversity.<sup>1</sup> Although some of the effects of river fragmentation are well known—the effects of large dams on migratory fishes<sup>2</sup> and waterfalls on geographic distributions of freshwater animals<sup>3</sup>—many agents other than dams and waterfalls fragment river systems, and their effects on habitat and movement of organisms can vary widely. Because of time lags and interactions with other human impacts on freshwater ecosystems (e.g., climate change, species introductions), the effects of fragmentation are not usually expressed immediately, and so are prone to be underestimated. Managing freshwater biodiversity will require deliberate management of fragmentation. In addition, we believe that emerging theoretical and empirical studies of fragmentation in river networks have great potential to advance the general understanding of ecological fragmentation.

Although river networks are naturally fragmented by agents such as waterfalls, cascades, and beaver dams, human actions (damming, road building, water withdrawal, pollution/water quality barriers, and species introductions) have further divided these habitats into ever smaller patches. Human actions influence almost every freshwater ecosystem across the globe; only a few undammed rivers remain<sup>1</sup> and many of these are affected by culverts and other barriers. Anthropogenic fragmentation developed rapidly and at a pace that precluded the ability for aquatic species to evolve alongside, so these human actions are affecting the rich biodiversity that is harbored within freshwater ecosystems.<sup>4</sup> These anthropogenic effects may increase greatly as the full effects of existing barriers develop, as additional barriers are erected, and as fragmentation interacts with other human impacts (e.g., climate change) on freshwater ecosystems.

The goals of this review are (1) to explain how river systems differ from the terrestrial ecosystems

### Box 1. Glossary of terms related to habitat fragmentation and river networks

- Connectivity**—Can be either structural or functional. Structural connectivity is the physical connection between landscape elements or patches, while functional connectivity is the movement of genes, individuals, or populations between landscape elements.<sup>153</sup>
- Core habitat**—Habitat that is beyond the influence of edge effects.<sup>154</sup>
- Dendritic network**—River drainage network pattern that resembles the branching structure of an oak or chestnut tree.<sup>32</sup>
- Edge habitat**—Part of a patch near its perimeter in which environmental conditions differ from interior conditions in the patch as a result of interactions with the surrounding matrix.<sup>155</sup>
- Edge effect**—A change in environmental conditions or biological communities near the periphery of a patch as a result of interactions with the surrounding matrix.
- Headwater tributary**—A small stream in a river network.<sup>156</sup>
- Hyporheic zone**—A transition zone between the river channel and the underlying ground water.<sup>157</sup>
- andscape genetics**—The field of study combining landscape ecology and population genetics aimed at understanding the interaction of environmental processes and landscape features with population and individual genetic structure.<sup>135</sup>
- Lateral river axis**—Dimension of rivers that involves the exchange of materials and organisms between the river channel and the riparian zone/floodplain.<sup>5</sup>
- Longitudinal river axis**—Dimension of river that runs along a river as the water flows; channel to channel or river segment to river segment.<sup>5</sup>
- Mainstem**—The larger (and often the largest) streams in a river network.
- Matrix habitat**—Habitat between the target patch habitat.<sup>19,143</sup>
- Passability**—Attribute of a barrier that describes the ability of a focal organism to overcome or traverse through the barrier.<sup>7</sup>
- Patch habitat**—The remaining focal habitat (usually the original habitat before human alterations) following fragmentation.<sup>143</sup>
- Permeability**—Attribute of a barrier that describes the proportion of a focal population that is able to pass the barrier relative to the proportion that would pass if the barrier did not exist.<sup>158</sup>
- Riparian zone**—Transition zone between aquatic and terrestrial environments.<sup>159</sup>
- Vertical river axis**—Dimension connecting the river channel water column with the subsurface flow beneath the river bed.<sup>5</sup>

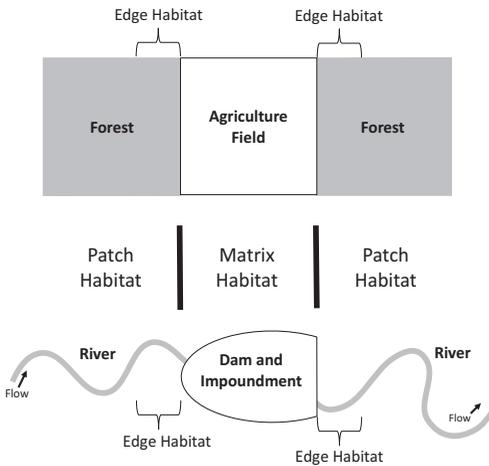
for which much of the theory of ecological fragmentation was developed; (2) to catalog the major agents that fragment river networks and briefly describe their effects; (3) to propose a framework for thinking about the effects of individual barriers and systems of barriers in river networks; (4) to discuss why it is difficult to know precisely how severely fragmentation affects freshwater biodiversity; and (5) to suggest how to best understand the consequences of deliberate management of river fragmentation. We conclude by identifying core areas for future research, including uses of new technology to detect rare dispersal events and implications for future restoration of freshwater habitats.

This review focuses on the *longitudinal* (see Box 1 for glossary of italicized terms) fragmentation of river networks, partly for reasons of space, but also

because longitudinal fragmentation is ubiquitous across riverscapes and has received considerable scientific attention. However, freshwater habitats other than river networks (e.g., lakes, wetlands) are important to freshwater biodiversity, as are other physical dimensions of connectivity in riverine ecosystems (*lateral* with the *riparian zone* and floodplain or *vertical* with the *hyporheic zone*).<sup>5</sup>

### An introduction to ecological fragmentation

Most work on ecological fragmentation has been done in terrestrial ecosystems, and the usual framework for describing and studying fragmentation (Fig. 1) reflects that origin. The focal habitat is usually some sort of primordial habitat, such as primary forest, which has been reduced to a series



**Figure 1.** Analogous parts of a terrestrial forest and a river split by a single fragmentation agent (agriculture field and impoundment, respectively). Patch and matrix habitat are labeled accordingly and locations for potential edge habitat are bracketed.

of disconnected patches by relatively inhospitable human-made habitats, such as agricultural fields. These are called *patch habitat* (i.e., the forest) and *matrix habitat* (i.e., the fields), respectively. This fragmentation reduces the connectivity of the habitat for plants and animals that depend on the forest habitat. The ability of a landscape to allow organisms to move through it has been called *connectivity*, *permeability*, or *passability*, and has been described with a large number of metrics.<sup>6,7</sup>

Fragmentation almost always affects habitat quality as well as connections between habitat patches.<sup>8</sup> Often, terrestrial researchers drill down into a single patch and identify *edge* and *core habitats*. Edge habitat is defined by the penetration of some characteristic/trait (e.g., core habitat species diversity or light availability) into the patch habitat, causing an *edge effect*. The impact of edge effects on species inhabiting these patches can be estimated using simple core-area models,<sup>9</sup> which define some penetration distance of the edge effect into the patch from the matrix habitat to estimate how much patch area is affected by the surrounding matrix versus what remains as unaffected patch-core habitat. Edge habitat is usually regarded as poorer quality for the focal species than core habitat, so the fragmentation harms the focal species by simultaneously reducing landscape connectivity, habitat quantity, and habitat quality. This terrestrial model is typically

discrete and two-dimensional (presumably because of the patchy nature of land conversion and the fact that the foundation theories of island biogeography and metapopulations are discrete), although other formulations would be possible.

