

Metapopulation persistence and species spread in river networks

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Abstract

River networks define ecological corridors characterized by unidirectional stream-flow, which may impose downstream drift to aquatic organisms or affect their movement. Animals and plants manage to persist in riverine ecosystems, though, which in fact harbor high biological diversity. Here we study metapopulation persistence in river networks analyzing stage-structured populations that exploit different dispersal pathways, both along-stream and overland. Using stability analysis we derive a novel criterion for metapopulation persistence in arbitrarily complex landscapes described as spatial networks. We show how dendritic geometry and overland dispersal can promote population persistence, and that their synergism provides an explanation for the so-called ‘drift paradox’. We also study the geography of the initial spread of a species and place it in the context of biological invasions. Applications concerning the persistence of stream salamanders in the Shenandoah river, and the spread of two invasive species in the Mississippi-Missouri are also discussed.

1 Introduction

Population persistence in riverine streams represents a long-standing issue in freshwater ecology (Speirs & Gurney, 2001; Lutscher *et al.*, 2010). These ecosystems are in fact characterized by strong unidirectional water flow, which imposes downstream drift to the movement of aquatic organisms. In the absence of mechanisms allowing for upstream colonization, the persistence of riverine populations would hardly be possible. This ‘drift paradox’ is especially relevant to non-sessile organisms with low self-propelled motion capacity, such as the larval stages typical of many freshwater species. To explain the long-term persistence of such populations several mechanisms have been proposed. As first empirically documented by Müller (1954) in Scandinavian freshwater ecosystems, many insect species compensate larval drift with upstream-directed flight of adults prior to oviposition (Müller’s colonization

26 cycle; see Müller, 1982). As an alternative explanation, Waters (1972) proposed an excess
27 production hypothesis, in which drifting organisms are supposed to be those who exceed
28 the balance of numbers at the local scale (thus implicitly assuming that drift represents an
29 extra-mortality term). Also, hydrodynamic stream heterogeneities have been shown to cause
30 organism retention in hydrodynamic in-flow refugia (e.g. Reynolds *et al.*, 1991; Lancaster &
31 Hildrew, 1993a,b).

32 The passive movement of an aquatic organism in a river system mainly results from the
33 combination of advection, as determined by the dominant uniform streamflow, and diffu-
34 sion, as determined by local streamflow heterogeneities. Active movement, occurring via
35 swimming, crawling or flying (either directly or through some dispersal vector) further in-
36 creases macroscopic diffusion – in some cases becoming the predominant source of motion.
37 These factors act within a distinctive landscape topology, usually characterized by a hier-
38 archical branching geometry endowed with universal scaling features (Rodriguez-Iturbe &
39 Rinaldo, 1997). Riverine ecosystems are in fact among the most representative examples of
40 dendritic ecological networks (Peterson *et al.*, 2013). Diffusive dispersal (Speirs & Gurney,
41 2001; Pachepsky *et al.*, 2005) and river network topology (Fagan, 2002; Campbell Grant,
42 2011) have been recently proposed as key factors for the persistence of riverine populations.
43 Topology is particularly important in constraining the dispersal of aquatic species lacking
44 life stages that can disperse overland (Fagan, 2002). This mode of dispersal has been both
45 theoretically postulated (Lutscher *et al.*, 2005) and experimentally observed (Carrara *et al.*,
46 2012) to facilitate the persistence of riverine populations. Dispersal can occur at different
47 life stages, most frequently early in the life history of aquatic organisms. As an example, in
48 a massive mark-recapture study (Campbell Grant *et al.*, 2010) of two lungless salamander
49 species in stream networks of Virginia, the newly metamorphosed (juvenile) salamanders
50 had the highest probabilities of dispersing to other stream reaches, thus being the primary
51 responsible for overland connections. While it is relatively common to find freshwater organ-

isms that begin their life cycle as motile and reach maturity as sessile (e.g. mussels), there are notable exceptions – as in the case of parasites with complex life cycles that involve intermediate hosts with low motility (e.g. snails) and final hosts with high motility (e.g. fish; see Blasco-Costa *et al.*, 2012).

