

How restructuring river connectivity changes freshwater fish biodiversity and biogeography

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[1] Interbasin water transfer projects, in which river connectivity is restructured via man-made canals, are an increasingly popular solution to address the spatial mismatch between supply and demand of fresh water. However, the ecological consequences of such restructuring remain largely unexplored, and there are no general theoretical guidelines from which to derive these expectations. River systems provide excellent opportunities to explore how network connectivity shapes habitat occupancy, community dynamics, and biogeographic patterns. We apply a neutral model (which assumes competitive equivalence among species within a stochastic framework) to an empirically derived river network to explore how proposed changes in network connectivity may impact patterns of freshwater fish biodiversity. Without predicting the responses of individual extant species, we find the addition of canals connecting hydrologically isolated river basins facilitates the spread of common species and increases average local species richness without changing the total species richness of the system. These impacts are sensitive to the parameters controlling the spatial scale of fish dispersal, with increased dispersal affording more opportunities for biotic restructuring at the community and landscape scales. Connections between isolated basins have a much larger effect on local species richness than those connecting reaches within a river basin, even when those within-basin reaches are far apart. As a result, interbasin canal projects have the potential for long-term impacts to continental-scale riverine communities.

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1. Introduction

[2] Ecologists have long recognized that the spatial domain in which an ecosystem is embedded plays an important role in structuring population dynamics [Wiens, 1976; Hanski and Gilpin, 1991; Hassell *et al.*, 1991; Dunning *et al.*, 1992], the evolution and pattern of dispersal [Wiens, 1976; Wiens *et al.*, 1993], species distributions [Pulliam and Danielson, 1991; With and Crist, 1995; With *et al.*, 1997], and population persistence [Roff, 1974; Fahrig and Merriam, 1994; Hanski, 1998; Hanski and Ovaskainen, 2000]. Theoretical studies on network connectivity involving patches of habitat linked in various combinations (e.g., nearest neighbor, random, etc.) demonstrate that the number and arrangement of connections between habitat patches can have large impacts

on system dynamics [Holland and Hastings, 2008; Ranta *et al.*, 2008]. Real landscapes are considerably more complicated and may or may not behave as predicted by such theoretical models for at least two reasons. First, real landscapes may be complicated by heterogeneity and fragmentation and may change over time as habitats, and connections between patches of habitat, change. Second, real landscapes rarely conform to the simplified geometries studied in these theoretical exercises.

[3] Because of their hierarchical, branching spatial structure, river networks feature spatial characteristics that warrant separate study from other, well-described habitat configurations [Grant *et al.*, 2007; Brown and Swan, 2010]. However, very few studies have considered the effects of changing network connectivity in real river networks (exceptions include studies on the effects of dam removal [Kuby *et al.*, 2005] and canal construction [Smith *et al.*, 2004] and the effect of out-of-network dispersal [Grant *et al.*, 2010]), and no studies have yet examined the impact of changing connectivity on basin-wide patterns of biodiversity and species richness.

[4] Interbasin water transfer (IBWT) projects, in which river connectivity is restructured via man-made canals, are an increasingly popular solution to address the world's growing water shortage and distribution crisis. The debate surrounding the feasibility, success, and suitability of interbasin linking to solve water supply problems encompasses economic, social,

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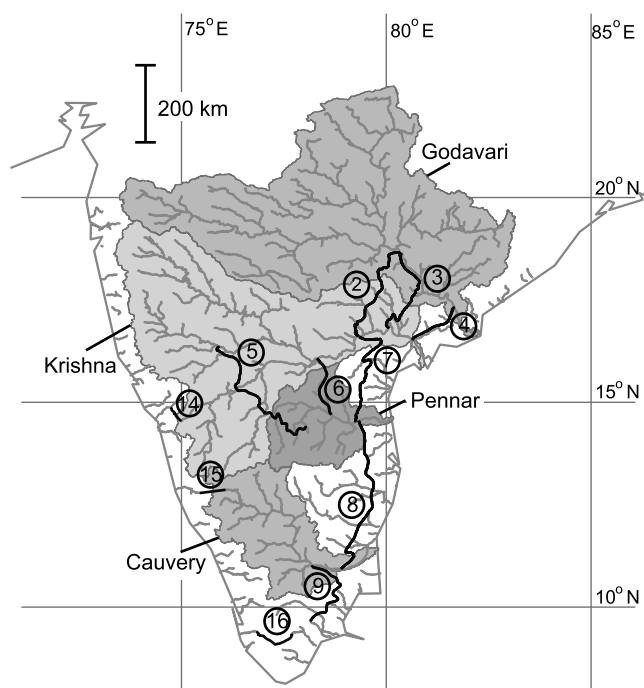


Figure 1. Map of the Indian Peninsula. Major rivers are shown in gray, and the 11 proposed links considered in the analysis are shown in black. The four major rivers basins involved are shaded and labeled. The links are numbered according to enumeration assigned by India's National Water Development Agency and correspond to the following canal projects: 2, Godavari (Inchampalli)–Krishna (Nagarjunasagar); 3, Godavari (Inchampalli)–Krishna (Pulichintala); 4, Godavari (Polavaram)–Krishna (Vijayawada); 5, Krishna (Almatti)–Pennar; 6, Krishna (Srisailem)–Pennar; 7, Krishna (Nagarjunasagar)–Pennar (Somasila); 8, Pennar (Somasila)–Palar–Cauvery (Grand Anicut); 9, Cauvery (Kattalai)–Vaigai–Gundar; 14, Bedti–Varada; 15, Netravati–Hemavati; 16, Pamba–Achankovil–Vaippar.