Several aspects of this conventional framework apply poorly to river systems. First, when thinking about longitudinal connectivity (as opposed to lateral connectivity with the riparian zone), it seems most natural to conceive of river networks as *dendritic* or one-dimensional rather than two-dimensional (e.g., Refs. 10–14). Fully aquatic organisms such as fish essentially always move in the channel (except in rare instances in which they are passively moved over land), and even species with aerial or terrestrial life stages often disperse chiefly along stream channels.<sup>15–17</sup> This changes the analysis of fragmentation and connectivity from the conventional model, both because the specific dispersal pathway across the landscape is known so precisely and because the shape of the habitat network is altered. The dendritic or one-dimensional shape of river networks often also makes them more susceptible to fragmentation effects (e.g., smaller average fragment size and greater fragment size variance across a fragmented network) than terrestrial systems.<sup>11</sup>

Second, water flow in river networks often introduces very strong asymmetry in edge effects. The edge effects of some barriers (notably dams) can extend well upstream of the barrier, but, as will be discussed below, it is common for the edge effects of barriers such as dams, water withdrawals, and waste outfalls to extend very far (even hundreds of kilometers) downstream.<sup>18,19</sup>

Third, although patch-dynamics approaches have been used in river systems,<sup>20–22</sup> the prevalence of diffuse rather than discrete patch edges in river systems may challenge traditional frameworks. For example, a wastewater outfall creates a chemical barrier, and it is difficult to delineate the downstream boundary of that (degraded) edge habitat patch. Therefore, to apply to river networks, the patch-matrix framework might be modified for continuous gradients or conceptualized as multiple patches of transitional habitat through a gradient.<sup>23</sup>

Fourth, edge effects are usually regarded as negative for the focal species in terrestrial ecosystems, but some riverine edge effects, notably the downstream effects of low dams, may be positive

even for riverine species (i.e., not weedy or edge species)—for example, species richness and abundance of riverine fish and mussels is often enhanced downstream of low-head dams, and riverine freshwater mussel species immediately downstream of a mill dam grow faster and to a larger size than conspecifics upstream of the impoundment or even farther downstream in the same river.<sup>24,25</sup> Thus, models of riverine fragmentation may have to allow for both positive and negative edge effects.

Fifth, the permeability of many barriers in river networks varies with discharge (the amount of water flowing down the channel). Low dams that are passable during high water may be effective barriers when flows are low, and stream channels that are continuous and passable most of the year may fragment into a series of unconnected pools during dry periods. Consequently, the fragmentation of a river network may change greatly between storm events, from wet to dry season, from wet years to dry years, or as flows change as a result of water withdrawals or climate change. Studies of terrestrial fragmentation have only recently considered the time-variance of abiotic forces (e.g., temperature/wind/light in terrestrial matrix habitat or discharge in rivers), except over successional time,<sup>26</sup> and it may be more important in river networks at both short and long time scales than in terrestrial systems.

For these and other reasons, conceptual frameworks developed to describe and study fragmentation in terrestrial ecosystems will likely need to be extended and modified to apply to river networks.<sup>23</sup> It may even be worthwhile for stream ecologists to develop conceptual models of fragmentation *de novo* rather than adapting ill-fitting terrestrial frameworks, although stream ecologists have tended to apply theory developed elsewhere rather than develop their own theory.<sup>27</sup> Finally, we note that because fragmentation in river networks offers a constrained system for studying habitat fragmentation, they may be promising settings in which to study the general effects of fragmentation on ecosystems.

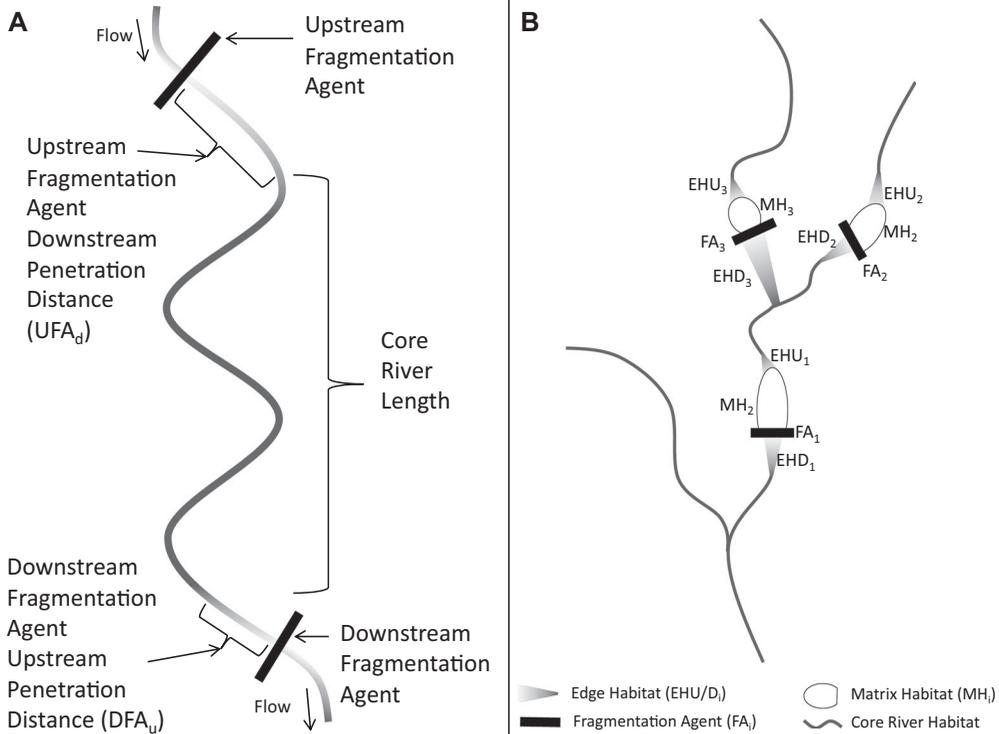
### **A conceptual framework for barriers in river networks**

We offer a simple framework for assessing the effects of barriers in river networks. Let us begin by considering the effect of a single barrier. A barrier has two effects on biodiversity: it blocks movement of

organisms to some degree, expressed by its permeability, and it creates edge habitat (Figs. 1–3). Both of these effects can range from trivially small to complete (no movement past the barrier, lethal habitat conditions in the edge). Edge habitats can extend both upstream and downstream and, with a few exceptions (perhaps, beaver dams or run-of-river dams in flat terrain), downstream edge effects usually extend farther than upstream edge effects. Likewise, permeability is usually asymmetric, and is higher for organisms moving downstream than upstream.

There are several key differences from the usual treatment of fragmentation in terrestrial habitats. As we have already noted, it is most natural to think of the river network as one dimensional around a single barrier, in contrast to the two-dimensional terrestrial system. Interpatch distance is commonly used as a metric of patch isolation in terrestrial systems,<sup>28,29</sup> but it is clearly inadequate as a measure of movement between locations in a river network that may be separated by a high dam; both distance and barrier permeability will be important. Edge effects around some riverine barriers are positive for even some core species,<sup>24</sup> so the model has to allow for both positive and negative edge effects. Because edge effects in river systems often have diffuse boundaries, particularly on the downstream side, it may be more useful to model the stream network as continuous rather than as a series of discrete patches, and asymmetry of permeability and edge effects should probably be the default assumption in models of fragmentation in river networks because such asymmetries can have strong effects on population persistence (e.g., Refs. 30 and 31). Finally, both permeability and edge effects may be strongly stage or time dependent, so depending on the purpose of the model, it may be necessary to incorporate temporal variation into the model, or at least use time- or stage-specific parameter values, such as maximum annual permeability or permeability during a spawning migration.

