

# Landscape-Scale Spatial Population Dynamics in Human-Impacted Stream Systems

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**ABSTRACT** / The movement of individuals among populations can be critical in preventing local and landscape-scale species extinctions in systems exposed to human perturbation. Current understanding of spatial population dynamics in streams is largely limited to the reach scale and is therefore inadequate to address species response to spatially extensive perturbation. Using model simulations, I examined species response to perturbation in a drainage composed of multiple, hierarchically arranged stream-patches connected by in-stream and overland pathways of dis-

persal. Patch extinction probability, the proportion of initially occupied patches extinct after 25 years, was highly sensitive to the extent of species occupancy and perturbation within the drainage, longitudinal species distribution, perturbation decay rate and the covariance pattern of stochastic effects on colonization and extinction probabilities. Results of these simulations underscore the importance of identifying and preserving source populations and dispersal routes for stream species in human-impacted landscapes. They also highlight the vulnerability of headwater specialist taxa to anthropogenic perturbation, and the strong positive effect on species resilience of habitat rehabilitation when recolonization is possible. Efforts to conserve and manage stream species may be greatly improved by accounting for landscape-scale spatial population dynamics.

Spatial population dynamics, the demographic contribution of the movement of individuals among populations, can reduce the probability of species extinction in landscapes exposed to anthropogenic perturbation (Levins 1970, Fahrig and Merriam 1994, Monkkonen and Reunanen 1999, Hanski and Ovaskainen 2000). Research on spatial dynamics of resident stream organisms is largely limited to individual stream reaches (Sheldon 1984, Pringle and others 1988, Sheldon and Meffe 1994, Palmer and Poff 1997). However, anthropogenic perturbation often encompasses whole streams or drainages of multiple streams (Sedell and others 1990, Zwick 1992, Allan and Flecker 1993, Poff and others 1997, Ward 1998, Jones and others 2000). To effectively conserve and manage resident stream species we must expand the scale of our understanding of spatial dynamics in stream systems to match that of perturbations experienced by these systems.

Improving understanding of landscape-scale spatial dynamics in stream systems requires significant theoretical and methodological advances. Existing theory on landscape-scale spatial population processes does not address implications of the linear and hierarchical habitat structure of stream systems (Strahler 1964), nor of

associated flow-mediated dispersal rates (Palmer and others 1996, Fonseca 1999, Skalski and Gilliam 2000). Likewise, delineation of habitat patches appropriate to the scale of management and quantification of inter-patch dispersal rates require modification of current sampling approaches (Hankin 1984, Frissell and others 1986, Pringle and others 1988, Moilanen 1999, Hanski and others 2000).

The objective of this study was to generate initial predictions of how landscape-scale spatial dynamics may mediate species response to perturbation in stream systems. I used simulation models to meet this objective. I defined the landscape as a headwater drainage composed of first, second and third-order streams (Strahler 1964, Vannote and others 1980). I defined a patch as a continuous stream segment between upstream origin and downstream confluence, in the case of first-order patches, or between upstream and downstream confluences. Where possible, model parameters were derived from my research on *Gyrinophilus porphyriticus* (Plethodontidae), a large salamander (11–21 cm total length) restricted to headwater streams of the eastern United States (Petranka 1998, Lowe and Bolger 2002). I have shown timber harvest to be an important perturbation to *G. porphyriticus* populations. Along with few other empirical studies in stream systems (Gagen and others 1998, Dunham and Rieman 1999, Labbe and Fausch 2000, Gilliam and Fraser 2001), this research has also explicitly assessed landscape-scale spatial population dynamics.

**KEY WORDS:** Spatial population dynamics; Landscape ecology; Stream; Dispersal; Extinction; Colonization; Metapopulation

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I investigated patch extinction probability under the influence of four sets of factors known or suspected to affect drainage-scale species response to perturbation: (1) species distribution and perturbation extent (Hanski and others 1996, Harding and others 1998, Welsh and Ollivier 1998), (2) longitudinal abundance and overland dispersal rate (Gadgil 1971, Dougherty and Sheldon 1982, Palmer and others 1996, Ferguson 2000), (3) perturbation decay rate and time delay between perturbation events (Flecker and Feifarek 1994, Ward 1998, McCabe and Gotelli 2000), and (4) covariance, variance and spatial correlation pattern of stochastic effects on patch colonization and extinction probabilities (Gyllenberg and Hanski 1997, Palmqvist and Lundberg 1998, Hiebeler 2000). I selected these factors based on their amenability to empirical evaluation in the field, likely sensitivity to management decisions, and general applicability to resident stream organisms.

