

Patterns of dispersal through stream networks respond simply to multiple structural modifications

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Abstract: Planning of catchment-scale programs of stream restoration requires an ability to predict the combination of small-scale projects that will provide the greatest ecological benefit. However, we lack the tools to predict where within stream systems restoration should be undertaken to achieve maximum ecological benefit, or to quantify the cumulative effect of multiple small-scale projects.

Stream systems form Dendritic Ecological Networks (DENs), which differ from other ecological networks in terms of their complexity, and possible routes of dispersal for organisms. The restricted topography of a DEN means that a single intervention in a network may have greater consequences than would such an intervention in a network of less restricted topography. Moreover, the strong directional connectivity inherent in stream systems suggests that multiple interventions in a network will interact, leading to a network-scale effect that may be more than just the sum of the parts. These properties appear to make planning restoration actions in stream networks a *complex* problem, best suited to approaches such as numeric optimization.

We developed a framework to describe the movement of fish throughout stream networks, and how those patterns of movement are affected by changes to habitat quality and reduced connectivity caused by barriers to passage. We used this framework to investigate the nature of interactions between multiple restoration projects designed to improve either habitat quality or connectivity.

Contrary to the expectations outlined above, our mathematical analysis showed that the interaction amongst multiple projects is small, and that under almost all circumstances, the total network-scale effect of multiple restoration projects is well-approximated by the sum of individually predicted effects. Interactions among multiple projects to improve connectivity will only be large when two projects cause very large increases in connectivity, *and* when those two projects are also close together. The predictions of the mathematical analysis were confirmed by simulation analyses. These conclusions apply to equilibrium conditions within dendritic networks, and the transferability of such conclusions to dynamically evolving systems is not yet known. However, even if non-additivity emerges in the dynamic evolution of a system, near-additivity will always be inherent in the underlying equilibrium framework.

These findings are immediately important for planning of stream restoration programs. Rather than having to consider many combinations of projects using advanced approaches such as optimization, managers can rank individual projects by their expected individual benefit, and implement the top ranked projects. The framework can be implemented with the type of data that exist for many stream systems, and can readily consider multiple species and ontogenetic behavioural changes. In circumstances where additivity of effects cannot be assumed, the framework can still be used to assess the effects of combinations of projects.

More generally, these findings are important for the field of riverine landscape ecology. Whilst rivers have become increasingly viewed as landscapes in their own right, it has been suspected that the topological restrictions of DENs may affect population processes in these landscapes. Accordingly, there have been recent calls for theoretical research to better understand population processes within DENs. We have shown here both analytically and through simulations, that dispersal and movement through DENs responds more simply to interventions in the landscape than has previously been assumed. Accordingly, our work constitutes an immediately useful contribution to the research required to better understand these unique systems.

Keywords: *Dendritic Ecological Network (DEN), landscape ecology, fish, migration, connectivity, barrier, habitat, degradation, restoration, catchment-scale planning*

1. INTRODUCTION

In response to the human-induced degradation of running waters that has occurred the world over, river restoration has become a valuable industry with annual expenditure topping \$1 billion per year in the U.S. alone (Bernhardt et al., 2005). Addressing barriers to fish passage is one well-recognized form of river restoration, and a number of large-scale programs have been established around the world to improve fish passage (e.g. Barrett and Mallen-Cooper, 2006). Restoring fish passage is, however, expensive (Bernhardt et al., 2005), and barrier remediation programs are usually forced to address only limited subsets of barriers (O'Hanley and Tomberlin, 2005). But which combination of barriers should be chosen to achieve the best ecological outcome? To date this question has generally been addressed using localized scoring systems that are mostly driven by local information, and that thereby fail to place the barrier in a catchment context. Nor do such systems have any ability to assess how the remediation priority of a single barrier might change following remediation of another barrier (O'Hanley and Tomberlin, 2005).

The effects of in-stream barriers and other forms of habitat degradation on the movement of resident fish can only be modelled by considering the residence and dispersal of organisms among stream reaches of different qualities, with movements regulated by *connectivities* between the reaches. Importantly, it has been suggested that the fundamental dendritic structure of riverine networks may have uniquely important implications for population dynamics and persistence at the landscape scale (Fagan, 2002; Grant et al., 2007). Furthermore, the constraint of dispersal within dendritic networks implies that a single interventions (e.g. remediation of a barrier to passage) will have a much greater effect upon patterns of movement throughout an entire system than such an intervention might have within a terrestrial network of less restricted dispersal routes (Fausch et al., 2002).