Of course, most river systems contain many barriers, so a framework must consider the possibly interactive effects of multiple barriers. As in the case of a single barrier, multiple barriers affect both dispersal and habitat. The basin-wide effects of barriers on dispersal are most often evaluated using the dendritic connectivity index (DCI),<sup>7</sup> which is the probability that an organism can move



**Figure 2.** Identifying parameters of core-length model for (A) an individual river segment and (B) a system of barriers. For every fragmentation agent ( $FA_i$ ), there is an associated matrix habitat ( $MA_i$ ) and an upstream and downstream edge habitat ( $UEH_i$  and  $DEH_i$ , respectively).

between two randomly chosen points in the river network:

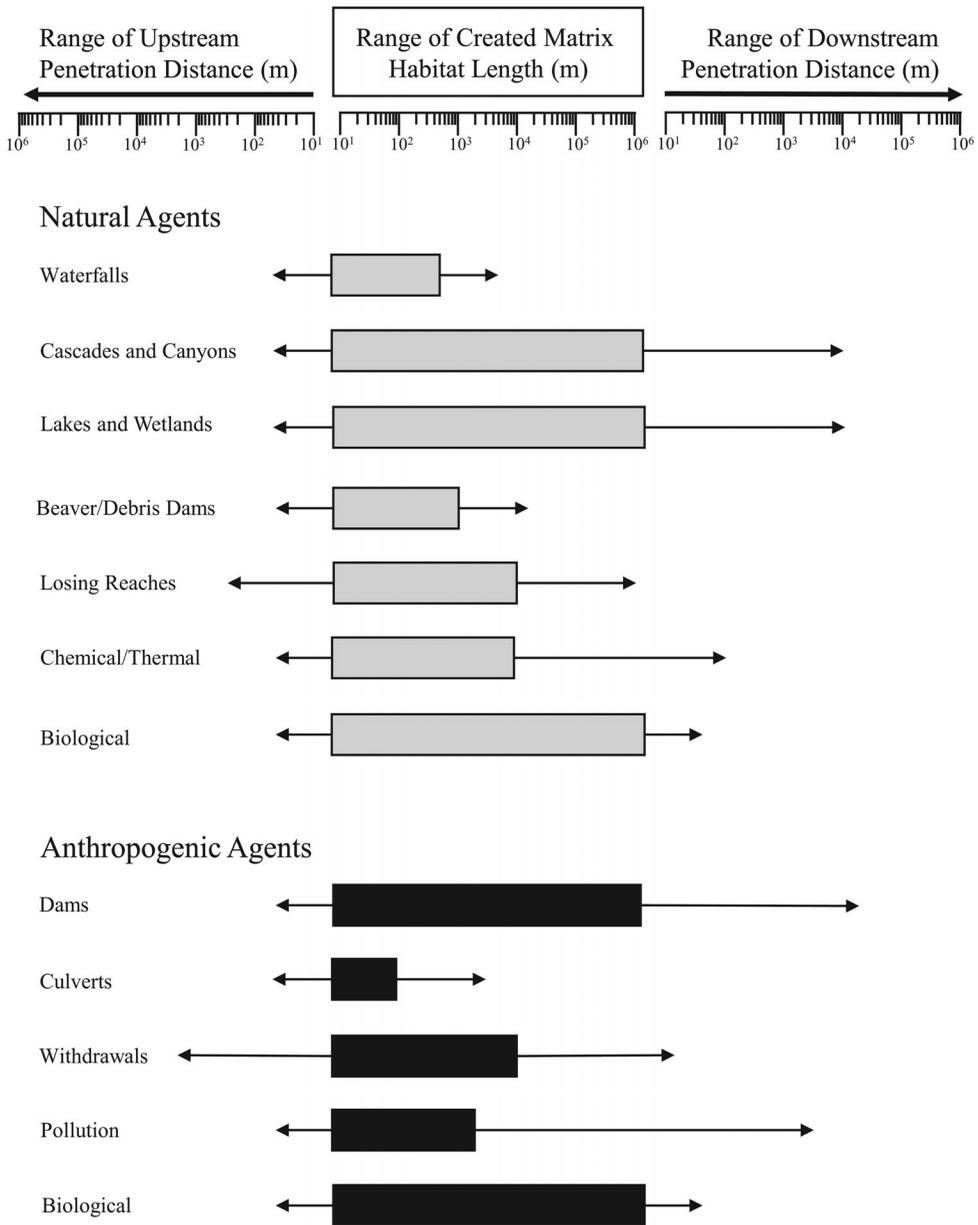
$$DCI = \sum_{i=1}^n \sum_{j=1}^n c_{ij} \frac{l_i}{L} \frac{l_j}{L} * 100, \quad (1)$$

where  $c_{ij}$  is the connectivity between sections  $i$  and  $j$ ,  $l_i$  is the length of section  $i$ , and  $L$  is the total length of stream channel in the network. If there are multiple barriers between  $i$  and  $j$ , their connectivities are assumed to be multiplicative, and  $c_{ij}$  is calculated as the product of upstream and downstream connectivity across barriers. Cote *et al.*<sup>7</sup> offered a modification for diadromous species (i.e., those that must reach the mouth of the network), and it would seem straightforward to make similar modifications to consider focal species that occupy only parts of the network (i.e., fourth-order streams and larger), or are obligate migrants between known parts of the network (i.e., potamodromous species). The assignment of equal importance to upstream and downstream connectivity could be inappropriate

for some purposes, and might also need to be modified.

In practice, it may be hard to estimate every  $c_{ij}$  precisely, especially for barriers whose effectiveness is incomplete or variable with stage (e.g., low dams, beaver dams, and culverts). In such cases, it would still seem worth exploring the utility of analyses using a modified *DCI* with simple ordinal assessments of connectivity based on expert opinion (e.g., 0 = never passable; 1 = rarely passable; 2 = partially passable).

In addition to considering the effects of multiple barriers on dispersal, it will be necessary to consider their edge effects, both upstream and downstream, to scale individual barriers up to cumulative systems of barriers. One first step would be to calculate the total amount of remaining core habitat and the total length of river that has been affected by habitat fragmentation (Fig. 2b). To calculate the remaining core habitat in a fragmented river network, begin by determining the total affected length (*TAL*) in the river network. The *TAL* is the sum of all matrix plus



**Figure 3.** Hypothesized range estimates for the length of matrix habitat created for various fragmentation agents (box length on log scale). Arrows represent the approximate range in upstream or downstream penetration distance for potential edge effects caused by each fragmentation agent.

edge habitats created by each fragmentation agent in the network, and is calculated as

$$TAL = \sum_{i=1}^n EHD_i + \sum_{i=1}^n EHU_i + \sum_{i=1}^n MH_i, \quad (2)$$

where  $n$  is the total number of fragmentation agents in the network,  $EHD_i$  is the downstream edge

habitat,  $EHU_i$  is the upstream edge habitat, and  $MH_i$  is the matrix habitat created by fragmentation agent  $i$  (Fig. 2b). The total remaining core length ( $TCL$ ) of the network is simply:

$$TCL = TNL - TAL, \quad (3)$$

where  $TNL$  is the total network length.

Although a statistic like the *TCL* may be useful for coarse evaluation and comparison among river networks, it has several shortcomings. First, like the *DCI*, it is highly species dependent, and will need to be evaluated separately for different species or guilds of species. Second, it does not consider the quality of either the core habitat or the affected habitats, although it is highly unlikely that core habitats will all be suitable or affected habitats will all be unsuitable for the focal species.

In addition, the network-wide effects of a system of barriers will depend on the shape of the drainage network. River networks vary in shape and network branching structure depending on the geology of the landscape.<sup>32</sup> Models suggest that these details will affect metapopulation functioning and the effects of barriers (e.g., Refs. 13 and 33). Finally, and as we discuss next, all metrics of fragmentation and connectivity are functions of the characteristics of the fragmentation agents, which vary widely. While this quantitative approach provides a method of conceptualizing fragmentation, connectivity, and habitats, the continuous and nondichotomous nature of river systems makes the approach a starting point at best.

### Type and extent of fragmentation agents in river networks

Fragmentation may be caused by any agent that decreases the movement of organisms, either upstream or downstream, such that the organism is impeded (but not necessarily completely blocked) from moving between two patches of suitable habitat. Causes of fragmentation in river networks are highly varied (Table 1), and barriers in river networks range in form, permeability, permanence (Fig. 4), spatial location (position within the river network), and abundance (frequency or density within a river basin).