and environmental spheres [World Wildlife Fund, 2007; Fairless, 2008], which complicates efforts to evaluate these programs. Despite the number of large-scale interbasin water transfer projects that have been completed or are being developed around the world [Davies *et al.*, 1992; Snaddon and Davies, 1998; Stefferud and Meador, 1999; Ghassemi and White, 2007], such projects usually proceed with very little understanding of the ecological consequences involved (as noted also by Davies *et al.* [1992] and Fairless [2008]). Nevertheless, it is reasonable to assume that by introducing dispersal routes where none previously existed, man-made canals that restructure river connectivity have the potential to alter landscape-scale patterns of species distribution and diversity.

[5] While some traction on issues of riverine complexity and reconfiguration can be gained via theoretical models that represent river networks as simple branching structures [Fagan, 2002; Lowe, 2002; Labonne *et al.*, 2008; Fagan *et al.*, 2009; Goldberg *et al.*, 2010; Grant 2011], assessing the ecological consequences of such projects is hampered by the complex geometry of real river systems and corresponding patterns of connectivity [Labonne *et al.*, 2008]. The ecological impacts of the network restructuring that accompanies interbasin water transfer projects occur on both

the short (ecological) time scale and on the long (evolutionary) time scale. Whereas short-term dynamics such as ecological invasion and competitive exclusion involve the detailed biology of the species involved, the long-term metacommunity consequences are mediated to a larger extent by abiotic factors such as the newly linked network geometry. Species-specific information for affected river basins is often insufficient for a full consideration of the short-term ecological dynamics expected following completion of IBWT projects. In contrast, a focus on long-term consequences can provide insight into the enduring effects of such a project on the diversity and distribution of freshwater species.

[6] Here we explore the biogeographic consequences of reconfiguring river geometry using an empirically derived riverine landscape. We investigate the response of a theoretical fish community to alterations in river network structure in the form of canal links within and between disparate parts of the larger network. This strategy allows us to explore the relevant biogeographic issues in a general way while still attending to the inherently complex geometry of real-world river networks. To do this, we use a neutral metacommunity model. The neutral theory of biodiversity and biogeography [Caswell, 1976; Bell, 2001; Hubbell, 2001] posits ecological equivalence among individuals of different species. Neutral models include few parameters, yet they have demonstrated utility in replicating broad patterns of diversity across scales in a wide range of systems [Volkov *et al.*, 2003; Olszewski and Erwin, 2004; Walker and Cyr, 2007].

[7] We use a neutral model as a starting point for understanding the potential impacts of IBWT projects for two reasons: (1) it has been shown to simultaneously capture a suite of biodiversity patterns in a large-scale river system (the Mississippi–Missouri River System (MMRS) [Muneepeerakul *et al.*, 2008; Bertuzzo *et al.*, 2009]), and (2) it presents a mechanism for generating biologically realistic patterns of biodiversity without detailed empirical data on the spatial ranges of individual fish species and their pairwise ecological interactions, information that is typically unavailable or incomplete [Ghosh and Ponniah, 2008].

2. Data and Methods

[8] One real-world example of network restructuring by IBWT is provided by India's proposed Inter Basin Water Transfer project [Gourdj *et al.*, 2005; Fairless, 2008; Jain *et al.*, 2008] (see Figure 1). We use India's river network and canal link plan as a geometric framework from which we develop theoretical predictions for the impacts of canal links on patterns of biodiversity. Our primary goal is to understand the impacts of human modifications to riverine geometry rather than comment on specific potential impacts of the Indian IBWT project.

[9] The network geometry for our analysis was based on the HYDRO1k data set provided by the U.S. Geological Survey and derived from their 30 arc sec digital elevation model of the world (ETOPO30). Data on streams, including metadata on length and stream order, were downloaded as ArcGIS shapefiles. Our study area (~1600 km long × 1000 km wide) included all basins from the Godavari Basin and south, a region encompassing most of the Indian Peninsula and 11 of 16 proposed canals in the peninsular component of the IBWT project (Figure 1). Precise geographical details on the proposed

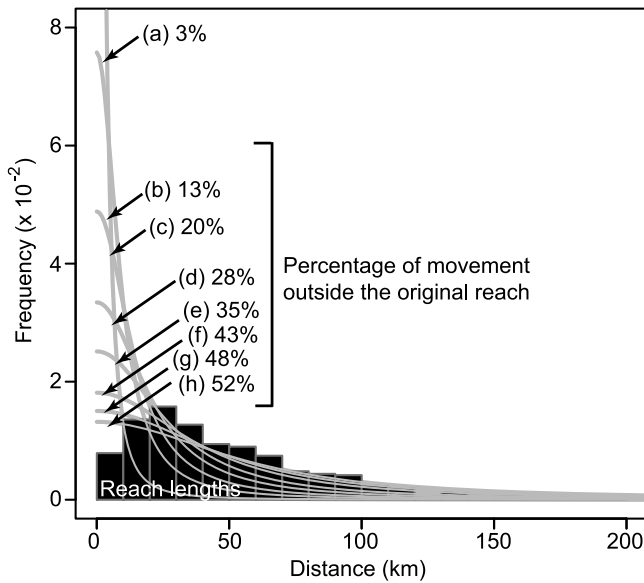


Figure 2. Movement kernels used in analysis. All kernels use $p = 0.18$. The parameter u varies as follows: a, $u = 10$; b, $u = 100$; c, $u = 250$; d, $u = 550$; e, $u = 1000$; f, $u = 2000$; g, $u = 3000$; h, $u = 4000$. The distribution of reach lengths in the Indian river network (Figure 1) is included for reference (black histogram).

canal links were not available, and shapefile layers were constructed manually on the basis of geocorrected JPEG maps provided by India's National Water Development Agency (<http://nwda.gov.in>).