## Methods

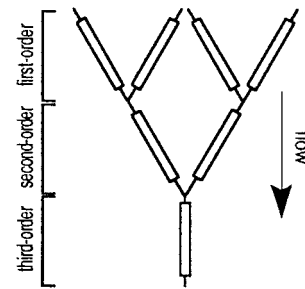
I derived the mathematical elements for a model of landscape-scale spatial population dynamics in headwater drainages by modifying the incidence function metapopulation model (Hanski 1991). By explicitly incorporating the spatial arrangement of patches and variability in local abundance, the incidence function model provides an effective tool for assessing the role of spatial dynamics in perturbed systems.

### Species Distribution

I varied the number of initially occupied first-order patches to generate a range of species distributions within the drainage. Occupancy was randomly assigned to four possible positions within a template of four first-order patches, two second-order patches and one third-order patch arranged in a strict hierarchy (Strahler 1964) (Figure 1). To match observed patterns of *G. porphyriticus* distribution, all patches downstream of initially occupied first-order patches were also initially occupied. All initially occupied patches were open to post-extinction recolonization. Initially unoccupied patches were not open to future colonization. This methodology reflects the assumption that initial species distribution represented a stable state where all suitable patches were occupied.

### Local Abundance

Expected local abundance of patch  $i$  ( $A_i$ ) was calculated in each time step (i.e. year) of model iteration. I incorporated three factors known to influence the local abundance of *G. porphyriticus* in this calculation:



**Figure 1.** Schematic representation of the spatial and hierarchical structure of stream-patches (open rectangles) within a focal drainage used to simulate spatial population dynamics in *Gyrinophilus porphyriticus*.

stream order, the presence of predatory brook trout and the occurrence and timing of perturbation (i.e. timber harvest). I assumed the area of all stream-patches to be constant.

I used the following equation, modified from Moilanen and others (1998), to calculate  $A_i$ :

$$A_i = \exp(-\delta[o_i - 1])(1 - f_i \epsilon_F)(1 - h_i \epsilon_H \exp[-\tau t])a. \quad (1)$$

The parameter  $a$  represents the maximum abundance of the focal species within the stream continuum (e.g. abundance in first-order patches for a headwater specialist such as *G. porphyriticus*). In these simulations  $a$  was set at 100 (Table 1), a value derived from survey and mark-recapture data from fishless first-order streams not exposed to timber harvest for over 30 years. The parameter  $\delta$  scales  $a$  to the order ( $o$ ) of patch  $i$ . I derived the value of  $\delta$  (3) by fitting an exponential function to relative abundance values from surveys of first through third-order streams throughout the northeastern United States (Lowe unpublished data).

The variables  $f_i$  and  $h_i$  describe the incidence of fish and perturbation in patch  $i$ ; 0 when absent, 1 when present. Fish occupancy was assigned to first-order patches at year 0 based on a probability of 0.5 (Lowe and Bolger 2002). Perturbation was randomly and independently assigned to a defined number of occupied first-order patches. This number effectively represents the spatial extent of perturbation in the drainage. The parameter  $\epsilon_F$  is the proportional reduction in  $a$  when fish are present (i.e.  $f_i = 1$ ). The parameter  $\epsilon_H$  is the proportional reduction in  $a$  when perturbation occurs (i.e.  $h_i = 1$ ). The parameter  $\tau$  scales  $\epsilon_H$  to the number of years elapsed since perturbation occurred ( $t$ ), thereby assuming locally driven recovery by the resident population. I refer to  $\tau$  as the perturbation decay rate. Values of  $\epsilon_F$ ,  $\epsilon_H$  and  $\tau$  used in simulations (0.63,