For simplicity, we distinguish anthropogenic from natural barriers, and recognize three broad classes of barriers: physical barriers that prevent movement of organisms (e.g., dams, culverts, and dry sections of channel); habitat barriers in which physicochemical conditions discourage or prevent movement (e.g., thermal or chemical pollution, large lakes or reservoirs that are inhospitable to riverine specialists); and biological barriers, such as dense populations of predators, competitors, or

diseases. Some barriers (e.g., hypolimnetic release dams) belong to more than one of these classes.

Most barrier types exist within specific environments (e.g., waterfalls and cascades usually exist where topographic variation is large enough to generate these steep-slope reaches) and therefore cluster within portions of a river network rather than being evenly distributed.<sup>34</sup> The location and abundance of barriers thus vary widely within and across regions in predictable ways (Table 1).<sup>35</sup> Anthropogenic barriers cluster not only where the underlying geology or landscape is favorable, but also where humans need them. For example, point-source pollution outfalls (chemical pollution barriers) are clustered in urban areas, and culverts are more numerous in areas with high road densities (including roads in rural and less-developed areas such as forests). Dams cluster where geology, topography, and climate meet appropriate conditions for dam structural integrity, storage, and flow requirements. Therefore, very large high-head dams are less frequent in areas of very low relief, particularly in comparison to the more ubiquitous low-head dams that typically pepper regions of moderate relief. For instance, in North Carolina, dams are more abundant on the Piedmont (4–7 dams/100 km<sup>2</sup> or 7–12 dams/100 km of stream), an area of moderate relief, than on the flatter Coastal Plain (~1 dam/100 km<sup>2</sup> or ~3/100 km of stream) (data modified from Ref. 36).

As already mentioned, many of these fragmentation agents also alter habitat. In the following section, we briefly catalog the common causes of fragmentation in river networks, their frequency and spatial distribution, and their effects on habitat and movement of organisms.

#### *Natural fragmentation agents*

Waterfalls, steep cascades, and canyons are physical barriers that generally exist in landscapes of high relief or where streams cross resistant geologic strata (e.g., Niagara Falls, the Fall Line in the southeastern United States).<sup>34,37–39</sup> These features can cover either long or short sections of channel (Fig. 3). Many waterfalls have little edge effect on either upstream or downstream habitat. In contrast, cascades and canyons can extend for hundreds of kilometers (the 504-km-long Tsangpo Canyon along the Yarlung Tsangpo River in Tibet) of river and create large matrix habitat patches between river

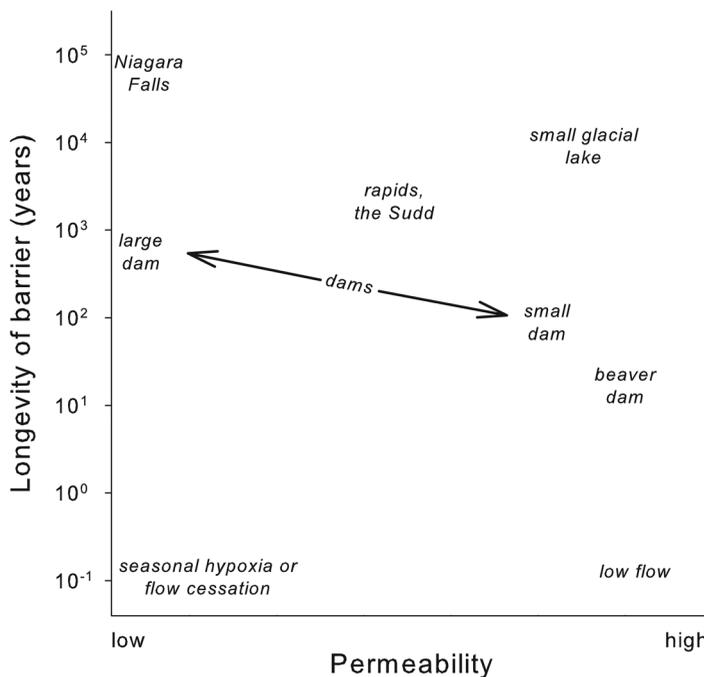
**Table 1.** Major fragmentation agents, their origin (natural or anthropogenic), primary barrier form (with secondary and/or tertiary forms), and what drives their distribution and frequency across the landscape

Fragmentation agent	Origin	Barrier form	Distribution and frequency driver
Beaver/debris dam	Natural	Physical (habitat, biological)	Riparian habitat
Culvert	Anthropogenic	Physical	Road density
Dam	Anthropogenic	Physical (habitat, biological)	Geologic, topographic, and climatic
Lake/wetland	Natural	Physical (habitat, biological)	Topographic/geologic
Losing reach/intermittent river	Natural or anthropogenic	Physical	Topographic/human
Pollution barrier	Anthropogenic	Habitat	Human population density
Species introduction/human harvest	Anthropogenic	Biological	Human population density
Thermal barrier	Natural or anthropogenic	Habitat	Human population density
Waterfall/cascade/canyon	Natural	Physical	Topographic

segments. Depending on the canyon, edge effects may extend downstream, but it is likely that upstream edge effects on habitat will be minimal. Waterfalls, cascades, and canyons are significant for restricting dispersal of fully aquatic organisms (e.g., see Ref. 3). However, for semiaquatic organisms with terrestrial life stages or aquatic organisms with resistant life stages (e.g., seeds of aquatic plants, resting eggs of crustaceans), these short interruptions of the channel are only minor barriers, especially if flight (e.g., many aquatic insects) over the barrier is possible.<sup>40</sup> Long cascades/canyons may be effective

barriers even for aquatic organisms with terrestrial or resistant life stages (e.g., seeds, resting/dormant eggs) and riparian species.<sup>41</sup>

Natural lakes have a variety of origins, including glacial, tectonic, coastal, riverine, and volcanic formation, and typically cluster according to the mechanism of origin.<sup>42,43</sup> Most of these lakes greater than 1 ha are derived from glacial processes, so river networks in glaciated regions tend to have higher densities of natural lakes.<sup>44,45</sup> The largest lakes extend for hundreds of kilometers (Caspian Sea, Laurentian Great Lakes) and can constitute nearly complete



**Figure 4.** Hypothesized relationship between barrier permeability and longevity, with some typical fragmentation agents plotted.

habitat barriers for riverine organisms<sup>46,47</sup> because of their lack of flow and distinctive physical and chemical conditions. The downstream edge effects of lakes can be considerable, with distinct physico-chemical conditions and benthic communities in their outlets;<sup>48</sup> upstream edge effects apparently have not been noted.

Wetlands that interrupt the river network may also function as barriers that change habitat conditions such as current speed, water temperature, and substratum type. Wetlands may also produce water chemistry that is stressful to typical riverine species, such as low dissolved oxygen, low pH, or high dissolved organic carbon, in and downstream of the wetland.<sup>49</sup> It is difficult to assess the importance of wetlands as barriers in river networks because global inventories of wetlands are often made by summing their cumulative surface areas rather than enumerating them within a river network,<sup>50,51</sup> but they are at least regionally important.

Beaver dams and large woody debris dams are common physical barriers similar in their material composition and partial permeability. Although both commonly occur as small-scale (<10 m of stream channel) barriers on small streams,<sup>52,53</sup> complexes of multiple beaver dams and ponds may cover kilometers of stream,<sup>54</sup> and large woody debris jams have been reported to cover hundreds of kilometers of channel on a large river.<sup>52,55</sup> Beaver dams were common (~10 dams/km of stream<sup>56</sup>) throughout much of the range of the North American beaver (*Castor canadensis*). The European beaver (*Castor fiber*) is not as well known for building dams (they dig bank burrows instead of building dams to form a moat around their dens), so streams in its range probably were less affected by damming.<sup>57</sup> The geographic extent and numbers of beaver dams have fluctuated wildly in recent centuries, as both species were trapped to very low population densities before starting to recover, and as North American beavers were introduced into Europe and Tierra del Fuego.<sup>58,59</sup> Woody debris dams are presumably common throughout the range of forests.<sup>52</sup> Beaver dams and large woody debris barriers are probably fairly permeable to most stream-dwelling organisms, especially during high flow, but may be effective barriers during low flow.