Given that the strong directional connectivity imposed upon river systems by the flow of water means that interventions in one part of a system may propagate in effect to distant parts of that system (Fausch et al., 2002), it seems reasonable to assume that the effect of multiple interventions across a river network will amount to more than just the sum of their individual effects. Thus one must prioritize amongst possible *combinations* of potential restoration projects. However, prioritizing amongst combinations of projects is an exponentially more complex problem than prioritization based on estimation of individual effects, as numbers of combinations can easily reach billions. Such problems can be addressed using optimization algorithms, and this is the approach that has been employed in the only two studies of which we are aware that examine the efficient removal of fish barriers (Kuby et al., 2005; O'Hanley and Tomberlin, 2005).

A major drawback of using optimization-based approaches is that results pertain only to the case study under investigation, and that little in the way of general solutions can be drawn from any particular study. These considerations motivated our attempt to develop an analytically tractable framework to address the effects of modifications to stream networks, and to use this framework to describe both generally and analytically the ways by which patterns of fish movement through stream networks are affected by modifications.

2. THE ANALYTIC FRAMEWORK

The analytic framework is based around the concept of the value of a stream segment (hereafter reach) as determined by its intrinsic quality, and its accessibility from the remainder of the stream network. We conceive of the stream system as a Dendritic Ecological Network (DEN; Grant et al., 2007), with the basic unit of our DEN being the reach. Each reach is defined by three properties: habitat quality (q), and an upstream and downstream *connectivity*, respectively denoted u and d . A consideration of reach length is implicit within the q parameter, and without any loss of generality for the present analysis all segments may be presumed of unit length. Habitat quality represents the intrinsic value of the reach to a particular fish taxon and takes a value in the interval (0,1), where 0 is 'totally uninhabitable' and 1 is 'perfect'. The connectivities define probabilities of fish being able to pass from that reach to the adjacent downstream or upstream reach. Thus, for example, passage between some reach, i , and the adjacent upstream reach, $i+1$, will be defined through the values of u_i and d_{i+1} , which represent a single barrier. Barriers are reflected in decreased values of u , d , or both, with a connectivity of zero implying a totally impassable barrier. Any intervention in a stream network through, for example, habitat remediation, or the removal of a barrier, will affect the values of one or more of q , u , or d .

For each reach within a stream network, the framework evaluates the probabilities of fish being able to migrate from any and all other places within a network to that reach, as well as from that reach to all others. The full complement of these probabilities forms a matrix of transition probabilities between every pair of reaches within a network, or a finite Markov chain spanning all pairs and not just nearest neighbours. This matrix is used to calculate a *score* for each reach, representing the equilibrium proportions of a population

expected within that reach when fish move according to those transition probabilities. These scores can be obtained either through repeated iteration of the transition probabilities from any initial distribution until convergence, or as the eigenvector of the transition matrix corresponding to the unitary eigenvalue (Kemenev and Snell, 1976).

The transition probabilities, p_{ij} , representing movement from reach i to reach j , are fractions, with the numerator being the quality of reach j , weighted by the product of all connectivities traversed between i and j , and the denominator containing the sum of all such values for *all* reaches accessible from i (Figure 1). The transition probability p_{ij} thus measures the relative ‘appeal’ of reach j compared to that of all other reaches accessible from i . These transition probability matrices contrast with the majority of previous studies of diffusion processes upon networks (see refs. in Albert and Barabasi, 2002), which implement nearest-neighbour matrices with non-zero values only for nodes separated by a single edge. Representing diffusion as a nearest-neighbour process implies that, in the context of Figure 1, the probability of fish relocating from Reach 1 to Reach 2 is independent of the quality of Reach 3. For cogent agents such as fish, we believe that habitat qualities of an entire network should be considered to inform such decisions. Otherwise, for example, salmon would never migrate upstream through poor breeding habitat. Our matrix thus represents all possible paths of diffusion within an entire network, and incorporates the additional refinement of being real-valued, rather than being a traditional zero-one binary matrix. As a simple example, consider a *linear* network of three reaches, numbered upstream from 1 (Figure 1). The transition probabilities *towards* Reach 2 are,

$$\begin{aligned} p_{12} &= u_1 q_2 / (q_1 + u_1 q_2 + u_1 u_2 q_3) \\ p_{22} &= q_2 / (d_2 q_1 + q_2 + u_2 q_3) \\ p_{32} &= d_3 q_2 / (d_3 d_2 q_1 + d_3 q_2 + q_3) \end{aligned} \quad (1)$$