Table 1. Values and descriptions of model parameters

Parameter	Value <sup>a</sup>	Description
$a$	100	Maximum local abundance
$\alpha_1$	0.14	Rate of upstream dispersal
$\alpha_2$	0.07	Rate of downstream dispersal
$\alpha_3$	0.05	Rate of in-stream dispersal between same-order streams
$\alpha_4$	0.02	Rate of overland dispersal between same-order streams
$\delta$	3	Sets relationship between patch order and local abundance
$e$	10	Derived from minimum local abundance where $E_i = 1^b$
$\epsilon_F$	0.63	Effect of fish on local abundance
$\epsilon_H$	0.81	Effect of perturbation on local abundance
$\tau$	0.06	Rate of $\epsilon_H$ reduction over time
$x$	1	Sets relationship between local abundance and extinction risk
$y$	1	Controls patch turnover rate
$\sigma_{st}^2$	0.02	Variance of stochastic effects on $C_i$ and $E_i^b$

<sup>a</sup>These values were used in simulations unless otherwise indicated.

<sup>b</sup> $C_i$  and  $E_i$  are extinction and colonization probabilities.

0.81, and 0.06, respectively) were estimated with regression and partial regression analyses of survey data on *G. porphyriticus* abundances in first-order streams throughout the northeastern United States (Lowe and Bolger 2002).

Because I did not have adequate survey data to independently assess the effects of fish and timber harvest in higher-order streams, I chose not to apply these effects to second and third-order patches. However, it is likely that these factors contributed to the estimated value of  $\delta$ .

#### Connectivity

Connectivity ( $S$ ) is the inverse of patch isolation, describing the relationship between the spatial and demographic structure of a metapopulation and the immigration dynamics to an individual patch (Hanski 1998). In calculating patch connectivity, I made the following assumptions: (1) that yearly dispersal is restricted to patches adjacent to one another by either in-stream or overland pathways, and (2) that distance between adjacent patches by either in-stream or overland pathways is constant.

I used the following equation to calculate the connectivity of patch  $i$ :

$$S_i = \sum_j p_j A_j \left( \sum_{r=1}^4 [\alpha_r n_r] \right), \quad (2)$$

where  $j$  represents the set of donor patches, those adjacent to patch  $i$  by either in-stream or overland

dispersal pathways. The variable  $p$  represents species incidence in a patch:  $p$  equals 1 when the species is present and 0 when the species is absent. Dispersal routes between patch  $j$  and  $i$  are specified by  $r$ -values. These routes are defined by both pathway (i.e. in-stream and overland) and, for in-stream pathways, direction of movement relative to the direction of flow (Table 1).

The  $\alpha_r$ -parameters represent density-independent, route-specific dispersal rates between  $j$  and  $i$ : the proportion of  $A_j$  dispersing from patch  $j$  to  $i$  via a given dispersal route in one year. Values of  $\alpha_1$  and  $\alpha_2$  were estimated from data on *G. porphyriticus* movement in a fishless first-order stream not exposed to timber harvest activities for over 50 years (Lowe unpublished data). Values of  $\alpha_3$  and  $\alpha_4$  were estimated based on the assumption that dispersal rates between same-order patches would be lower than rates between longitudinally-arranged patches due to the complexity of movement required. I assumed that physiological factors would reduce overland dispersal rate relative to in-stream dispersal rate between same-order patches. The variable  $n_r$  represents the incidence of a specific dispersal route between  $j$  and  $i$ : 0 when that route is absent, 1 when it is present.

#### Colonization and Extinction Probabilities

I used the following equation to calculate the yearly probability of patch colonization:

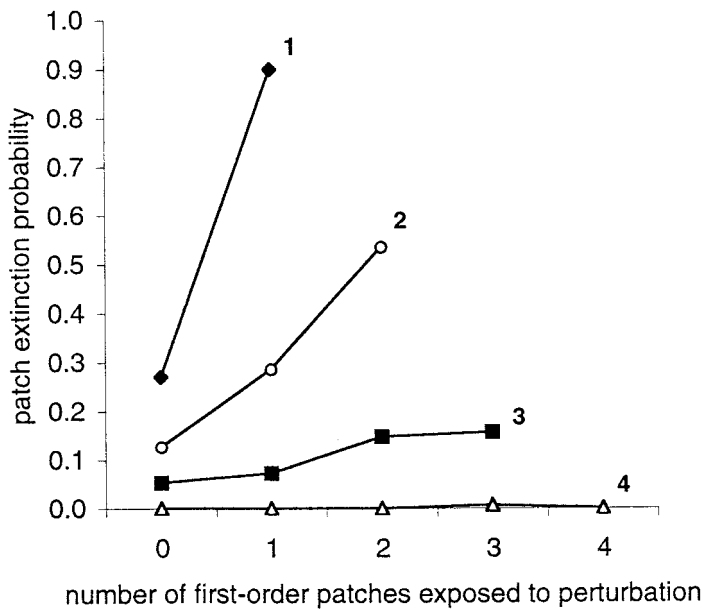
$$C_i = S_i^2 / (S_i^2 + y^2). \quad (3)$$

