REPORTS

CONNECTIVITY, FRAGMENTATION, AND EXTINCTION RISK IN DENDRITIC METAPOPULATIONS

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Abstract. Neither linear nor two-dimensional frameworks may be the most appropriate for fish and other species constrained to disperse within river–creek systems. In particular, the hierarchical, dendritic structures of riverine networks are not well captured by existing spatial models. Here I use a simple geometric model and metapopulation modeling to make three points concerning the ecological consequences of dendritic landscapes. First, connectivity patterns of river–creek networks differ from linear landscapes, and these differences in connectivity can either enhance or reduce metapopulation persistence compared to linear systems, depending on the details of dispersal. Second, habitat fragmentation in dendritic landscapes has different (and arguably more severe) consequences on fragment size than in either linear or two-dimensional systems, resulting in both smaller fragments and higher variance in fragment size. Third, dendritic landscapes can induce striking mismatches between the geometry of dispersal and the geometry of disturbance, and as is the case for arid-lands fishes, such mismatches can be important for population persistence.

Key words: colonization; connectivity vs. dispersal, influence on extinctions; creeks and rivers; dendritic landscapes; dispersal constraints, landscape imposed; fishes; habitat fragmentation; habitat geometry; hierarchical riverine networks; landscape ecology; river networks; rivers, conservation biology.

INTRODUCTION

Most studies of metapopulation-like dynamics involve species living in what can be roughly characterized as two-dimensional (2-D) landscapes. Examples include studies of butterflies (Harrison 1991, Wahlberg et al. 1996), small mammals (Pokki 1981, Lindemayer et al. 1999), and pool frogs (Sjögren 1991). In 2-D landscapes, dispersers might move between particular pairs of patches via any of several possible dispersal routes, but such routes likely differ in the frequency with which they are actually used. In contrast, Gotelli and Taylor's (1999) study of metapopulation dynamics for 41 fish species in the mainstem of Oklahoma's (USA) Cimarron River involves what can be characterized as a linear landscape. Unlike 2-D systems, dispersers restricted to linear landscapes cannot move between distant patches without first passing through (and perhaps colonizing) the same series of intervening patches.

However, neither the linear nor 2-D metapopulation frameworks may be the most appropriate for species whose habitats feature alternative geometries. In par-

ticular, and in contrast to the linear nature of the Cimarron River system (Gotelli and Taylor 1999), many river–creek systems feature a hierarchical dendritic structure that is not well captured by any of the array of existing metapopulation models. Such landscape-imposed dispersal constraints would be especially important for fish and other entirely aquatic species, that, unlike many stream insects, lack life stages that could disperse (or be dispersed) over land. For such species, altered patterns of connectivity in dendritic landscapes require reconsideration of the notion of patch isolation, in which spatially "nearby" patches may actually be quite remote (e.g., Dunham and Rieman 1999). In a sense, applications of standard metapopulation approaches force hierarchical systems to conform unrealistically to linear or 2-D landscapes.

Here I use a simple geometric model, metapopulation modeling, and empirical data to make three points concerning the ecological consequences of dendritic landscapes. First, altered connectivity patterns of river–creek networks can, depending on the details of dispersal and among-patch correlations in extinction risk, either enhance or reduce metapopulation persistence compared to linear systems. Second, habitat fragmentation in dendritic landscapes has different (and arguably more severe) consequences on fragment size than in either linear or 2-D systems. Third, dendritic

landscapes can induce striking mismatches between the geometry of dispersal and the geometry of disturbance that have important consequences for population persistence. These consequences of dendritic landscape structure are then discussed in the context of arid-lands fishes.

There is increasing interest in several kinds of fragmentation that commonly affect river–creek systems (papers in Minckley and Deacon [1991], Rahel et al. 1996), the natural patchiness that riverine landscapes exhibit (e.g., Horwitz 1978, Gotelli and Taylor 1999, Palmer et al. 2000), and the difficulties of maintaining persistent local populations in moving environments (Speirs and Gurney 2001). This paper illustrates the need to study how dynamic processes operating in hierarchical river–creek systems may differ from or resemble processes in more ''conventional'' landscapes.