[10] In our application of the neutral model, we assigned a habitat capacity to each individual stream reach (i.e., the stream section between two confluences) proportional to the maximum flow accumulation of the stream segment, which is itself proportional to the upstream watershed contributing area. In each time step, one “fish unit” (a fish unit can be thought of as a subpopulation of fish of the same species) dies at random somewhere in the system, and the resulting habitat capacity is filled either by a dispersing species from within the basin (with probability $1 - \nu$) or through the creation of an entirely new species by “diversification” (with probability ν). Diversification is simply a collective term for mechanisms responsible for introducing new species to the system, such as speciation and immigration from outside the network. The average number of new species introduced to the system (ν times total habitat capacity) in one generation is θ , where generation is defined as the average time required for complete turnover of the populations. Mean habitat capacity and the diversification rate, two free parameters in the model, were fixed to the values that best fit the data available for the MMRS [Muneepeerakul *et al.*, 2008]. Species dispersal distance (x) was stochastic and was driven by a movement kernel based on the “2Dt” function used by Clark *et al.* [1999],

$$f(x) \propto \frac{p}{\pi u \left(1 + \frac{x^2}{u}\right)^{p+1}},$$

which is governed by two movement parameters, p and u . The parameter p controls the shape of the distribution, with larger values tending to a Gaussian distribution and smaller

values to a Cauchy distribution, while u is a scale parameter that allows more long-distance dispersal as the value increases (Figure 2) [Clark *et al.*, 1999]. We varied these parameters to investigate the effects of different dispersal distributions on the spatial patterns of fish biodiversity. We assumed unbiased movement with equal upstream and downstream movement probabilities based on a previous study of another large river network [Muneepeerakul *et al.*, 2008] and verified that this assumption did not alter our conclusions by using additional analyses that included both upstream- and downstream-biased dispersal. Distances between different stream reaches were measured following the branches of the stream network (which always yield distances greater than or equal to the corresponding Euclidian distances). Where canal links created multiple paths between a pair of reaches, we used the shortest distance from among the possible pathways. With the exception of the specific movement kernel described above, the details of the neutral model used in this analysis are given by Muneepeerakul *et al.* [2008].

[11] In other work [Muneepeerakul *et al.*, 2008; Bertuzzo *et al.*, 2009], we were able to use empirical data on species distributions to parameterize the movement component of the neutral model. However, comprehensive empirical data for freshwater fishes in India is currently lacking [Ghosh and Ponniah, 2008]. Consequently, we established biologically realistic values on the basis of another river system of similar spatial scale. The parameter set found to maximize the fit of the model to the MMRS data was ($p = 0.18$, $u = 550$). From this starting point, we created a series of different movement scenarios by varying u (leaving p fixed at 0.18; Figure 2).

[12] To quantify the impacts of network restructuring, we considered local species richness (LSR) (i.e., the number of species in each reach), total species richness in the network (TSR), and the rank-occupancy curve. Note that we considered occupancy (i.e., the number of reaches in which a species is present) and not abundance (i.e., the number of individuals of a given species) because the former is more consistent with the kind of empirical data typically available, especially over large geographic areas.

[13] To understand the impact of network linking on patterns of biodiversity for a random link between two river basins, we selected a random set ($N = 50$) of stream reaches in the largest basin (the Godavari) and linked them to a single order 1 (headwater) stream reach from the second-largest basin (the Krishna) (Figure 3a). To explore the role of stream order on changes in LSR, we repeated our analysis for the three segments downstream of our first-order reach (Figure 3a). To contrast the results of such interbasin linking with the impact of creating intrabasin links, we also considered the impact of a random set of intrabasin links ($N = 25$), as well as a paired comparison in which a link was created between two order 1 (headwater) stream reaches within a single basin and then between two different basins. Finally, we considered the potential impact on LSR and TSR of the 11 proposed canals in our study area, taken individually and collectively.