Despite their importance, diffusive dispersal, landscape geometry, stage-dependent movement and exploitation of multiple dispersal pathways have not yet been analyzed together to yield a comprehensive description of the conditions leading to the persistence and spread of riverine populations. Classical approaches in fact include the analysis of reaction-advection-diffusion (Speirs & Gurney, 2001; Pachepsky *et al.*, 2005), integro-differential (Lutscher *et al.*, 2005) or integro-difference equations (Lutscher *et al.*, 2010) in simple one-dimensional (1-D) landscapes. Dendritic geometries have been considered in simulation studies of individual-based models (Fagan, 2002; Campbell Grant, 2011) and in matrix population models applied to stage-structured populations in networks of habitat patches (Goldberg *et al.*, 2010). This study is particularly interesting because it is devoted to the analysis of branching spatial structure and life history on the asymptotic growth rate of a riverine population – with clear implications for population persistence. Also, some analytical results for the persistence of a population subject to advection and diffusion on a tree graph have been provided recently by Ramirez (2012).

Here, we use stability analysis to derive a spatially explicit persistence criterion for riverine metapopulations. A technically similar approach has recently been used in an epidemiological context to determine invasion thresholds for pathogens of waterborne diseases (Gatto *et al.*, 2012, 2013). We analyze a model network for a riverine metapopulation with two developmental stages (juveniles and adults) in which individuals are allowed to move according to multiple stage-dependent dispersal pathways, typically along the hydrological network and overland. We use the criterion to study the effects of contrasting geometries and different ecohydrological conditions on metapopulation persistence. We also analyze a

78 case study pertaining the persistence of a metapopulation of stream salamanders inhabiting
79 the Shenandoah river (Virginia, US). As the conditions for metapopulation persistence in a
80 river ecosystem correspond to those for species spread, we discuss how to use our framework
81 in the context of biological invasions, for which the analysis of dispersal pathways is crucial
82 to focusing mitigation and conservation efforts. To that end, we study retrospectively two
83 recent biological invasions of a large fluvial system (namely, the spread of the zebra mussel
84 and of the Asian carp in the Mississippi-Missouri river system, MMRS).

85 2 Material and methods

86 The model

87 We consider a prototypical aquatic metapopulation living in a river network made of n
88 nodes (Fig. 1a), each of which represents a river stretch where local ecological conditions are
89 identical. We assume that the species has two ecologically distinct developmental stages, thus
90 we split the population in young (non-reproductive) individuals (Y) and adult (reproductive)
91 individuals (A). Movement from node to node can occur through different pathways, either
92 along the stream network or overland. Local demographic processes (birth, growth and
93 death) and dispersal dynamics in each node i of the river network are described by the
94 following system of $2n$ ordinary differential equations

$$\begin{aligned}
\frac{dY_i}{dt} &= -\mathcal{M}_Y(Y_i, A_i)Y_i - \gamma Y_i + \mathcal{N}(Y_i, A_i)A_i - \sum_{h=1}^{N_Y} l_h \left(Y_i - \sum_{j=1}^n P_{hji} Y_j \right) \\
\frac{dA_i}{dt} &= -\mathcal{M}_A(Y_i, A_i)A_i + \gamma Y_i - \sum_{k=1}^{N_A} m_k \left(A_i - \sum_{j=1}^n Q_{kji} A_j \right), \tag{1}
\end{aligned}$$

95 where: $\mathcal{M}_Y(Y_i, A_i)$ [$\mathcal{M}_A(Y_i, A_i)$] is the (possibly) density-dependent per-capita mortality rate
96 for juveniles [adults]; γ is the rate at which young individuals become adult ($1/\gamma$ thus being

97 the average duration of the juvenile phase); $\mathcal{N}(Y_i, A_i)$ is the (possibly) density-dependent
 98 natality rate of adults; $l_h [m_k]$ is the rate at which young [adult] organisms undergo disper-
 99 sal along to the h -th [k -th] pathway ($h = 1..N_Y$ [$k = 1..N_A$] being the number of possible
 100 dispersal mechanisms for juveniles [adults]); and $P_{hji} [Q_{kji}]$ is the fraction of young [adult] or-
 101 ganisms moving from node j to node i through the h -th [k -th] dispersal mechanism available
 102 to juveniles [adults]. We assume that the mortality [natality] rate is a monotonically increas-
 103 ing [decreasing] function of population density ($\partial\mathcal{M}_{Y,A}/\partial(Y_i, A_i) \geq 0$, $\partial\mathcal{N}/\partial(Y_i, A_i) \leq 0$ for
 104 any i), i.e. that there is no depensation or Allee effect. Note that the assumption of spatial
 105 homogeneity of the parameters can be relaxed, and that the model can also be easily ex-
 106 tended to describe populations with more complex age/stage structures. A comprehensive
 107 list of mathematical symbol is reported in Table 1.