and probabilities for the remaining combinations follow suit. Recalling that the scores, denoted s_i , are the equilibrium proportions of the population in each reach, s_i is obtained from the sum of all movements *to* reach i (including the self-transition $i \rightarrow i$) minus all movements *away from* that reach to all other reaches. Thus for Reach 2,

$$\begin{aligned} s_2 &= s_2 p_{22} + s_1 p_{12} + s_3 p_{32} - s_2 p_{21} - s_2 p_{23} \\ s_2 (1 + p_{22} - p_{21} - p_{23}) &= s_1 p_{12} + s_3 p_{32} \\ s_2 &= \frac{s_1 p_{12} + s_3 p_{32}}{1 - p_{22} + p_{21} + p_{23}} \end{aligned} \quad (2)$$

For the more general case of a linear network of N reaches, numbered upstream from 1, the transition probabilities for $i > j$ become,

$$p_{ij} \Big|_{j < i} = \frac{q_j \prod_{k=j+1}^i d_k}{q_i + \sum_{k=1}^i \left(q_k \prod_{m=k+1}^i d_m \right) + \sum_{k=i+1}^N \left(q_k \prod_{m=i}^{k-1} u_m \right)}, \quad (3)$$

and

$$p_{ji} \Big|_{j < i} = \frac{q_i \prod_{k=j}^{i-1} u_k}{q_j + \sum_{k=1}^{j-1} \left(q_k \prod_{m=k+1}^j d_m \right) + \sum_{k=j+1}^N \left(q_k \prod_{m=j}^{k-1} u_m \right)}. \quad (4)$$

For $i < j$, the d_m in the numerators of (3) are replaced by u_m , (vice-versa for [4]). The general version of (2) is,

$$s_i = \sum_{j=1}^N (s_j p_{ji}) - \sum_{j=1 \neq i}^N (s_i p_{ij}) = \frac{\sum_{j=1 \neq i}^N (s_j p_{ji})}{1 - p_{ii} + \sum_{j=1 \neq i}^N p_{ij}} \quad (5)$$

Each s_i depends upon all other $s_{j \neq i}$, and so (5) represents a system of simultaneous equations, the solution of which is the eigenvector corresponding to the unitary eigenvalue of the transition probability matrix, $[p_{ij}]$. In a practical application, this matrix would be used to calculate scores, but the primary aim of this analysis is to demonstrate the explicit effects upon reach scores of modifications to q , u , or d . As such, the analysis below is conducted on the basis of (3) to (5), noting that we have shown elsewhere that conclusions from the analysis of linear streams are equally valid for dendritic networks (Padgham and Webb, submitted).

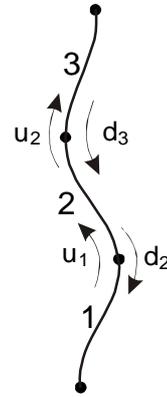


Figure 1. The linear network examined in (1) and (2). With reference to Reach 2, the absolute score (σ) of that reach is σ_{22} ; while $\sigma_{21} = q_1 d_2$; $\sigma_{23} = q_3 u_2$. The denominators of transition probabilities are the sum of all such scores, with numerators being these σ scores so that, $p_{2i} = \sigma_{2i} / \sum \sigma_{2j}$.

3. ANALYTIC EFFECTS OF MODIFICATIONS TO REACHES

We first examine the effects of single modifications, followed by examination of interactions between multiple modifications.

3.1. Quality

If a single reach of quality q_A is modified to $q'_A = q_A + \Delta q$, the transition probability p_{AA} becomes,

$$p'_{AA} = \frac{q_A + \Delta q}{q_A + \Delta q + \sum_{i=1}^{A-1} \left(q_i \prod_{j=i+1}^A d_j \right) + \sum_{i=A+1}^N \left(q_i \prod_{j=A}^{i-1} u_j \right)} \quad (6)$$

This equation represents one transition probability among N possibilities, and thus will have an expected value in the order of $1/N$. The proportional contribution of the Δq components in the numerator and denominator will thus approximately be $1 + \Delta q$ and $N + \Delta q$ respectively, with the former representing a much larger *relative* contribution when N is large. Thus, the additional Δq in the denominator may be ignored to an approximation accurate to $\sim 1/N$, leaving the transition probability as,

$$p'_{AA} \approx p_{AA} + (\Delta q/q_A) p_{AA} \approx p_{AA} (1 + \Delta q/q_A) \quad (7)$$