MODEL STRUCTURE AND ANALYSES

To illustrate some unique aspects of river–creek systems, I consider two different patch geometries: a linear system and a bifurcating dendritic network (Fig. 1). For convenience, I explore the consequences of varying the number of patches by reference to the dimensions of bifurcating dendritic networks (complete binary trees in the terminology of graph theory [Gross and Yellen 1999]) whose tree depth (the number of ''levels'' of patches, Fig. 1B) is denoted by the integer n. For the bifurcating dendritic networks discussed here, a tree of depth n always has $2^n - 1$ patches and $2^n - 2$ connections among patches. Naturally, alternative representations of dendritic landscapes are possible (e.g., landscapes featuring asymmetrical branches or unbranched ''stems''), but as a starting point I consider a balanced geometry that lends itself to mathematical characterization.

The branchiness of dendritic networks influences patch connectivity and isolation in different ways than occurs in the linear geometries (or in two-dimensional ''terrestrial''-type geometries). For example, for the dendritic geometry studied here, 2^{n-1} patches (i.e., just over half) could be recolonized from only one direction should they go extinct, whereas just under half the patches in a dendritic landscape could be recolonized from three directions. Consequently, the connectivity of dendritic landscapes contrasts with that in the linear case (in which two patches are restricted to unidirectional recolonization). One consequence of this pattern of connectivity is that as the number of patches in a metapopulation increases, the fraction of somewhat-isolated patches stays constant in the dendritic geometry but diminishes quickly in the linear geometry.

Point 1: The interplay between connectivity and dispersal influences metapopulation persistence in dendritic landscapes

A well-established tenet of metapopulation dynamics is that connectivity influences metapopulation persis-
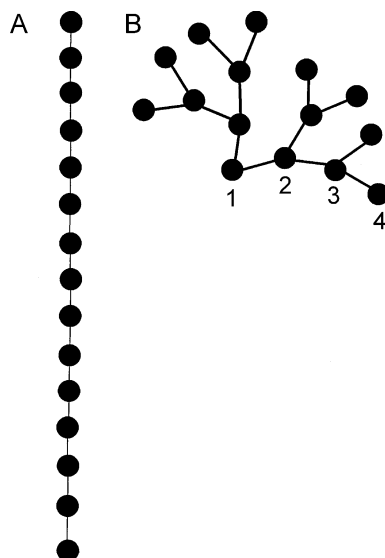

FIG. 1. Alternative geometries for metapopulation dynamics: linear arrangement of (A) patches and (B) dendritic arrangement featuring a hierarchical array of four ''levels'' of patches. Solid circles represent patches of habitat, and line segments represent possible dispersal pathways.

tence (Hess 1996). However, dendritic landscapes expand the range of possible relationships between connectivity and persistence. To see this, consider a discrete-time metapopulation model in which each patch has an independent probability e of going extinct per time step, but also has a probability c of being recolonized via dispersal from each of its immediately neighboring patches (provided those patches are themselves occupied). In simulating such a model, I assume that the initial condition is total occupancy and that extinction happens before dispersal in each time step. Simulations indicate that dendritic and linear geometries yield equivalent metapopulation persistence times when the probability of patch-to-patch colonization is low relative to the risk of local extinction (Fig. 2). This similarity across geometries holds for both two-way colonization (i.e., both ''upstream'' and ''downstream'') and one-way colonization (e.g., the riverine ''drift paradox'' [e.g., Müller 1954]). In contrast, when the probability of colonization is higher, an interaction emerges between landscape geometry and the directionality of dispersal that influences metapopulation persistence. With two-way colonization, the enhanced connectivity of dendritic landscapes is an asset, resulting in longer metapopulation lifetimes than in comparably sized linear landscapes (Fig. 2A). In contrast, the altered connectivity of dendritic landscapes becomes a liability with one-way dispersal, and the magnitude of this disadvantage increases with the number of patches in the metapopulation (Fig. 2B).