The parameter  $y$  controls patch turnover rate by limiting the effect of connectivity ( $S_i$ ) on colonization probability (Moilanen and others 1998). For simplicity, this parameter was set at 1 in all simulations.

I used the following equation to calculate the probability of patch extinction:

$$E_i = (1 - C_i)e / A_i^x. \quad (4)$$

The parameter  $x$  scales  $A$  to a specific functional relationship between extinction probability and local abundance. I set  $x$  at 1 for these simulations, thereby assuming extinction to be a simple declining exponential function of local abundance. The parameter  $e$  is derived from  $A_0$ , the minimum local abundance for which yearly extinction probability is 1, by the equation  $e = A_0$ .  $A_0$  was set at 10 for these simulations. My survey and mark-recapture data indicate that this is a conservative estimate of the minimum number of *G. porphyriticus* individuals present in occupied first-order streams. This calculation of extinction probability includes a rescue effect, or decrease in extinction probability due to immigration. Inherent in this method of modeling a res-



**Figure 2.** Model predictions for the relationship between patch extinction probability, the extent of species distribution (number of initially occupied first-order patches, in **bold**) and the extent of perturbation in a simulated headwater drainage. Species occupancy was assigned to higher-order patches downstream of initially occupied first-order patches. Perturbation was assigned to the specified number of initially occupied first-order patches at year 0.

cue effect is the assumption that the negative effect of emigration on large populations is smaller than the positive effect of immigration on small populations (Moilanen and others 1998).

#### Iteration and Analysis

I calculated the yearly colonization probability ( $C_i$ ) for each patch based on the patch occupancy pattern from the previous year. Next, I calculated the extinction probability ( $E_i$ ) for each occupied patch. Actual colonizations and extinctions were then adjusted for stochastic effects by multiplying  $C_i$  and  $E_i$  values by random values drawn from a normal distribution with a mean of 1 and defined variance ( $\sigma_{st}^2$ ; Moilanen and others 1998).

In simulations addressing the role of stochastic effects in species response to perturbation, I varied the magnitude of  $\sigma_{st}^2$  and the occurrence (covariance versus no covariance) and directionality (positive versus negative covariance) of covariance of stochastic effects on  $C_i$  and  $E_i$  values. I also varied spatial autocorrelation of stochastic effects by deriving either a single value for all patches or independent values for each patch. Otherwise, stochastic effects on  $C_i$  and  $E_i$  values were assumed to be independent (i.e. no covariance) and to be spatially autocorrelated. Baseline variance in stochastic effects ( $\sigma_{st}^2$ ) was set at 0.02 (Table 1), thus incorporating these effects but preventing them from obscuring patterns caused by variation in focal parameters.

I used the mean proportion of initially occupied patches extinct at year 25 of model iteration as the