For the probability of moving from reach A to another reach i , (3) may be similarly adapted to reveal that $p'_{Ai|i < A} \approx p_{Ai}$ within the order of $1/N$, as per above, while (4) yields $p'_{iA|i < A} \approx p_{iA} (1 + \Delta q/q_A)$. Similar extensions follow for cases $i \geq A$. Given these approximations, we may then adapt (5), to reveal that,

$$s'_A \approx \frac{\sum_{i=1 \neq A}^N [s'_i p_{iA} (1 + \Delta q/q_A)]}{1 - p_{AA} (1 + \Delta q/q_A) + \sum_{i=1 \neq A}^N p_{Ai}} \quad (8)$$

The last term in the denominator is the sum of $N - 1$ probabilities, which must on average be greater than the p_{AA} term by an order of $(N - 1)/(\Delta q/q_A)$. Thus, although the $\Delta q/q_A$ term may be quite large when restoring very degraded habitat, it would be unlikely to approach the scale of $N - 1$, and the change in the denominator may very generally be ignored. Finally, because a change in the equilibrium proportion of reach A effects compensatory changes in all other reaches (e.g. an increase in A necessitates slight decreases in all $i \neq A$), the effect on any reach $i \neq A$ will be $\sim \Delta q/N$, and thus $s'_{i|i \neq A} \approx s_i$, and we arrive at the approximation that,

$$s'_A \approx s_A \cdot (1 + \Delta q/q_A), \quad (9)$$

and the conclusion that the effect of Δq is approximately additive, and localised to the reach directly affected.

3.2. Connectivity

Changes in d or u primarily affect the adjacent reach in the downstream or upstream directions respectively. Here we consider the effect upon reach A of the change $d'_{A+1} = d_{A+1} + \Delta d$. The transition probabilities p_{Ai} of (4) – for all reaches, and not just $i < A$ – will be unaffected, because no movement *from* A will pass via d_{A+1} . Values of p_{iA} will change for all i passing through d_{A+1} , which is all $i > A$. Thus, (3) is recast as,

$$\begin{aligned} p'_{iA|i > A} &= \frac{q_A \prod_{j=A+2}^i d_j \cdot (d_{A+1} + \Delta d)}{q_i + \sum_{j=1}^{i-1} \left[q_j \prod_{k=j+1}^A d_k \cdot (d_{A+1} + \Delta d) \cdot \prod_{k=A+2}^i d_k \right] + \sum_{j=i+1}^N \left(q_j \prod_{k=i}^{j-1} u_k \right)} \\ &= \frac{q_A (1 + \Delta d/d_{A+1}) \prod_{k=A+1}^i d_k}{q_i + \sum_{j=1}^{i-1} \left[q_j (1 + \Delta d/d_{A+1}) \prod_{k=j+1}^i d_k \right] + \sum_{j=i+1}^N \left(q_j \prod_{k=i}^{j-1} u_k \right)} \end{aligned} \quad (10)$$

and thus by the same reckoning as for (7) above,

$$p'_{iA} \approx p_{iA} \cdot (1 + \Delta d/d_{A+1}). \quad (11)$$

Because the modification only affects those $p'_{iA|i > A}$, the change in the value of s'_A is reduced from (9) to,

$$s'_A \approx s_A \cdot \left(1 + \frac{\Delta d}{d_{A+1}} \frac{N - A}{N} \right). \quad (12)$$

We now introduce the complication of multiple barrier modifications, through considering the effect upon reach A of the two changes, $d'_{A+1} = d_{A+1} + \Delta d_{A+1}$, and $d'_{B>(A+1)} = d_B + \Delta d_B$. As above, p_{AA} and p_{Ai} are unaffected, while the products within p_{iA} become [cf (10)],

$$\begin{aligned} \prod_{j=A+1}^i d_j &\rightarrow (d_{A+1} + \Delta d_{A+1}) \cdot \prod_{j=A+2}^{B-1} d_j \cdot (d_B + \Delta d_B) \cdot \prod_{j=B+1}^i d_j \\ &= \prod_{j=A+1}^i d_j \cdot \left(1 + \frac{\Delta d_{A+1}}{d_{A+1}} + \frac{\Delta d_B}{d_B} + \frac{\Delta d_{A+1} \Delta d_B}{d_{A+1} d_B} \right) \end{aligned} \quad (13)$$