In smaller streams, or in streams and rivers flowing through arid and semiarid regions, intermittent flow conditions can naturally fragment the river

network. When streams lose flow, the normally continuous aquatic system becomes a series of disconnected pools, where the deeper areas retain water and associated organisms. While intermittent streams were initially ignored in the ecological literature, a classic study by Stanley, Fisher, and Grimm<sup>60</sup> drew attention to the effect of drying on essentially reconstructing a continuous ecosystem into a series of distinct, individual ecosystems for potentially long periods of time. They showed that much of the theory that had been developed in terrestrial ecology with regard to shrinking patches could be applied, in relatively short time windows, to contracting aquatic ecosystems in dryland regions. In one sense, these fragmented pools create refugia, which then serve as a source of colonists once the stream rewets.<sup>61–66</sup> In another sense, there is increased competition for resources within these refugia—resources that become scarcer as the isolation continues. While most studies of fragmentation via drying have focused on small streams, the theory should apply to larger systems as well, although the complete, natural loss of flow in large systems is less likely than in the more characteristically flashy small streams.

Habitat barriers also occur naturally in rivers, both large and small. Natural habitat barriers include thermal barriers,<sup>67</sup> hypoxic reaches in and downstream of wetlands,<sup>49</sup> or where tributaries with distinctive water chemistry converge<sup>68</sup> to restrict movement of organisms. Such barriers are uncommon or absent from many river systems. Natural habitat barriers are likely partially permeable, and their permeability is very species specific, depending on individual tolerances to temperature and water chemistry. Consequently, the size of the matrix habitat created by these agents (which is the thermal or chemical plume itself) will be variable according to species as well.

Finally, purely biological barriers that do not affect physical (beaver dams) or chemical (anoxia from high rates of microbial decomposition) conditions must be important in natural river networks as well, although they seem not to have received much research attention. Examples would include the presence of a predator in a *mainstem* river that reduces dispersal of a prey species from one tributary to another<sup>69</sup> or a strong competitor in some parts of the network that increases the distance and reduces the connections between viable

populations of a species in a river network. For some aquatic invertebrates, the presence of a fish predator in a stream alters invertebrate behavior by reducing their affinity to drift downstream, and consequently may encourage isolation of populations in *headwater tributaries*.<sup>70</sup> Additionally, terrestrial predators can be barriers to aquatic species, as in the case of bears consuming salmon during annual spawning runs.<sup>71</sup>

### *Anthropogenic fragmentation agents*

Dams are the most important way humans fragment river networks worldwide<sup>72,73</sup> because of their large numbers and extensive ecological impacts. In the United States, the National Inventory of Dams records ~87,000 dams taller than ~3 m,<sup>74</sup> and >2 million impoundments exist with dams less than 3 m tall in the United States.<sup>75</sup> Often, these small dams are excluded from analyses because the grain size of the geographic information system data is too coarse to determine their relationship with streams and rivers (impoundments appear isolated from the river network rather than having stream connections).<sup>36</sup> Dams vary widely in permeability, from high dams with large impoundments that are nearly complete barriers to fully aquatic organisms and strong barriers even to species with terrestrial or resistant stages, to low dams with small impoundments that pose no barrier to species with terrestrial or resistant stages, and are passable at least during high water even by fully aquatic species. Although most of the world's dams are small, there are enough large dams of very low permeability to fishes and other organisms that they are fragmenting and eliminating many riverine populations (e.g., Refs. 2, 17, and 76), or affecting their genetic structure and connectedness (e.g., Refs. 77–80).

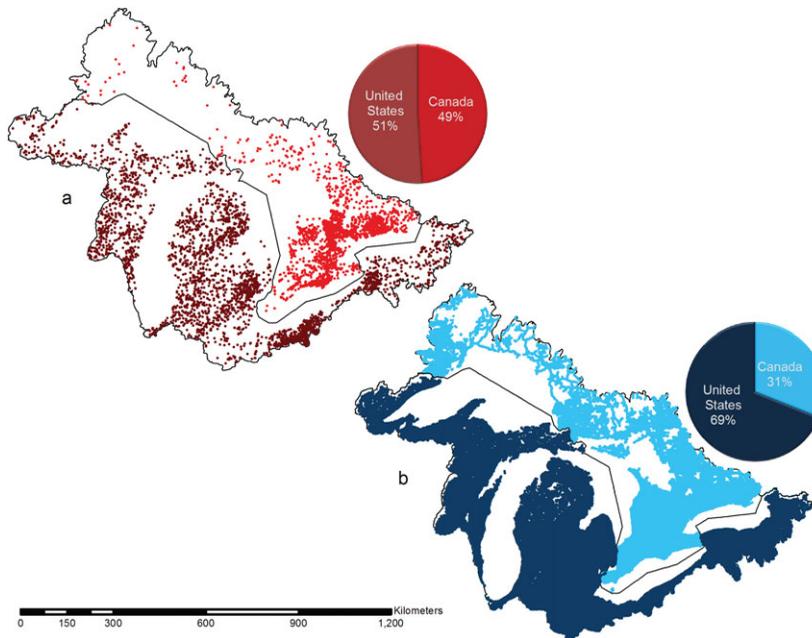
Dams can have strong and spatially extensive edge effects both upstream and downstream, which have been studied extensively by ecologists.<sup>81–83</sup> The reservoir impounded by the dam, which can be very large (hundreds of kilometers), creates a habitat barrier in the form of lake-like conditions in the place of a free-flowing river. Riverine populations in tributaries to the reservoir, newly isolated by the habitat barrier of the reservoir, may be subject to high rates of extirpation.<sup>84</sup> Populations of predatory fishes, such as smallmouth bass in and around the reservoir, may also serve as a biological barrier reducing movement between sections of river.<sup>85</sup>

There are comparable downstream impacts which can similarly expand for substantial distances downstream. Depending on the structure and operations of the dam, hydrology, temperature, water chemistry, and sediment composition and dynamics may be very severely affected, completely restructuring aquatic habitat far downstream of the dam.<sup>81</sup> Thus, in many moderately to heavily dammed modern river systems, the entire mainstem of the river may consist of edge habitats whose characteristics are determined by dam operations.

Though generally more permeable than even small dams, culverts and other road-crossing structures are increasingly recognized as limiting aquatic organism dispersal.<sup>86–90</sup> Road crossings and culverts usually greatly outnumber dams (Fig. 5), and their impacts are typically concentrated in the headwater reaches of watersheds. Old culverts in steep terrain are especially likely to be impermeable.<sup>86,91</sup>

The alteration of hydrology at the local and regional scale through groundwater and surface water withdrawals can create an anthropogenic amplification of drought-induced fragmentation. Because such anthropogenic withdrawals are far more prevalent in dry regions, the streams and rivers of these areas will already be susceptible to flow losses; human actions exacerbate such impacts, thus making these ecosystems more fragmented than they were previously.<sup>92</sup> As humans continue to move into arid regions and continue to effectively alter the hydrology of these regions, there has been considerable attention to how these ecosystems are being affected by fragmentation, particularly as these systems shift from being occasionally fragmented to being dry, and perhaps only occasionally actually connected.<sup>93–95</sup> The potential role of climate change in amplifying this drying tendency is now also being considered, particularly for how it might alter connectivity of stream networks.<sup>96</sup>

Anthropogenic habitat (chemical and thermal) barriers are observed mostly as pollution barriers to organism movement.<sup>68,97</sup> Pollution barriers can occur via low dissolved oxygen concentrations or high water temperatures unsuitable for species to inhabit.<sup>97</sup> Inputs of labile organic matter (e.g., sewage, paper pulp waste) and eutrophication are common causes of low dissolved oxygen concentrations, while hot water discharges from power plants or outfalls draining urban landscapes can elevate stream temperatures.<sup>98</sup> Point source inputs create



**Figure 5.** Comparison of the number of (a) dams and (b) culverts/road crossings within the North American Great Lakes basin. Figure reprinted from Ref. 86.

matrix habitat with distinct upstream boundaries, but downstream boundaries can be diffuse as a result of physical mixing, inputs from tributaries and ground water, and biogeochemical reactions. Thus, similar to the diffuse, long downstream effects of a dam (which is a singular point), a point source of chemical or thermal pollution will often create a diffuse, long downstream type of new habitat that is a continuum, but most distinct at its upstream edge.