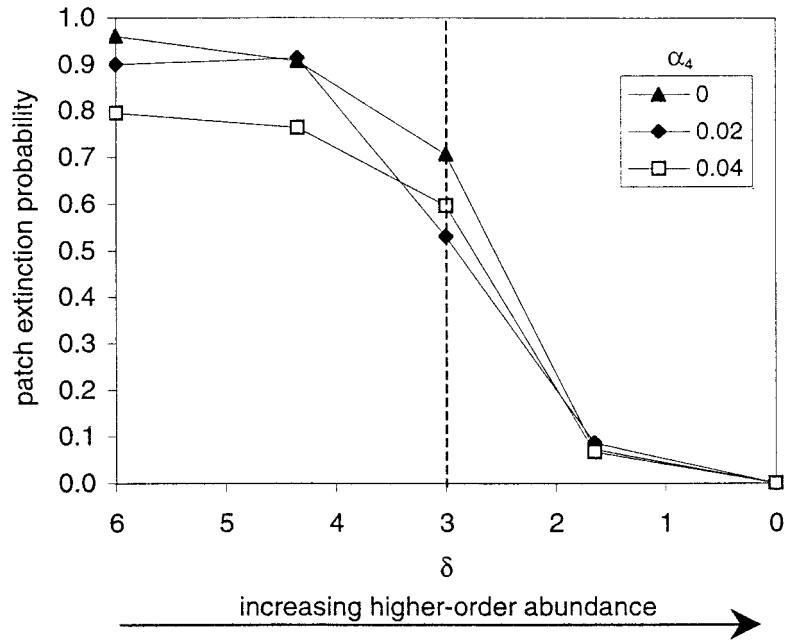
response variable in assessing simulation results. I refer to this variable as patch extinction probability. Individual extinction probabilities were based on 100 replicate model runs. I chose to evaluate simulation results at year 25 because I considered this to be a temporal scale relevant to land management decisions. Patch occupancy stabilized by year 25 across the range of parameter values.

#### Results

The extent of species distribution and the extent of perturbation interact to determine patch extinction probability (Figure 2). For example, applying a perturbation to two patches in a drainage composed of four initially occupied first-order patches versus a drainage composed of two initially occupied first-order patches increases predicted extinction probability from 0 to 0.54. Extinction probabilities greater than 0.2 are limited to drainages of only one or two initially occupied first-order patches.

Abundance in higher-order patches may have a significant influence on patch extinction probability (Figure 3). Under estimated dispersal rates, an increase in abundance in second-order patches from 1 to 5 ( $\delta = 4.5$  and 3.0, respectively) reduces extinction probability from 0.91 to 0.53. Further increases in higher-order abundance also result in marked declines in extinction probability. Overland dispersal has the strongest effect on extinction probability when longitudinal range is restricted (i.e. at high  $\delta$ -values).

**Figure 3.** Model predictions for the relationship between patch extinction probability, longitudinal abundance pattern, and overland dispersal rate ( $\alpha_4$ ). Species abundance in higher-order patches decreases with increasing values of  $\delta$ . The vertical dashed line represents the estimated  $\delta$  value of 3. The estimated  $\alpha_4$  value of 0.02 is represented by the closed diamonds. Species occupancy was initially assigned to two first-order patches and higher-order patches downstream. Perturbation was assigned to initially occupied first-order patches at year 0.