Following the progression from (10) to (11) we have,

$$p'_{iA} \approx p_{iA} \cdot \left(1 + \frac{\Delta d_{A+1}}{d_{A+1}} + \frac{\Delta d_B}{d_B} + \frac{\Delta d_{A+1} \Delta d_B}{d_{A+1} d_B} \right). \quad (14)$$

This only applies to those reaches $i > B$, and so, with the addition of a further barrier, (12) becomes,

$$s'_A \approx s_A \cdot \left[1 + \frac{\Delta d_{A+1}}{d_{A+1}} \frac{N-A}{N} + \left(\frac{\Delta d_B}{d_B} + \frac{\Delta d_{A+1} \Delta d_B}{d_{A+1} d_B} \right) \frac{N-B}{N} \right]. \quad (15)$$

Three key points should be noted concerning this result. Firstly, the fractions $\Delta d/d$ are not necessarily small, particularly when describing the complete removal of strong barriers to passage such as dams. The final, non-linear interaction may be large if (and only if) $\Delta d_{A+1} > d_{A+1}$ and $\Delta d_B > d_B$. Secondly, (14) can only be constructed in reference to a point, $i > B$, if it is to include the effects of both modifications, and thus (13) must include the product of all intervening connectivities between the two points. This product will decrease in expected value with increasing distance between A and B . Thus, non-linear interactions between multiple modifications are likely only to have significant effect when the two modifications are also close together. However, and lastly, for this result to hold, connectivities may never equal zero, because the presence of a total barrier between two interventions (u or $d = 0$) severs the network into two fragments. Consideration of interactions between modifications in these fragments is meaningless, as the network is not a single system.

To conclude, the effects of two modifications to connectivity within a single network may be approximated by the additive effects of the individual modifications. The interactive effects – the final term of (15) – will very generally be negligibly small, and may be ignored (although cases where this term may be non-negligible are considered below). Furthermore, higher-order interactions will on average be smaller again.

4. NUMERICAL SIMULATIONS

To verify the analytical results, we performed numerical simulations on linear stream networks of twenty equal-length reaches. Including greater numbers of reaches had no additional effect. For each simulation, values of q , u , and d for each reach were randomly chosen from a uniform (0,1) distribution. Using the matrix of transition probabilities illustrated by (1), we quantified the *total* effect of choosing either 2 or 3 barriers at random and ‘restoring’ full connectivity to them by setting the u_i , d_{i+1} to 1; then compared the effect to the summed individual effects of restoring each barrier. Effects of modifying qualities (q) were similarly examined. It is important to note that such simulation analyses do not require any of the simplifying assumptions made during the analytical analysis. The change in a network in response to intervention is manifested as a change in the eigenvector described above. Sums of absolute differences between the normalized eigenvectors before and after modifications quantify population redistribution, and also provide an analogue for *absolute* changes in network quality. Using this quantification, the underestimates were expressed as 1 minus the ratio of summed to total effect for all possible second- and third-order interactions.

The simulations verify all the predictions of the analytical analysis (Table 1). The average 50th percentile underestimate for second-order interactions resulting from modifications to connectivity lies an order of magnitude beneath the $1/N$ limit predicted above (here 5%), and that from third-order interactions yet another order of magnitude below that. Modifications to quality exhibit smaller interactions than do modifications to connectivity. Finally, interactions decrease rapidly with increasing separation between modifications.

5. DISCUSSION

Large-scale plans for ecosystem restoration or conservation require an ability to determine the most efficient use of finite resources. Rarely can entire ecosystems be restored, and so restoration must be targeted at those

combinations of small-scale projects expected to provide the greatest overall benefit. We currently lack methods for making such predictions (Palmer and Bernhardt, 2006).

We developed a framework to explore the effects of multiple interventions in stream networks. While this combinatorial problem has previously been assumed to be complex in nature, and has thus been addressed using optimization procedures, we have shown that for most circumstances, effects of multiple barrier or habitat

interventions will approximately equal the sum of individual effects. This has important implications for catchment-scale planning of barrier remediation programs. Most importantly, under almost all circumstances there will be no need to examine the interactive effects of multiple interventions. Rather, one need only to score each individual potential intervention, and use these ratings to prioritize works.