3. Results

[14] In our analysis, the creation of new interbasin links increases LSR but has no consistent impacts on TSR (Figures 3b and 3c). The increase in LSR is a saturating

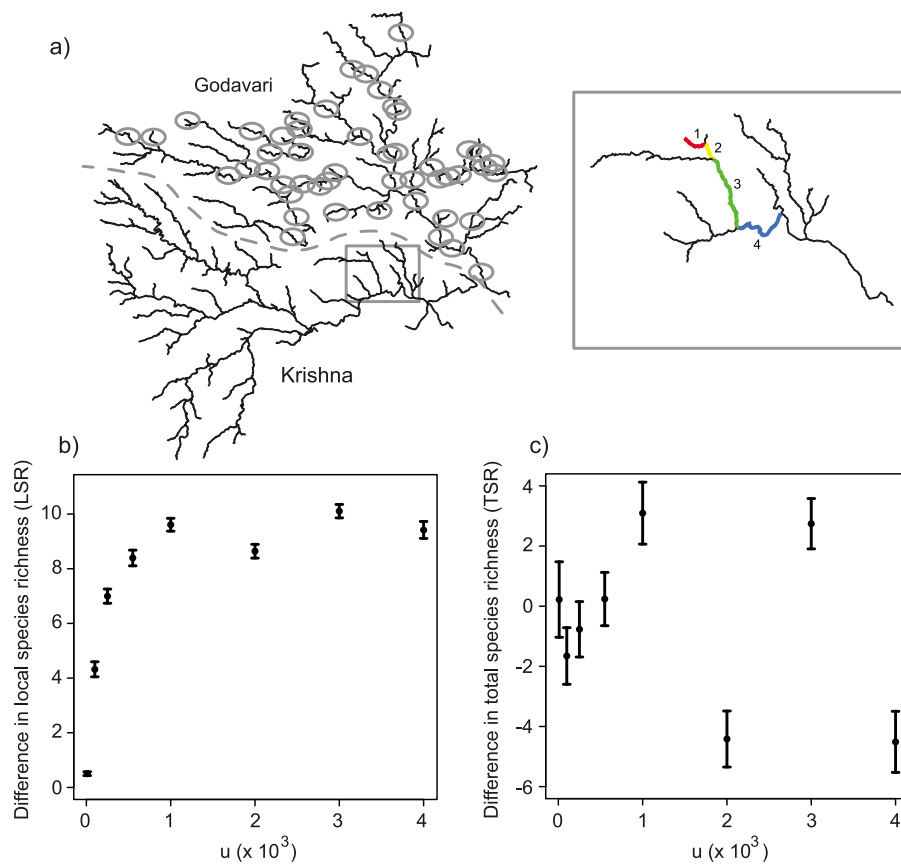


Figure 3. (a) Randomly selected links involved in the simulation of network linking. In each case, the Krishna reach indicated by the gray box is connected to one of the 50 Godavari reaches indicated by gray ovals. The dashed gray line is a visual guide to the division between the two basins. The enlargement shows an expanded view of reaches within the gray box, showing the first-order (red), second-order (yellow), third-order (green), and fourth-order (blue) reaches used in the interbasin linking analysis. Mean (\pm SE) differences in (b) local and (c) total species richness (after linking minus before linking) as a function of the movement parameter u (using a first-order stream in the Krishna basin as a connection point for the interbasin links to the Godavari basin). For each scenario, $N = 50$ realizations.

function of increasing long-distance dispersal (Figure 3b), whereas there is no corresponding relationship with TSR (Figure 3c). Common (i.e., more widespread) species become more common, whereas there is no change in occupancy among the least common species (Figure 4). These results remain true when habitat capacity is redefined as being proportional to reach length (see Figure S1 in the auxiliary material).¹ As LSR increases with stream order (see Figure S2), linking two fourth-order streams leads to a larger increase in average LSR than linking two smaller (first- and second-order) streams (Table 1). All stream reaches within a newly connected basin experience an increase in LSR, although there is a spatial decay moving away from the point of connection (see Figure S3). Longer links (i.e., connecting more distant basins) have a smaller impact on LSR (not shown) because fewer fishes travel those longer distances bridging the two basins, and this effect is most significant with the most localized (smallest u) movement kernels. Nevertheless, LSR increases after linking even for the most distant connection (596 km) and the

most localized movement kernel ($u = 10$), even though less than 0.05% of all fish movements extend as far as the link length.

[15] The increase in LSR with interbasin linking is robust to changes in the diversification rate (see Figure S4), to changes in the total amount of habitat available (see Figure S5), and to upstream or downstream dispersal bias (see Figure S6). Increasing the diversification rate and the total amount of habitat available increases LSR under either the linked or unlinked scenario and increases the change in LSR associated with interbasin linking (see Figures S4 and S5), whereas LSR and the change in LSR with linking decrease with either upstream or downstream dispersal bias (see Figure S6).

[16] Whereas interbasin links have a significant influence on patterns of local species richness, intrabasin links do not. We see no change in basin-wide average LSR as a result of creating additional links between reaches that are in the same river basin (Figures 5 and S3). This remains true even when linked reaches are distant from each other in the original network and the canal linking them is made artificially short.

¹Auxiliary materials are available in the HTML. doi:10.1029/2010WR010330.