Biological barriers of human origin may also be important in modern river networks. Fresh waters have been heavily invaded by nonnative species, many of which have strong ecological effects<sup>99</sup> and could therefore affect connectivity in river networks. In particular, the very widespread introductions of large, predatory fishes (e.g., Salmonidae, Esocidae, large catfishes, *Micropterus* spp.) may have been especially effective in reducing network connectivity for small fishes and other prey. On the other hand, the very large harvest of species such as predatory fishes in many fresh waters<sup>100</sup> could increase connectivity for prey species. Likewise, the spread of diseases such as amphibian chytridiomycosis, salmonid proliferative kidney disease,<sup>101,102</sup> and crayfish plague may have substantially reduced con-

nectivity for some species. Introduced competitors may be important as well. Zebra mussels eliminate or reduce populations of unionid mussels in large rivers and lakes, but not in headwater streams.<sup>103</sup> Remaining unionid populations in these headwater streams are presumably less connected than they were before zebra mussels arrived. Thus, it seems likely that biological barriers are important in some river networks today, although they have not received much formal study, especially within the context of habitat-fragmentation effects. The sizes, shapes, and edge effects are presumably highly varied, depending on the ranges, habits, and effects of the causative and target species.

Although many river systems are naturally fragmented, it would be a mistake to conclude that additional anthropogenic fragmentation of river networks is therefore unimportant. Anthropogenic barriers often are numerous and highly impassable, create spatially extensive edge habitats in which environmental conditions may be entirely novel or harsh to riverine biota, and can exist in regions where natural fragmentation is minimal. Consequently, dismissing anthropogenic fragmentation because natural fragmentation exists would be misleading.

## Net effects of anthropogenic fragmentation

How has the widespread fragmentation of river networks affected freshwater biodiversity? We know that many river networks are now highly fragmented, and that fragmentation may contribute to the loss of the populations isolated in the fragments, thereby affecting the composition of communities,<sup>13,104</sup> but the overall effects of fragmentation are not yet clear. Some studies have reported strong effects of fragmentation (e.g., Refs. 76, 90, 105, and 106), leading to general statements such as “habitat fragmentation is one of the major causes of local and regional species extinctions in fresh water ecosystems,”<sup>104</sup> whereas other studies have been unable to detect the effects of fragmentation, or found its effects to be less severe than the effects of other drivers (e.g., Refs. 107–109).

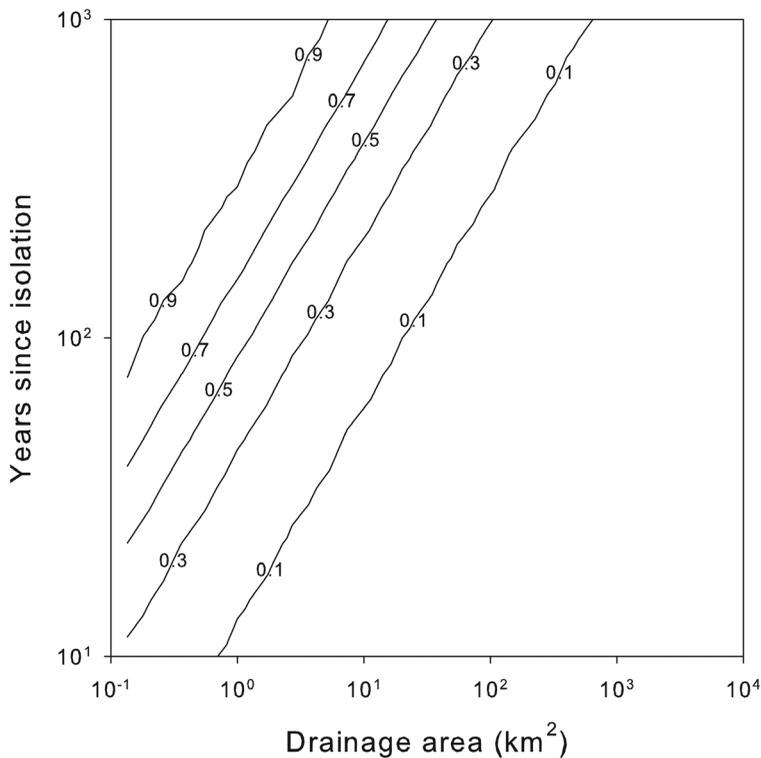
Several factors may contribute to this lack of clarity about the effects of fragmentation. First, population losses following fragmentation are often the result of interactions with other drivers, rather than a simple effect of fragmentation. That is, although some losses will result from demographic or genetic problems in very small populations, many isolated populations will be eliminated by droughts,<sup>110</sup> floods, chemical spills, diseases, and so on, and then will be unable to recover because of their isolation. Such losses may be attributed to the proximate cause of the loss, but are properly viewed as a joint result of the proximate cause and fragmentation—both causes are necessary to eliminate the population. This class of fragmentation loss will become increasingly important as climate change and other human pressures on fresh waters intensify and increase local extinction rates,<sup>111</sup> so it is important not to overlook it.

Second, unlike population losses from chemical spills, droughts, or diseases, which occur more or less instantaneously, the full extent of population losses from fragmentation may not be expressed for a long time after the initial fragmentation (Box 2). This time lag occurs because isolated populations are lost as a result of demographic stochasticity, genetic degradation (from inbreeding depression and/or genetic drift), or the impact of some infrequent environmental stress (see above), none of which occurs immediately after fragmentation. Indeed, the full effects of fragmentation may take centuries or even millennia to play out (Fig. 6).<sup>112</sup>

This suggests that studies performed soon after fragmentation (even decades after fragmentation) will underestimate its effects (sometimes severely), and generate a discrepancy in the time scales between rapid time-sensitive conservation action and slow metapopulation response to fragmentation.

Third, almost all agents of fragmentation in river networks also have strong effects on habitat quality. Some of these effects are beneficial, even to riverine species,<sup>24</sup> and they usually increase habitat heterogeneity within the river network (e.g., Refs. 60 and 113). Because increased habitat heterogeneity often increases biodiversity,<sup>114</sup> the effects of fragmentation on dispersal and habitat heterogeneity may have opposing effects on biodiversity in the river network. However, some of the increased biodiversity at the basin scale that results from this habitat transformation may consist of species that were not present or prominent in the natural river network, such as standing-water species in reservoirs. Some feel that this artificial biodiversity may have less value than natural biodiversity.<sup>115</sup> Furthermore, because many of these standing-water species (e.g., largemouth bass) are widely introduced and have broad ranges, fragmentation may decrease across-basin or global biodiversity (by eliminating riverine endemics) while increasing within-basin biodiversity (by encouraging broadly distributed standing-water species). Nevertheless, some kinds of fragmentation may increase network biodiversity, whereas other kinds may decrease biodiversity (Fig. 7), so it seems unlikely that river fragmentation will always harm biodiversity. Given the long time lags, we suspect that most forms of anthropogenic fragmentation will decrease biodiversity, however, because they have developed rapidly (compared to the pace of evolution), they are pervasive, have large effects on permeability and habitat, and often are placed into networks that historically lacked natural barriers.