Differences among landscape types also occur when extinction events are correlated among patches. For example, when all patches in a metapopulation are ac-

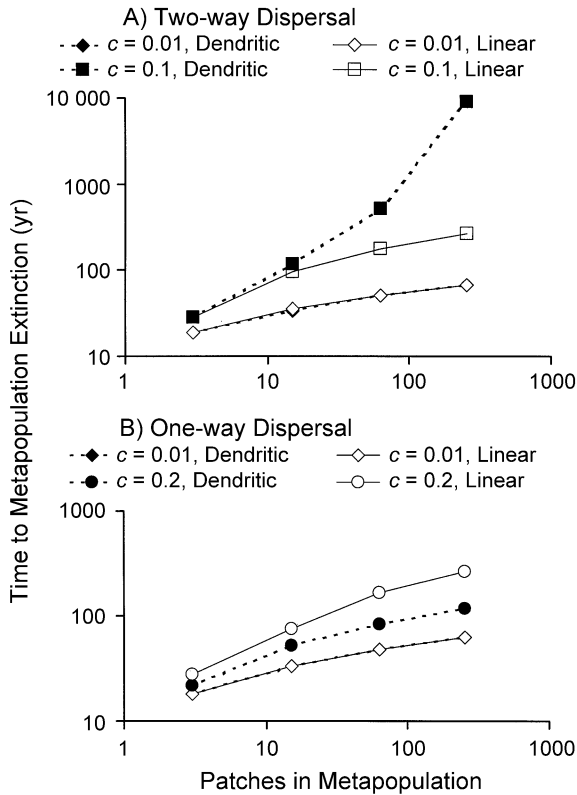## A) Two-way Dispersal
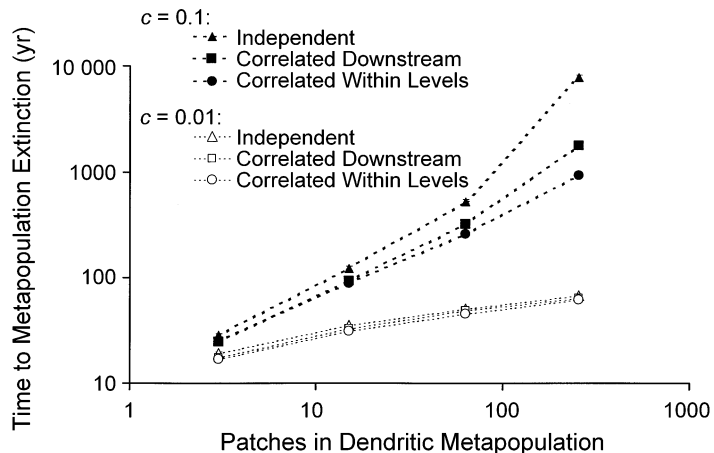

B) One-way Dispersal

FIG. 2. Mean metapopulation lifetimes for systems of patches arranged in linear vs. bifurcating dendritic networks. Probabilities of colonization per time step are given by the parameter c (c = probability of being recolonized via dispersal from each immediately neighboring occupied patch). In all cases, probabilities of extinction per patch per time step were 0.1, initial conditions featured complete occupancy, and 1000 replicates were simulated (though confidence intervals were too small to display on the logarithmic axes). Note that symbols overlap for $c = 0.01$. In panel (A) both up- and down-stream dispersal occurs, whereas in (B) only downstream, ''drift'' dispersal is possible. Persistence times in two-dimensional grid systems (not shown here) far exceed those of linear and dendritic landscapes.