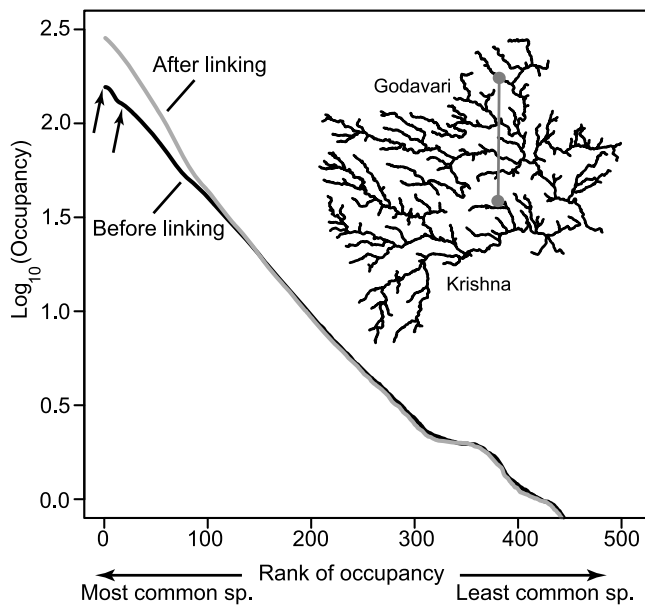


Figure 4. Rank-occupancy plot for the entire peninsular river system, resulting from one of the 50 canal links shown in Figure 3a. The y axis represents the number of reaches in which a given species exists, and the x axis represents the rank of occupancy for all of the species in the system. The most common species occurs in 129 more reaches (out of 456 reaches total) after the additional network link. The arrows point to plateaus that result from the complete occupation of the two largest basins in the system (see section 4).

[17] Finally, we see that the combination of all 11 canals considered in this analysis has a significant impact on the LSR of fishes in this empirical network (Figure 6). Disregarding stray fluctuations resulting from the inherently stochastic nature of the model, the impact for any given canal is restricted to the basins being connected. Nevertheless, the broad spatial extent of the proposed project means that the cumulative result of the 11 canal links is a significant increase in local species richness relative to the original geometric configuration in most of the river reaches considered.

4. Discussion

4.1. Overview and Synthesis

[18] Linking rivers is an example of out-of-network connectivity, which on theoretical grounds, is expected to

strongly influence the stability and composition of populations living in branching riverine networks [Grant *et al.*, 2007; Chaput-Bardy *et al.*, 2009; Fagan *et al.*, 2009]. New links added in a river network allow for the dispersal of species between reaches that in the absence of stream capture or orogenic events over geological time scales, would either be more difficult (intrabasin linking) or impossible (interbasin linking). Network theory in two-dimensional systems suggests that these dispersal pathways can be of critical importance to system dynamics and stability [Dunne *et al.*, 2002; Hill *et al.*, 2002; Holland and Hastings, 2008; Ranta *et al.*, 2008]. We used the empirical river network of the Indian Peninsula and plans for a suite of IBWT canals to structure our investigation of the potential effects of out-of-network links on local and system-wide patterns of fish biodiversity in complex river networks and to contrast the effects of permanent connections within and between hydrologically unconnected river networks. We investigated the sensitivity of these results to stream order (network position) and dispersal behavior.

[19] Our results agree with the predictions of neutral theory despite the explicitly spatial structure added via the dispersal kernel and the branching geometry. Mixing two nonspatial communities is predicted to have no effect on the rank-abundance curve [Purves and Pacala, 2005], which is consistent with our findings that total species richness is unaffected by the linking of two separate river basins. The before- and after-linking rank-occupancy curves (as opposed to rank-abundance curve; Figure 4) reveal a difference in the spatial spread of common species driven by the finite size of individual basins, beyond which common species can occupy no more reaches. This saturation of “occupation space” leads to a plateau in the rank-occupancy curves that differs before and after network linking and is an artifact of the relative size of the river basins and the extent of long-distance dispersal. Empirical rank-occupancy curves may not include a similar saturation in occupancy.

[20] Although limited in its capacity to predict the precise consequences of an IBWT project for any given species (discussed in more detail below), the neutral model provides us with one platform for understanding the potential landscape-scale consequences of such a massive hydrological manipulation of a river system. It also represents one of the few examples in which the restructuring of an empirically derived, and spatially explicit, ecological network is examined for its macroecological consequences. The number and scale of these types of water transfer projects provide considerable motivation to continue efforts to understand general rules for the impact of network manipulation on riverine species and biogeographic patterns.

Table 1. Increase in Local Species Richness When Linking Reaches of Various Orders ($p = 0.18$, $u = 550$)^a

Order	Order			
	1	2	3	4
1	8.08 ($\sigma = 0.97$, $N = 8$)	8.07 ($\sigma = 1.15$, $N = 16$)	8.52 ($\sigma = 1.17$, $N = 16$)	8.77 ($\sigma = 0.93$, $N = 14$)
2		7.79 ($\sigma = 0.78$, $N = 8$)	8.32 ($\sigma = 1.12$, $N = 16$)	8.22 ($\sigma = 1.07$, $N = 14$)
3			8.85 ($\sigma = 0.61$, $N = 8$)	8.66 ($\sigma = 0.54$, $N = 14$)
4				9.47 ($\sigma = 0.50$, $N = 6$)

^aOne standard deviation and sample size are shown in parentheses. Differences are statistically significant (t test with $p = 0.05$ Bonferroni corrected for 45 comparisons) for $2 \rightarrow 1$ versus $4 \rightarrow 4$ and for $2 \rightarrow 2$ versus $4 \rightarrow 4$. The comparison $1 \rightarrow 1$ versus $4 \rightarrow 4$ is barely nonsignificant because of the small sample size.