Fourth, the effects of fragmentation depend on the size of the resulting fragments. The effects of fragmentation should be most severe for small populations in small basins, because such populations should be most subject to the demographic, genetic, and environmental problems that extinguish local populations. In practice, this means that fragmentation effects should be most severe in small fragments of river basins, as has been observed (e.g., Refs. 76 and 110). Indeed, the analysis of Hugueny



**Figure 6.** Contours estimating the probability of extinction for isolated populations of resident (i.e., nondiadromous) fish as a function of the drainage basin size and time since the basin was isolated, based on analyses of postglacial losses by Hugueny *et al.*<sup>106</sup> These estimates are very approximate, and probably underestimate extinction rates in modern drainage basins that are heavily affected by human activities, but illustrate the strong dependence of species losses in isolated basins on the size of the basin and time since isolation.

*et al.*<sup>106</sup> suggests that the dependence of extinction rates on fragment size may be very steep (Fig. 6), so that populations in small fragments can be at high risk of loss from fragmentation at the same time that populations in moderately large fragments are nearly immune from this risk.

Fifth, the effects of fragmentation are different on different kinds of species<sup>40,80</sup> and take different amounts of time to be expressed. It has long been known that obligate diadromous species, such as many salmonids and alosines, are severely and immediately affected by fragmentation (e.g., Refs. 116–118). It is perhaps less well appreciated that potamodromous fish species (those that migrate entirely within river systems, sometimes over very long distances) are common in river networks,<sup>119,120</sup> and these species should also be strongly and quickly affected by fragmentation. At the other end of the spectrum are species that may truly be relatively insensitive to fragmentation (habitat general-

ists with strong dispersal through flying adults or passively dispersed resting stages). Finally, nonmigratory species with weak dispersal abilities, which constitute a large fraction of riverine species, should be sensitive to fragmentation, but may respond much more slowly than migratory species, which may lead to an underestimate of the effects of fragmentation.

All of this suggests that it is unreasonable to expect a single, simple signal of fragmentation that applies across all systems, species, and barriers, and that a comprehensive analysis of the effects of fragmentation will require careful consideration of species biology, disturbance regimes, other human impacts, network characteristics, barrier attributes, and time. Moreover, these considerations suggest that it will be easy to underestimate the long-term effects of fragmentation. Yet, at the same time, current understanding suggests that fragmentation can be a powerful change agent for aquatic ecosystems.

## Box 2. Extinction debt and freshwater fragmentation

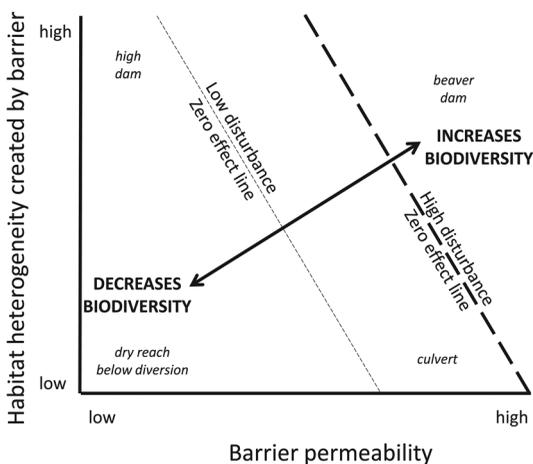
Extinction debt is the number of species that are destined to become extinct in the future as a delayed result of past events.<sup>160</sup> In the context of fragmentation, these could be species that will be lost as a result of demographic stochasticity or catastrophic events operating on isolated populations many years after the initial fragmentation. Extinction debt is highly relevant to river fragmentation because the dynamics of biodiversity change arising from fragmentation may be slow, and in particular much slower than those caused by other driving variables (e.g., overharvest, pollution, and disease). Consequently, the extinction debt arising from fragmentation may be especially large, and the eventual effects of fragmentation may be much greater than they appear to be from short-term studies. Extinction debt is likely to be largest for basins that were severely and recently fragmented, and where disturbances that eliminate local populations (e.g., desiccation, pollution, and disease) are frequent; species that are long-lived, rare, or poorly dispersing; and populations that are near the extinction threshold (i.e., where populations are nearly large enough to persist).<sup>161,162</sup> Although extinction debt is thought to be large in fragmented river networks<sup>152,161</sup> and has been the subject of discussion and modeling,<sup>160–162</sup> it has rarely been estimated in nature.<sup>152,162</sup>

## Management implications

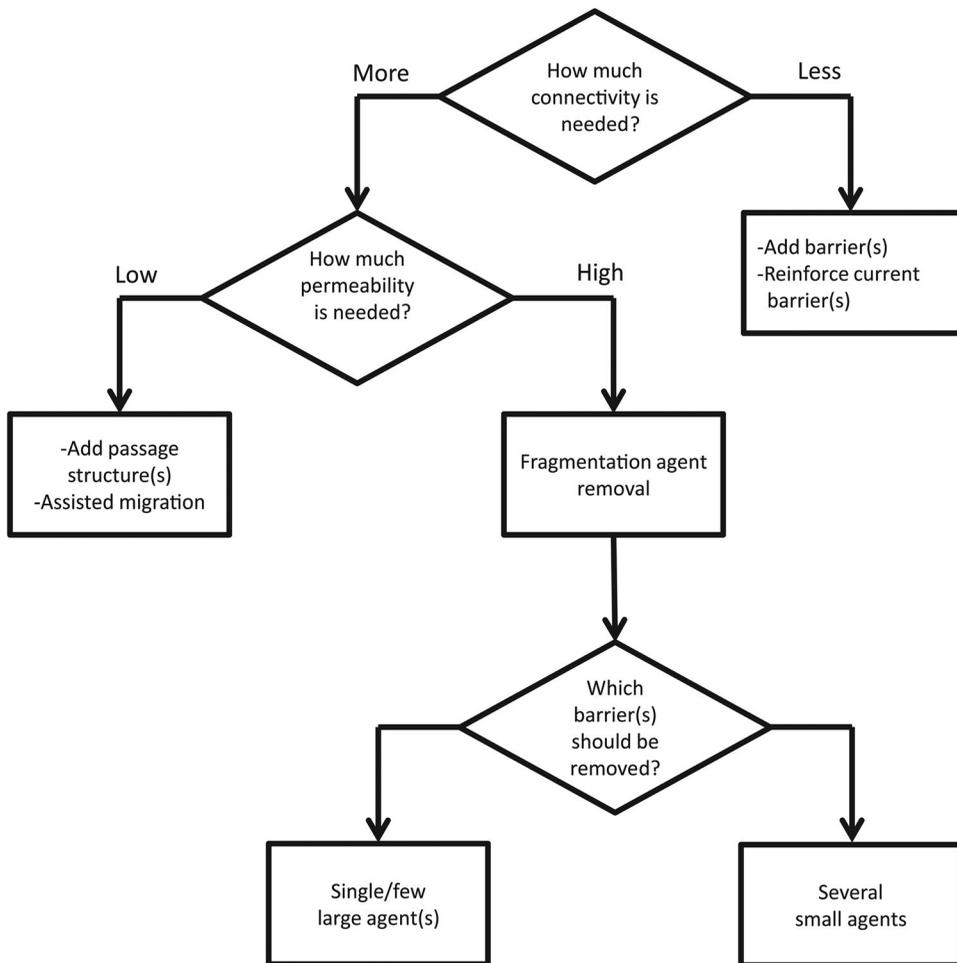
Natural resource managers and agencies whose role is species conservation (e.g., federal agencies such as the United States Fish and Wildlife Service, state agencies such as the North Carolina Natural Heritage Commission) are often faced with translating rapidly developing and evolving science into management practices. The development of ecological theories of extinction debt (Box 2) and habitat fragmentation may provide useful tools for species and

habitat managers, but translating those ideas into practices is necessary first. Fragmentation in a river network can be managed to protect the populations it contains by removing or adding barriers or by adjusting their permeability (by adding fish passage structures,<sup>121</sup> replacing culverts,<sup>122</sup> and similar actions) (Fig. 8). Although reducing fragmentation has been the usual goal of conservation and restoration projects, increasing fragmentation can be a valuable tool to reduce the spread of invasive or nuisance species.<sup>123,124</sup> Rather than simply assuming that fragmentation should be restored to natural levels, a conservation planner must first decide on the optimal level of fragmentation to reach the conservation goal.<sup>125</sup> Next, the manager needs to be able to predict the effects of adding, removing, or modifying particular barriers at specific points in the network and to understand the practical and political feasibility of the potential management options.