cessible from all other patches and extinction risks are uncorrelated among patches, persistence times scale exponentially with the number of patches in a fragment (Nisbet and Gurney 1982). The addition of among-patch correlations in extinction risk to such models causes metapopulation persistence times to scale only logarithmically with patch number (Gilpin 1990). Simulation studies undertaken for this paper indicate that correlated extinctions also reduce metapopulation lifetime in dendritic systems, although the magnitude of the effect depends upon the nature of the correlation. I considered two kinds of correlation structure. First, I examined the effects of extinctions that were correlated within levels in the dendritic hierarchy. Such a correlation structure represents cases in which patches are more similar to nonadjacent patches than they are to their immediate neighbors. In such a scenario, elevation, stream gradient, or similar characteristics would be important determinants of extinction risk. For comparison, I also examined the effects of longitudinally (i.e., within-branch) correlated risks. This correlation structure is more representative of the downstream effects of flooding, fire-sediment discharge, or pollutant release.

Modeling these correlated extinction risks required decomposing the per patch extinction probability e into two parts, a local patch-specific risk (e_1), and a risk attributable to a hypothetical larger-scale process (e_2). When larger-scale extinctions occurred, they affected a focal patch and two other patches. For the within-level case, the extinction affected the nearest two patches at the same depth in the hierarchy, whereas for the longitudinal case the extinction affected the two patches immediately downstream from the focal patch. Fixed values for e_1 and e_2 pairs were chosen such that the overall per patch risk of extinction was equal to the per patch risk when all extinctions occurred independently among patches. In both cases, correlated extinction risks did not change the functional form of the scaling relationship evident in the case involving in-

FIG. 3. Mean metapopulation lifetimes for bifurcating dendritic networks subjected to correlated extinction risks. In all cases, metapopulations started from complete occupancy, total probability of extinction per patch per time step was 0.1, and values for c (the probability of being recolonized via dispersal from immediately neighboring patches) are as in the key. Again, 1000 replicates were simulated. In the scenarios featuring correlated extinctions (which affected three patches; see *Model structure. . . : Point 1. . .* for details), $e_2 = 0.024$. Note y-axis logarithmic scale.

dependent risks, but did greatly reduce the benefits accrued through increases in the number of patches in the metapopulation (Fig. 3).

Point 2: Fragmentation in dendritic landscapes affects fragment size in complex ways

As with terrestrial landscapes, river–creek systems are subject to numerous fragmentation events of both natural and anthropogenic origins. For example, desert streams of the southwestern United States have experienced substantial natural drying trends since the Pleistocene that have contributed to fragmentation and isolation of many stream systems (Deacon and Minckley 1974). Dam building and water diversion have amplified the effects and accelerated the rates of natural changes to the landscape, effectively disconnecting segments of habitat for desert fishes. In contrast to two-dimensional (2-D) landscapes where multiple routes of movement among patches are possible, pollution or other habitat degradation at specific points in dendritic landscapes can completely separate portions of the system.

A return to the simple geometric models (Fig. 1) helps clarify the effects of fragmentation. For example, relative to other geometries, random fragmentation in dendritic networks leads to an increased frequency of small fragments and increased variability in fragment size. To see this, consider how the consequence of a single fragmentation event (that completely eliminates any recolonization between two neighboring patches) varies among the different geometries. In a regular 2-D grid of patches, random disruption of a single recolonization pathway cannot subdivide the system into two isolated fragments. In fact, for some kinds of species, habitat fragmentation per se may be of little importance in 2-D systems until after there is substantial habitat loss (e.g., Andrén 1994, Fahrig 1997), though this is likely less true in metapopulations that are 2-D in nature but with patches distributed less regularly than on a grid (Urban and Keitt 2001). I focus the remaining discussion by drawing contrasts between fragmentation in dendritic and linear systems, in both of which every fragmentation event (including the first) results in habitat subdivision.