5.1. Practical Implementation

Any real dendritic network to which this system is applied is likely to consist of 10s to 100s of reaches, so the expected 1/N error will be very small. Our method for scoring and ranking stream interventions can be implemented with the type of data that commonly exist for many river systems. These are primarily the habitat quality ratings and the effectiveness of upstream and downstream barriers to passage, along with knowledge of the topology of a system. Sensitivity analyses of the parameters can also readily be done.

Our analysis is based on the general model. However, without loss of generality of the findings above, the framework can be readily adapted to analyse species with different habitat preferences and migration strategies. This is achieved through separate applications of the scoring system, using different values of *u*, *d* and *q*. These separate applications reflect differences in the use of a stream network by different species. The results can then be combined, with the method of combination dependent on the type of ‘assemblage-level’ result desired (see Margules et al., 2002). Equally important to inter-specific differences, are likely to be variations within species, including ontogenetic shifts in habitat requirements. Diadromous species provide perhaps the most extreme example of this, as they must travel between marine and freshwater environments to complete their life cycles. The different stages in such a species’ life history will require different applications of the scoring system, similar to that required for different species. Thus, the framework can readily accommodate differences in habitat specialization, and in dispersal and recruitment patterns.

5.2. Limits to the Results

We have noted that near-additivity of individual intervention effects is not universal. However, even in such cases, the general framework based on habitat quality and transition probabilities remains valid. Thus, even though the framework was used to develop an argument for near-additivity, it also allows for the examination of non-additive interactions through direct application of the full matrix of transition probabilities.

The most likely situation through which near-additivity may be violated will be where two modifications cause relatively large changes to connectivity, *and* where the two modifications are close together. The large hydraulic changes caused by dam removal, for example, may also have large effects on effectiveness of barriers immediately downstream, leading to such a combination. However, if the new parameter values can be estimated, then the framework presented here can be used to assess network sensitivity to these major interventions, by adjusting *all* affected reaches to their new values, and comparing the properties of the entire – old and new – networks. Hypothetical removal of total barriers to passage can similarly be considered.

The analytic analysis assumes that population distributions are uniform among reaches to within an order of magnitude. Although this may be violated on occasion, the results of the simulation (where no assumption is

Order	%ile	% Underestimate at various inter-nodal distances								
		1	2	3	4	5	10	15	Avg	
C	2	50	1.94	1.61	1.31	1.14	0.90	0.28	0.03	0.55
		95	25.0	23.4	21.8	20.2	18.9	11.1	3.78	12.01
	3	50	0.27	0.20	0.13	0.09	0.06	0	0	0.04
		95	8.29	7.42	6.11	5.11	3.98	0	0	2.08
Q	2	50	0.22	0.13	0.11	0.11	0.10	0.07	0.05	0.08
		95	9.49	8.79	7.62	6.48	5.68	3.87	3.84	4.98
	3	50	0.01	0.01	0	0	0	0	0	0.00
		95	1.07	0.85	0.70	0.58	0.49	0	0	0.29

Table 1. 2nd and 3rd order underestimates arising from changes in connectivity (C) and quality (Q), as a function of inter-nodal distance. 50th and 95th percentiles are shown.

made) support the use of the assumption. The framework presented also only describes equilibrium conditions, and is thus not immediately adaptable to descriptions of dynamic changes in ecosystems. However, non-equilibrium dynamics are universally studied in response to perturbations from equilibrium conditions (e.g. Monasson, 1999). Thus, although non-additivity may emerge in the dynamic evolution of a system, near-additivity will always be inherent in the underlying equilibrium framework.

5.3. Conclusions

We have shown that, in terms of habitat quality and accessibility for fish, contrary to previous expectations, effects of multiple remediation projects in a stream network will very generally approximately equal the sum of effects of individual projects. Thus, relatively simple models can be used for catchment-scale planning of fish barrier and habitat remediation works, without having to employ more complex techniques such as optimization. Our general framework is extremely flexible, and can be tailored to different migratory life history strategies. Moreover, it may readily be implemented with the types of data commonly measured within many stream networks. Given the prominence of fish barrier works in stream restoration programs, these findings will have immediate benefits for planning of large-scale barrier remediation programs.

More generally, the occurrence of near-additivity of effects of interventions in DENs is an important finding for riverine landscape ecology. Riverine networks are being increasingly viewed as landscapes in their own right (Wiens, 2002), yet researchers suspect that many conclusions drawn from general theories of landscape ecology may not directly translate to dendritic riverine networks (Fagan, 2002). Our findings contribute directly to the recent and urgent call for theoretical research to better understand population processes within DENs (Grant et al., 2007).

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