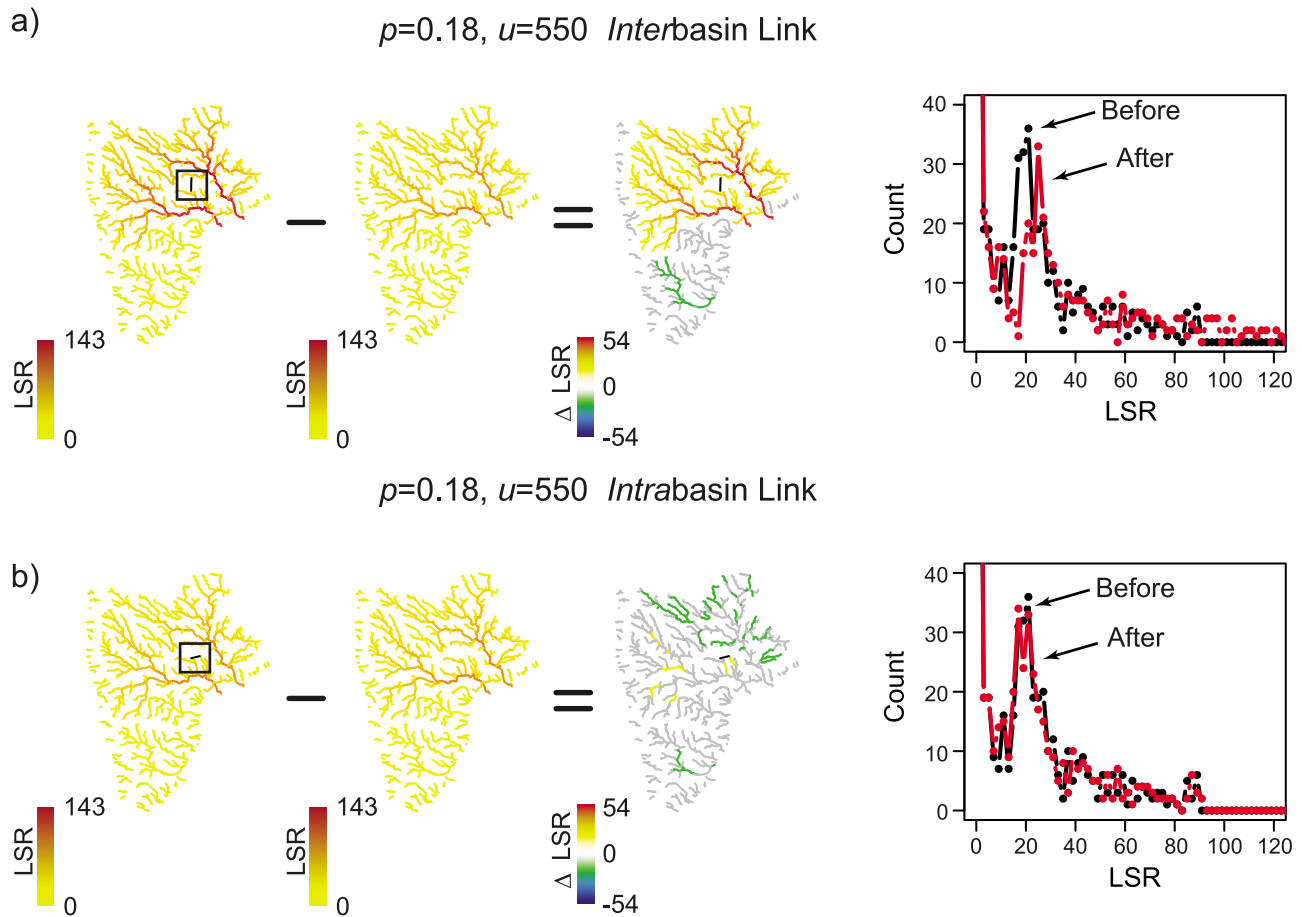


Figure 5. (left) Examples of the impact of (a) interbasin and (b) intrabasin linking on local species richness (LSR) for the Indian Peninsula river network, comparing theoretical canal links of equal length. (right) Histograms of LSR before and after linking. A shift toward higher LSR is seen for interbasin linking but not for intrabasin linking. All reaches with absolute differences (after minus before) smaller than the background stochastic variability are shaded in gray so as to emphasize reaches with large changes in local species richness. Note, however, that some reaches disconnected from the impacted basins show changes in LSR that slightly exceed this threshold. These changes reflect stochastic variability and are not ecologically significant.

[21] It is important to emphasize that our results do not simply reflect the transient dynamics involved in the interbasin dispersal of species upon the completion of a man-made canal. This is because the canal-linked and unlinked scenarios we compare each represent steady state conditions involving fish communities that are wholly independent of their respective starting conditions. In other words, the impact of network restructuring on local species and total species richness does not depend on the initial fish communities and would be the same whether the basins connected had the exact same or completely different fish communities prior to the canal. Nevertheless, increased dispersal accelerates the transition to equilibrium, as illustrated in Figure S7.