Treating the effects of a single fragmentation event as a uniform random discrete probability distribution (Rosner 1990), it is possible to quantify the expectation and variance of the distribution of fragment sizes. In a linear system with $2^n - 1$ patches, one can write the expected size of the *smaller* of the two remaining fragments as

$$E(\text{smaller})_{\text{linear}} = 2^{n-2} \tag{1}$$

while the variance in fragment size is

$$\text{Var}_{\text{linear}} = \frac{\frac{1}{6}(2^{3n}) - 2^{2n} + \frac{11}{6}(2^n) - 1}{2^{n+1} - 4}. \tag{2}$$
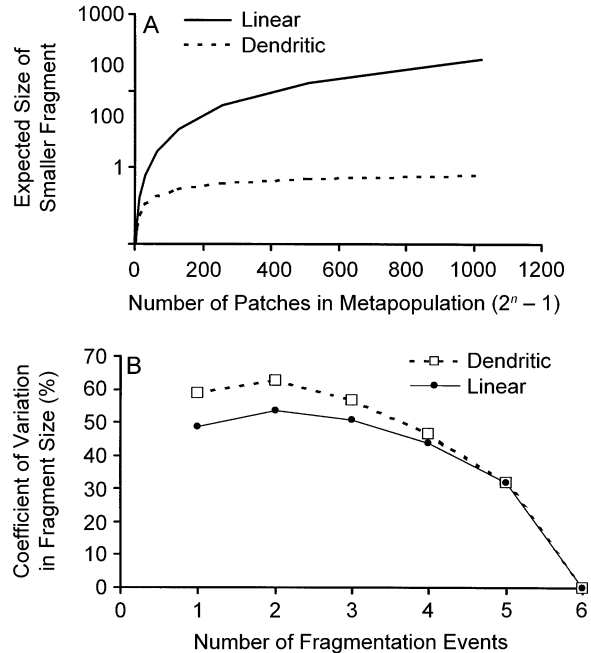
In contrast, for the dendritic system, the expected

FIG. 4. Impacts of fragmentation events on the structure of metapopulations with linear and dendritic geometries. Panel (A) gives the expected number of patches in the smaller fragment resulting from a single randomly placed fragmentation event. Note *y*-axis logarithmic scale. Panel (B) summarizes the effects of multiple randomly placed fragmentation events on the distribution of fragment sizes for linear and dendritic metapopulations with seven patches. The comparison is made in terms of the coefficient of variation of fragment size to scale out changes in expected fragment size due to increasing number of fragmentation events. When they occur, fragmentation events break a single dispersal pathway completely.

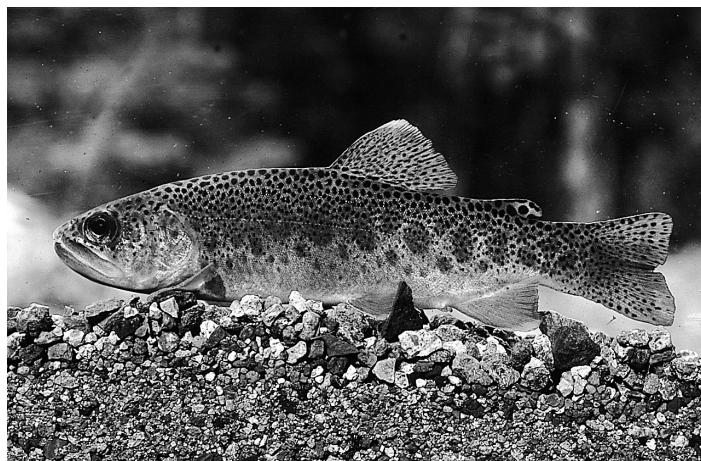size of the smaller fragment resulting from a single random fragmentation event is

$$E(\text{smaller})_{\text{dendritic}} = \sum_{i=1}^{n-1} \left[(2^i - 1) \frac{2^{n-i}}{2^n - 2} \right]$$
$$= \frac{2^n}{2^n - 2} \left(n - 2 + \frac{2}{2^n} \right) \tag{3}$$

while the variance for the dendritic system is

$$\text{Var}_{\text{dendritic}} = \frac{2^{3n-2} - n2^{2n} - n2^n + 2^{2n+1} - 7 \times 2^{n-2} - \frac{1}{2}}{2^n - 2}. \tag{4}$$