The adjustment of barrier permeability needs careful consideration (Fig. 8). Under certain conditions, barrier removal might not be feasible, necessary, or the best use of limited resources. Depending on the conservation goal, barrier modification to increase permeability for the target species may be sufficient. For example, minimum flows can alleviate the barrier effects of drying, fish ladders can alleviate the barrier effects of dams, and culvert alteration or improvement can alleviate the barrier effects of roads. These mitigation efforts are somewhat effective at



**Figure 7.** Riverine barriers may create opposing effects on basin-scale biodiversity by simultaneously decreasing permeability and increasing habitat heterogeneity. The balance between these effects depends on the frequency of population-threatening disturbances, as shown by the zero-effect lines at high and low disturbance rates.



**Figure 8.** Decision tree explaining the process by which habitat fragmentation could be managed in river networks.

alleviating habitat-connectivity problems, but do not address the habitat loss/degradation associated with each fragmentation agent; the broader impacts of water withdrawals, reservoirs, and roads would remain. Thus, the manager must assess the relative importance of connectivity as well as the potential for improving habitat. In fact, if only occasional connection between populations is necessary to improve metapopulation functioning or provide genetic supplementation, much lower levels of connection may be sufficient. In these cases, the manager may choose to ignore the barrier itself and instead use genetic supplementation (i.e., transplant a few individuals from an adjacent population to help maintain genetic diversity through time).<sup>126,127</sup> A manager needing to discriminate between these potential actions can use emerging

tools, including both direct empirical measures and gene-flow simulations.<sup>128</sup>

If it is necessary to remove barriers (high levels of connectivity and/or habitat restoration are needed), the next decision priority will be to determine which barriers should take priority given the limited funding available for defragmentation projects (Fig. 8). For example, if large runs of anadromous or potamodromous species are to be restored, then a particular or even multiple barriers may need to be removed entirely, because partial measures to restore fish passage are often ineffective at passing large numbers of fish.<sup>2</sup> Conservation managers will need to decide whether removing a single large barrier or several small barriers will benefit the target species more and whether there are keystone barriers whose removal would disproportionately

benefit the species. This analysis will require considering the cost and feasibility of removing each barrier, its potential benefit to the target species, and any side effects, either positive or negative, on other conservation targets or societal values. Historically, the status quo has been to remove any barrier within a river network for which funding can be obtained.<sup>36</sup> However, this ad hoc approach to managing fragmentation may not be the most efficient way to allocate limited funds. Instead, in cases where species conservation is a priority, managers should make surgical strikes against barriers that disproportionately affect the target species, even if this results in fewer overall structure removals.

One liability of very targeted approaches to connectivity restoration is that they often focus on a single (often rare) species or small group of species. When alleviating fragmentation for a particular species, we may be oblivious to the continuing effects of fragmentation that persist in the broader community. This unawareness sets up the base conditions for extinction debt (Box 2) in which we assume that the unmanaged species are unaffected by fragmentation, but instead are just not yet presenting the typical (or looked for) population declines that would indicate them as affected species. In the near future, rather than being limited to individual or pairs of species,<sup>129,130</sup> it will be routinely possible to empirically evaluate population genetics for multiple species across a watershed through emerging molecular techniques currently being applied to microbial communities.<sup>131</sup> One of the first instances of this approach in vertebrate communities occurred using fish metagenomes to compare community-level genetic diversity among four exploited fishing regions across the globe.<sup>132</sup> Similar evaluations at smaller spatial scales will likely be forthcoming, which would allow managers to examine communities rather than use umbrella species for conservation efforts. These molecular techniques are part of a broad set of tools and research arenas that are emerging in the field of aquatic science.

## Research horizons

There are many promising avenues for future research related to habitat fragmentation. Without attempting a complete or prioritized list, we offer several suggestions for new ways to investigate fragmented river networks as well as areas of research

that we believe are currently in need of detailed evaluation. Research on fragmented river networks could benefit from applying landscape genetic methods, better monitoring, evaluating fragmentation at the watershed scale rather than at individual barriers, developing practical models to predict management actions, and developing dynamic (as opposed to equilibrium) models to evaluate the effects of fragmentation.

Rapidly developing molecular techniques are making quantitative measurement of population genetic isolation and rare dispersal events possible.<sup>133</sup> The use of landscape genetics can determine what landscape and environmental variables are correlated with genetic divergence of populations and potentially help managers find support for answers to the first two questions in the decision tree (Fig. 8).<sup>134,135</sup> One of the major difficulties in studies of terrestrial landscape genetics is the uncertainty surrounding pathways of gene flow between fragmented populations; the primary method for determining these pathways (least-cost path analysis) has been criticized for several reasons.<sup>136</sup> In river networks, tracking of fully aquatic species (as well as many species with terrestrial life stages<sup>15–17</sup>) is not burdened with this uncertainty because the river network defines the route that species take between sections of the fragmented river network. Therefore, river networks provide excellent study systems to evaluate basic questions surrounding resistance to gene flow.

We offer one word of caution when employing population genetics in fragmentation research. The population genetics of long-lived species (e.g., some species of freshwater mussel<sup>137</sup> or fish<sup>138</sup>) may not have had enough time to respond and equilibrate to the fragmentation agents they are being used to evaluate.<sup>139</sup> For example, freshwater mussel species that can live for decades<sup>140</sup> may not be appropriate to study the impacts of dams and dam removals because too few generations would have passed to detect population genetic divergence.<sup>141</sup> Understanding the history of both the landscape and organism will be necessary to interpret the genetic impacts of modern fragmentation using these methods.

Monitoring the effects of barrier removal or addition in rivers should provide invaluable data for understanding the dynamics and reversibility of fragmentation. Defragmentation occurs regularly in

river networks when dams are removed, pollution barriers are remediated, or culverts are replaced.<sup>122</sup> Similar restoration efforts in terrestrial habitats where mature forests are reestablished between previously isolated stands are not as common, and when these types of efforts do occur, they likely take much longer to develop than in rivers. Therefore, assessment of recovery following defragmentation in rivers could accelerate our understanding of habitat and species reaction to defragmentation.

Evaluating fragmentation using watershed-scale units for comparison will be beneficial for understanding how fragmentation varies globally as well as regionally between adjacent basins. Understanding fragmentation necessarily requires the comparison of systems of barriers with varying amounts and types of fragmentation.<sup>142,143</sup> Currently, simulations may be the best approach for research on multiple fragmented watershed units. However, as remote sensing data become more accessible, statistics characterizing watershed-scale river network fragmentation may soon become simple, easy-to-generate predictors for population and habitat models.

Finally, developing practical models (i.e., those that can be parameterized using data that are likely to actually be available) to predict the effects of proposed management actions (removing, adding, or changing the permeability of barriers), at the watershed scale should be a priority for applied aquatic ecologists. Several such models chiefly based on applications of graph theory and other habitat optimization/barrier removal prioritization models have now been developed,<sup>144–150</sup> which could be a promising foundation for future work. In addition, it would be useful to develop dynamic models of the effects of fragmentation on biodiversity. Most existing models of the effects of fragmentation on biological communities are equilibrium, so we know little about the pace at which biodiversity responds to fragmentation (but see Refs. 106 and 151). It will be necessary to understand the dynamics of change, as well as the ultimate effects of fragmentation, if we are going to manage fragmented river networks effectively.

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## Conflicts of interest

The authors declare no conflicts of interest.

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