4.2. Contextualization of Specific Results

[22] LSR increases with stream order (see Figure S2), and as a result, the network position (i.e., stream order) of the linked reaches influences the impact of interbasin linking (Table 1). Larger fourth-order streams greatly facilitate the

potential exchange of species between linked basins, leading to a larger increase in LSR compared to links between smaller (first- or second-order) reaches. When two basins are linked to form a larger “metabasin,” the pool of potential immigrants to all of the reaches in the two original basins and, subsequently, the local species richness, increases. The extent to which the interbasin link influences the pool of potential immigrants for any given reach will depend on the length of the link itself (longer links have a smaller effect), the dispersal kernel, the position of the linked reaches within the river network, and the distance from the focal reach to the point of connection, an effect that is seen in the spatial decay of LSR with distance from the link (see Figure S3). This spatial component implies that reaches in close proximity to the canals should be considered explicitly in the assessment of potential ecological impacts and surveyed in advance for rare, endemic, or economically important species that may be disproportionately impacted.

[23] The rank-occupancy curve in Figure 4 demonstrates the log linear relationship between rank and occupancy

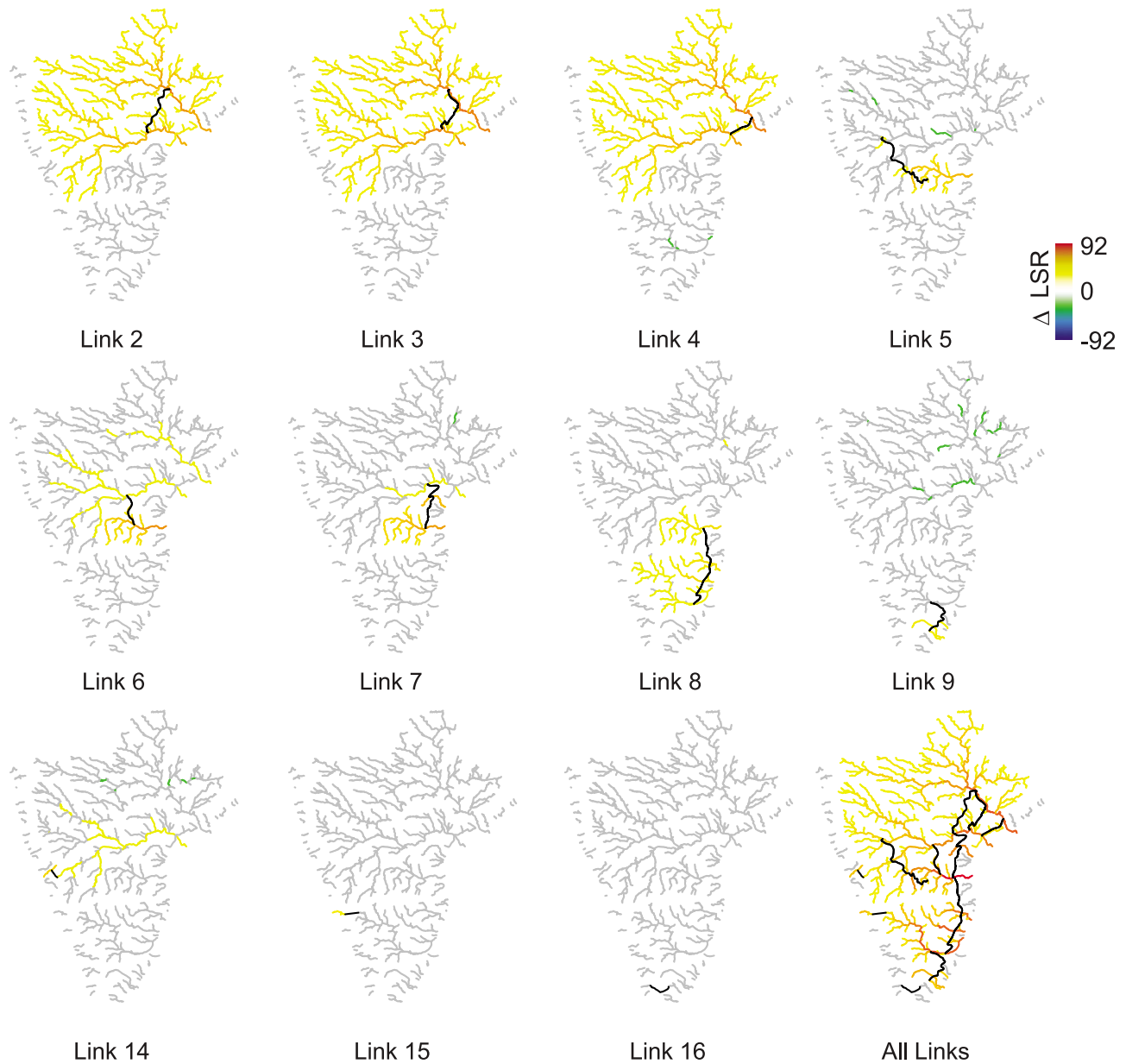


Figure 6. Impact of the 11 proposed interbasin water transfer peninsula links in our study area on patterns of local species richness (using $p = 0.18$, $u = 550$). All reaches with absolute differences (after minus before) smaller than the background stochastic variability are shaded in gray so as to emphasize reaches with large changes in local species richness. Note, however, that some reaches disconnected from the impacted basins show changes in LSR that slightly exceed this threshold. These changes reflect stochastic variability and are not ecologically significant. The links are numbered according to enumeration assigned by India's National Water Development Agency (see Figure 1).