As the number of patches in the metapopulations increases, the expected size of the smaller fragment resulting from a single fragmentation event scales as $2^n/4$ for linear systems (Eq. 1), whereas expected fragment size in the dendritic system is always $<n$ (Eq. 3; Fig. 4A). Consequently, the expected size of the smaller fragment resulting from a single fragmentation event will increase linearly in linear systems, but much more

PLATE 1. Pictured is *Oncorhynchus gilae* (Gila trout), which historically occurred in headwater tributaries in the upper Verde, San Francisco, and Gila rivers (Arizona and New Mexico). Having been extirpated from most of its native range, the species now occurs naturally in a few isolated headwater streams in New Mexico. Introduced or reestablished populations occupy a few other streams there and in Arizona.
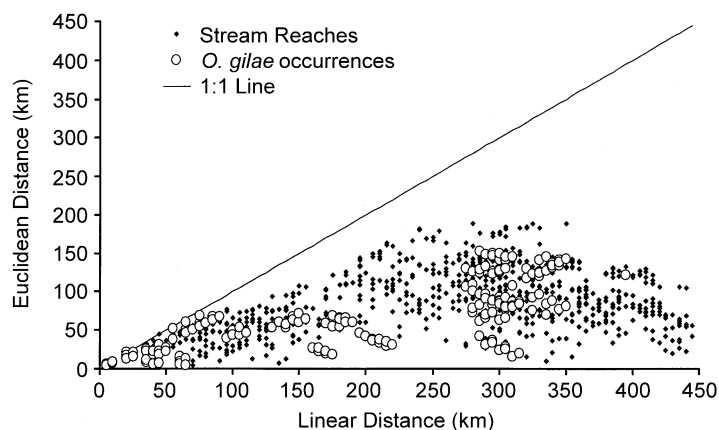
slowly in dendritic systems. Obviously, if the expected size of the smaller fragment is smaller in dendritic landscapes than in linear ones, the opposite must be true for the expected size of the larger fragment. This difference accounts for the effect of fragmentation on the respective variances of the different systems, in which dendritic systems will on average have a higher variance in fragment size than the corresponding linear systems (Eq. 4 > Eq. 2).

As one moves from single to multiple fragmentation events, quantifying the number of possible ways in which fragmentation could affect the systems' subdivision becomes difficult, necessitating numerical studies. First, in dendritic landscapes, increasing fragmentation rapidly leads, on average, to systems featuring several small and one or a few larger fragments. In contrast, uniformly random fragmentation in linear landscapes results in fragments that are more evenly sized. When the degree of fragmentation is considered as a proportion of the total possible, the variation in fragment size in the dendritic system will exceed that of the linear system for low and intermediate (but not extreme) degrees of fragmentation (Fig. 4B).

Point 3: Dendritic landscapes can induce mismatches between the geometry of dispersal and the geometry of disturbance

In dendritic landscapes the linear (stream course) distance separating two patches may be very different than the Euclidean distance between them (Fig. 5). That is, "as the trout swims" is different than "as the crow flies." Such patterns can have important dynamic consequences. For example, consider the case of headwater streams that drain opposite sides of a mountain and flow into separate river systems whose confluence is many kilometers downstream. Patches at the branch tips in such a dendritic landscape would be remote from the perspective of a species constrained to move through that landscape, but given their close proximity, these same patches could face a high correlation in extinction risk due to disturbances not constrained to the dendritic landscape (as in Fig. 3). This happens in real systems. Brown et al. (2001) demonstrate how forest fires in mountainous regions near the Arizona–New Mexico border have caused correlated extirpation of populations of the endangered Gila trout (*Oncorhyn-*

FIG. 5. Comparison of Euclidean and linear (i.e., stream course) distances separating stream reaches in the upper Gila River, Arizona and New Mexico, USA (above the confluence of the Gila and San Simon Rivers). Stream courses were digitally broken into 5-km-long segments, and the linear and Euclidean distances separating the centers of all possible pairs of segments were calculated. Solid points are a representative sample of these pairwise distances, designed to flesh out the shape of the resulting polygon of points. Open points indicate pairwise distances between extant populations of Gila trout (*Oncorhynchus gilae gilae*).

chus gilae gilae; see Plate 1) that exhibit such ''isolated but nearby'' relationships.