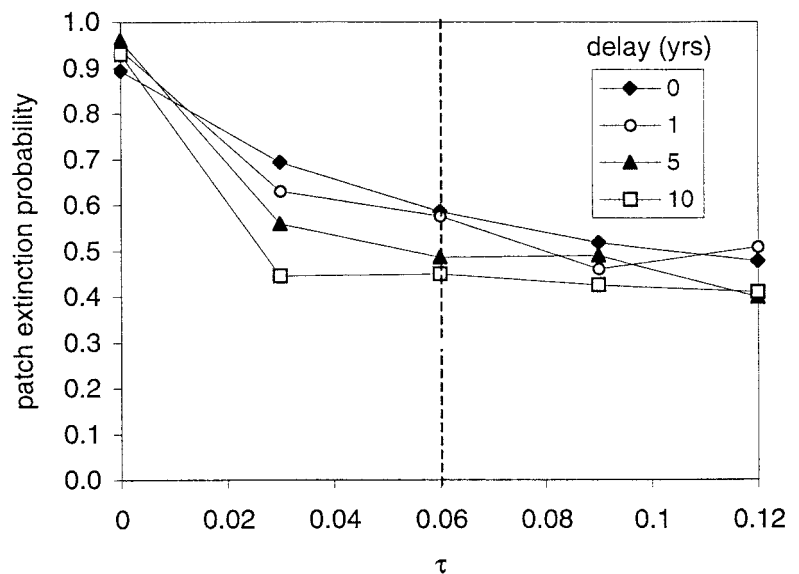


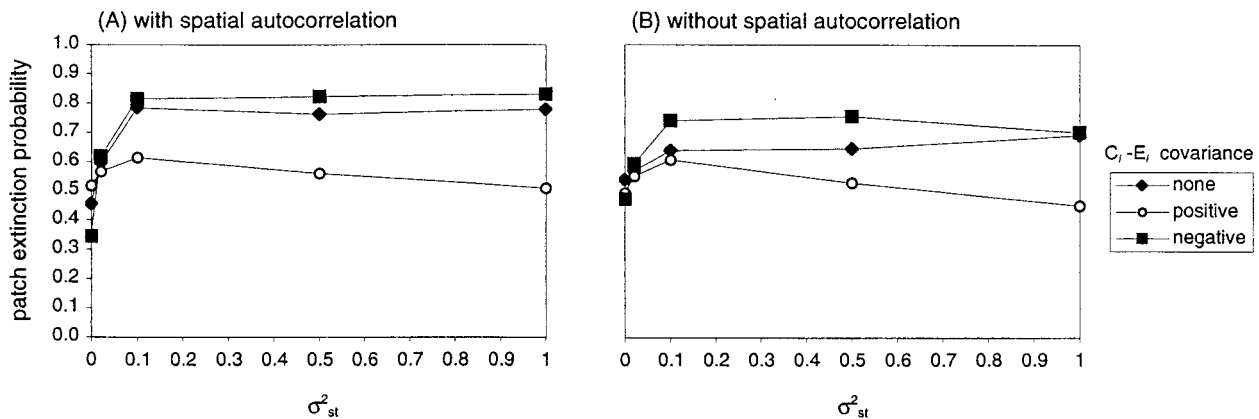
Modest reductions over time in perturbation impact may have a strong effect on extinction probability (Figure 4). For example, with no delay, increasing the decay rate from  $\tau = 0$  to 0.06, corresponding to  $\epsilon_H$  at year 10 of 0.81 versus 0.44, reduces extinction probability from 0.89 to 0.59. Increasing the time between perturbation events tends to decrease patch extinction probability at low  $\tau$ -values.

Figure 5 illustrates the relationship between extinction probability and the covariance pattern of stochastic effects on  $C_i$  and  $E_i$  values. With spatial autocorre-

lation of stochastic effects, no covariance and negative covariance result in higher extinction probabilities than positive covariance at most values of  $\sigma_{st}^2$ . For example, at  $\sigma_{st}^2 = 0.1$ , extinction probabilities without covariance, with negative covariance and with positive covariance are 0.78, 0.81, and 0.61, respectively. The value of  $\sigma_{st}^2$  has a strong effect on extinction probability below a value of 0.1, particularly with no covariance and negative covariance of stochastic effects. Removal of spatial autocorrelation dampened this effect of  $\sigma_{st}^2$ -magnitude and resulted in reductions of extinction

**Figure 4.** Model predictions for the relationship between patch extinction probability, perturbation decay rate ( $\tau$ ), and the time delay between perturbation events. The estimated  $\tau$ -value of 0.06 is represented by the vertical dashed line. Species occupancy was initially assigned to two first-order patches and higher-order patches downstream. Perturbation was assigned to one initially occupied first-order patch at year 0 and to the second after the specified delay.





**Figure 5.** Model predictions for the relationship between patch extinction probability, variance of stochastic effects on colonization and extinction probabilities ( $\sigma_{st}^2$ ), covariance of stochastic effects on colonization and extinction probabilities, and drainage-scale spatial autocorrelation of these effects (panels A and B). Species occupancy was initially assigned to two first-order patches and higher-order patches downstream. Perturbation was assigned to initially occupied first-order patches at year 0.

probabilities under no-covariance and negative-covariance scenarios.

## Discussion

Perturbation in drainages composed of one or two initially occupied first-order streams led to considerably higher extinction probabilities than in drainages composed of more than two occupied first-order streams. Although these results suggest that drainage-scale effects on resident species may be minimized by centering harmful activities in drainages with high densities of occupied streams, this strategy is subject to several important qualifications. The resistance to perturbation exhibited by extensively occupied drainages in these simulations is contingent on the occurrence of inter-patch dispersal. Without proof of dispersal among streams and assurance that activities will not reduce inter-stream dispersal rates, this strategy is clearly a risk. The value of this strategy also depends on the response variable of interest. Patch extinction probability is an accurate indicator of drainage-scale response to perturbation. However, it obscures the absolute number of predicted patch extinctions. As variance in the extent of occupancy of focal drainages increases, the strategy above may maximize drainage-scale resistance without minimizing the absolute number of patch extinctions. Which of these two response measures is most relevant will depend on the spatial and temporal scope of conservation goals. Finally, the productivity and stability of drainages with high densities of occupied streams may be the best reason to minimize their exposure to human impacts. These high-density drainages may be

sources of colonists to other drainages and critical refugia for stream species during periods of large-scale habitat alteration (e.g., climate change).