expected from a neutral model over a large range of ranks (occupancy is monotonically related to abundance; see supplementary information of *Muneepeerakul et al.* [2008]). Note that the slight saturation of occupancy for the most common species (a double saturation for the “before” curve and a single saturation at higher occupancy for the “after” curve) stems from the complete occupancy of the most common species throughout entire basins. The “double humps” (arrows in Figure 4) are due to the saturation of species in the two largest basins (the 156-reach Godavari and the 131-reach Krishna), and the single point of satura-

tion in the after curve is due to those species that completely occupy the combined 287-reach metabasin created by the canal link. As individuals are chosen at random for dispersal, common species have a numerical advantage over rare species in their capacity for dispersal and colonization of new reaches. Therefore, it is not surprising that common species become even more common after linking, although their increase in absolute abundance (not shown) is much smaller than their increase in occupancy (Figure 4). In other words, common species are able to occupy a much larger set of reaches after the link is added (in some cases, going from

complete occupancy of a single basin to complete occupancy of the new larger metabasin) even if their absolute abundance only increases slightly.

[24] We find no impact on local or total species richness when links are added within a single basin because the pool of potential immigrants has not changed significantly, even if the distances between different reaches have changed. Differences in community composition likely increase with increasing distance, so that common species are likely to occupy both reaches being linked by shorter canals. Conversely, distant reaches may provide greater opportunity for exchange of new species, but the longer canal links restrict the number of individuals that are able to utilize the link.

[25] Although IBWT projects are typically considered as a single entity, individual canal projects can vary considerably in their contribution to plan goals, feasibility, and timeline for completion. It is therefore crucial that we consider the ecological impact of each individual component of the project [Korse, 2004]. The spatial extent of impact (i.e., the total length of affected river reach) varies widely among the various proposed links (Figure 6) because the impacts on local species richness are basin-wide and the basins being connected by the various canal projects vary widely in size. When the entire plan calls for multiple connections between two river basins (e.g., Figure 6, links 2–4 or 5–7), the relative expected impact on local fish species richness can be included, along with social and economic considerations, in the process to decide which canal projects should be given priority. Each individual link results in a smaller change in LSR relative to the plan as a whole (Figure 6, all links plot), particularly for rivers impacted by multiple proposed canals (e.g., links 5–7).

[26] Although the neutral model assumes per capita equivalence of all individuals (including equal movement probability distributions), we can use our findings on the influence of long-distance movement to suggest potential consequences for fishes with different dispersal characteristics. For example, increased long-distance dispersal increases the chance that a species will encounter an interbasin link and, subsequently, reaches beyond it in the other basin. By considering a range of different dispersal kernels, we can make an inference regarding the more realistic scenario in which fishes differ in their movement probabilities. More highly dispersive fishes will have a greater chance of transiting the added network link than species with very limited movement capabilities. Therefore, we would expect that the spatial distribution of highly dispersive fish species will be more strongly impacted by the IBWT project.

4.3. Caveats and Limits to Interpreting Results From the Neutral Model

[27] The neutral model does not account for competitive or predator-prey interactions among species. Species interactions may be important when, for example, a new carnivorous (or larvivorous) fish is added to a river reach where smaller prey fish are vulnerable. Interbasin transport of such consumers in North America, including both accidental and intentional introductions, has dramatically reduced the spatial distribution, occupancy, and/or abundance of native fish species in some river basins [Fagan *et al.*, 2005; Minckley and Marsh, 2009]. Increased network connectivity resulting from an IBWT project may exacerbate problems with

the spread of nonnative fishes accidentally or intentionally introduced by aquaculture-related activities. In extreme cases this could lead to the local extinction of some species and, in cases of high endemism, global extinction as well [Olden *et al.*, 2006; Vitule *et al.*, 2009]. We note, however, that in one of the few empirical tests of the ecological consequences of canal-mediated interbasin linking, such interactions were found to be less important than increased opportunities for dispersal, supporting the case for neutral community models as an appropriate framework for analysis [Smith *et al.*, 2004].

[28] Our analysis does not consider any effects of man-made canals separate from their impacts on connectivity. Canals and associated dams change habitat conditions, alter natural river dynamics, and modify the disturbance regime of affected basins, all of which may influence fish distributions in a way not currently accounted for in the neutral model [Martinez *et al.*, 1994; Bonner and Wilde, 2000; Kingsford, 2000; Gehrke *et al.*, 2002; Nilsson *et al.*, 2005, and references therein; Poff *et al.*, 2007].

[29] We have only addressed the impact of linking on the spread and distribution of fish species. There is additional concern that such basin-linking canals would permit the spread of disease-causing pathogens that might affect fishes in newly connected reaches above and beyond simple changes in the species composition of the fishes themselves [Daniels, 2004; Linder *et al.*, 2005]. These secondary effects are beyond the scope of our analysis but deserve further consideration to understand comprehensively the impacts such a project would have on ecosystem health and function.

5. Summary and Future Directions

[30] The aim of the current work is to investigate the effect of out-of-network linkages in river networks on patterns of biodiversity, and our results provide testable predictions against which future empirical evidence may be compared. To address more directly some of the issues specific to India's freshwater fish community, spatially explicit (preferably reach-scale) data on occupancy patterns will be required. We are currently developing a database of India's freshwater fishes that combines collection records, occupancy information gleaned from the published literature, and other regional or global fish databases with an occupancy model that will allow us to create a comprehensive and spatially explicit portrait of India's freshwater fish community. Future efforts will use this information to refine our predictions regarding the ecological consequences of India's IBWT project.

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