DISCUSSION

Characteristics and dynamics of dendritic landscapes can differ strikingly from those of linear or two-dimensional systems. The altered connectivity patterns of river–creek networks can affect metapopulation dynamics, alter the interplay between dispersal and fragmentation, and induce mismatches in the geometries of dispersal and disturbance. All these differences can have important consequences for population persistence. As a result, this work complements recent findings that highlight the ecological importance of the interplay between landscape connectivity and dispersal (e.g., Hess 1996, Hiebeler 2000, Urban and Keitt 2001, Vos et al. 2001).

When working with particular dendritic metapopulations, it will be important to consider several additional factors. The specific location of fragmentation events is one example. Have fragmentation events occurred with equal probability throughout the network, or have they clustered near the trunk (where resulting fragments would tend to be more evenly sized) or near the branch tips (where resulting fragments would be disproportionately small)? Which scenario occurs may well depend upon the kind of fragmentation in question. For example, navigation control dams will most likely cluster near the trunks, whereas other kinds of fragment-producing processes (e.g., fishing lakes, flood-control dams, off-stream diversions) may cluster near the branches.

Likewise, even in the absence of anthropogenic activities that actually subdivide landscapes, natural hierarchic variation in habitat quality, which could at least partially decrease connectivity within the system, should also be considered in the context of dendritic geometries. As a simple example, upstream and downstream reaches may differ greatly in abiotic conditions such as sun exposure and current velocity, such that downstream areas are sufficiently hostile to inhibit recolonization among headwater reaches (Brown et al. 2001). Unmack (2001) provides an interesting (and extreme) case of such hierarchic variation. In that example, persistent populations of Australian desert fishes occupy deep pools in upstream, canyon-bound refugia while downstream riverbeds dry completely on an annual basis. Recolonization is only possible during floods.

Because a little fragmentation in dendritic landscapes can substantially reduce the potential for recolonization, it compounds the significance of local extirpation events, whatever their cause. For Sonoran Desert fishes, historical fragmentation of species' ranges is a stronger predictor of local extinction risk than is the number of historical occurrences (Fagan et al. 2002), in part because human habitat modifications have dramatically reduced opportunities for recoloni-

zation during periods of high flow, largely eliminating this counterbalance against extirpations.

In addition to more detailed extensions in real systems, the dynamics of populations and communities in dendritic (or otherwise constrained) geometries also deserve further theoretical study. One possible approach would be to adopt incidence-function methodology (Hanski 1996). Though it was first applied to two-dimensional systems, the colonization matrix in an incidence-function model can also be used for dendritic landscapes (Dunham and Rieman 1999). In framing specific dendritic networks as metapopulations, however, one would need to take care to distinguish habitat patches from those portions of the network that merely act as pass-through corridors. Likewise, consideration should be given to whether the frequency of recolonization events is really low enough to generate true metapopulation dynamics (Harrison 1991). For example, Horwitz (1978), Osborne and Wiley (1992), and Taylor (1997) present case studies in which dispersal and an immigration–extinction balance may contribute to patterns of species richness in stream fish assemblages, but from the perspective of metapopulation dynamics at large, the generality of these findings is uncertain.

If incidence matrices were adapted to model stream fish metapopulations, one would include structural zeros to represent all the patch-to-patch connections that are impossible, given nearest neighbor dispersal (or dispersal over some other neighborhood) within the stream network. Given the relationships between (graph theoretic) graphs and matrices, this perspective would likely be informative. However, model frameworks that directly embrace the hierarchical geometry of river–creek systems could well provide different sets of insights.

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