Simulation results suggest that longitudinal patterns of species distribution and abundance (Dunn 1928, Wiggins and Mackay 1978, Osborne and Wiley 1992, Winemiller and Leslie 1992) may be important predictors of drainage-scale response to perturbation. These results indicate that species with restricted longitudinal ranges may experience increased extinction probabilities when exposed to perturbation relative to those maintaining even low local abundances across multiple stream orders. This prediction is based partially on a fundamental pattern of drainage configuration whereby an individual stream is always longitudinally contiguous with streams of higher and/or lower order, but not guaranteed to be adjacent to a stream of the same order. These findings reinforce the need to minimize impacts on headwater specialists such as *G. porphyriticus*. Headwater specialist taxa that are not capable of overland dispersal (e.g., fish) may be especially vulnerable to local extinction. For those species that are capable of overland dispersal, preserving overland dispersal routes should be a priority where impacts are inevitable. This may be achieved by maintaining corridors of intact terrestrial habitat between streams.

The post-perturbation response of key habitat conditions, those controlling local demographic rates, and spatial dynamics may interact to affect species resistance to perturbation at the drainage scale. *G. porphyriticus* abundance in isolated streams increases as fine sediments introduced at the time of timber harvest are subsequently flushed downstream (Lowe and Bolger

2002). Post-perturbation dynamics of stream sediment, coarse woody debris, and canopy cover may drive the local recovery of other species as well (Murphy and others 1981, Hawkins and others 1983, Ryan 1991, Fausch and Northcote 1992, Reeves and others 1993, Welsh and Ollivier 1998, Hauer and others 1999, Nislow and others 1999), and may be predictable using current information (Reid and Dunne 1984, Garman and Moring 1991, Montgomery and Buffington 1997, Mitchell 1999, Bragg 2000, Johnson and Jones 2000). By restricting potentially harmful activities to drainages where predicted habitat recovery rates are high or by modifying activities to increase recovery rates of key habitat attributes, managers may greatly increase the drainage-scale resistance to perturbation of resident species. In systems where the decay rate of perturbation impacts is low, a time delay between activities may also increase drainage-scale species resistance.

Fluctuations in water discharge may be an important source of stochastic effects on colonization and extinction probabilities in streams (Chapman and Kramer 1991, Flecker and Feifarek 1994, Feminella 1996, Kupferberg 1996, Labbe and Fausch 2000). Perturbation acting to uncouple these effects may significantly increase extinction probabilities in managed drainages. Modest increases in the variance of stochastic effects on colonization and extinction probabilities may also increase extinction probabilities in systems where these effects currently exhibit low variance. Species occurring in systems where stochastic effects currently display high variance may be unaffected by further increases in the variance of these effects. The overall reduction in extinction probabilities with removal of spatial autocorrelation of stochastic effects agrees with other theoretical and empirical investigations (Palmqvist and Lundberg 1998, Koenig 1999).

Accounting for landscape-scale spatial dynamics may significantly improve predictive models of the response of stream species to habitat perturbation (Fausch and others 1988, Harding and others 1998, Ward 1998). Likewise, efforts to conserve and manage stream species may be made more effective by adjusting the extent, location, and practice of human activities to capitalize on the mitigating effects of these dynamics. Results of this study underscore the importance of identifying and preserving source populations and dispersal routes for stream species in human-impacted landscapes. They also highlight the vulnerability of headwater specialist taxa to anthropogenic perturbation, and illustrate the positive synergistic effect that maintaining recolonization capacity and rehabilitating local habitat can have on the resilience of stream species to perturbation. I hope that this study will lead to further refine-

ment of our understanding of landscape-scale spatial population dynamics in stream systems.

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