108 **Figure 1 and Table 1 about here**

109 **Connectivity structures and dispersal mechanisms**

110 Dispersal probabilities P_{hji} and Q_{kji} depend on the connectivity structure provided by the
 111 environmental matrix and the dispersal mechanisms relevant to the metapopulation being
 112 investigated. As for connectivity, we consider three hypothetical network structures for
 113 theoretical analyses and two real river networks (the Shenandoah river and the MMRS)
 114 for more realistic case studies. The hypothetical networks considered here are a 1-D lattice
 115 (Fig. 1b), a deterministic fractal, namely a Peano construct (Fig. 1c) and a so-called Optimal
 116 Channel Network (OCN, Fig. 1d; Rodriguez-Iturbe & Rinaldo, 1997). While the lattice
 117 geometry clearly represents an oversimplification of real river networks (although widely
 118 used to study population persistence in riverine ecosystems; see e.g. Speirs & Gurney, 2001;
 119 Lutscher *et al.*, 2005), Peano's topological measures match closely those of real river networks.
 120 OCNs represent a further step forward, in that their topological and metric properties are

121 virtually undistinguishable from those of real river networks.

122 As for dispersal pathways, the first and foremost mechanism to be considered in a riverine
123 setting is along-stream aquatic dispersal, which may describe both hydrological drift and
124 active movement along river corridors (see Appendix S1 in Supporting Information). Other
125 mechanisms can be relevant to the dispersal of riverine populations as well. For instance,
126 flying or human/animal-mediated transport processes (Wilson *et al.*, 2009) could be only
127 partially constrained by river network geometry and flow direction (see e.g. Collier & Smith,
128 1998; Didham *et al.*, 2012, for empirical evidence concerning insect flight), thus potentially
129 providing aquatic organisms with suitable pathways for unbiased overland dispersal. This
130 can be described by e.g. an exponential kernel (Hanski & Ovaskainen, 2000), but other,
131 possibly *ad hoc*, mechanisms can obviously be introduced to describe dispersal in species-
132 specific case studies.

133 Dispersal probabilities are subsumed into connection matrices, namely $\mathbf{P}_h = [P_{hij}]$ and
134 $\mathbf{Q}_k = [Q_{kij}]$. We assume that $\sum_{j=1}^n P_{hij} \leq 1$ and $\sum_{j=1}^n Q_{kij} \leq 1$ for any i , h and k .
135 Specifically, row-wise sums can be less than one in the presence of absorbing boundary
136 conditions (see again Appendix S1) and/or costly dispersal (Casagrandi & Gatto, 1999),
137 which both imply the non-conservation of the abundance of dispersing organisms. Finally,
138 the union of the graphs associated with the matrices \mathbf{P}_h and \mathbf{Q}_k is assumed to be strongly
139 connected, so that it is always possible for the individuals of the focal species to find a path
140 between any two nodes of the river network via the available dispersal pathways.

141 **Derivation of persistence conditions**

142 Irrespectively of parameter values, the state \mathbf{X}_0 characterized by $Y_i = 0$ and $A_i = 0$ for
143 any i is a global extinction equilibrium for model (1). In the absence of an Allee effect,
144 metapopulation persistence is related to the stability of this equilibrium. In fact, if \mathbf{X}_0 is
145 stable the population cannot persist in any of the river network nodes. On the contrary, if

146 \mathbf{X}_0 is unstable, juvenile and adult abundances, even if initially small, are expected to grow
147 – thus granting metapopulation persistence. The condition for the extinction equilibrium
148 to switch from stable to unstable is that the Jacobian matrix \mathbf{J} of system (1) linearized
149 at \mathbf{X}_0 has one zero eigenvalue. Population persistence can thus be assessed by analyzing
150 how the eigenvalues of \mathbf{J} vary with model parameters, connectivity structures and dispersal
151 mechanisms.

152 **Spatial patterns of species spread**

153 In our framework, the condition under which a species can invade a river network corre-
154 sponds to that for metapopulation persistence. As such, if the global extinction equilibrium
155 is unstable, the dominant eigenvector of matrix \mathbf{J} pinpoints the direction in the state space
156 along which the system trajectories, after a transient period due to initial conditions, will
157 diverge from the equilibrium. Specifically, the components of the leading eigenvector cor-
158 respond to the evolving abundances of young or adult individuals in different locations of
159 the river network. The analysis of the dominant eigenvector of the Jacobian of system (1)
160 evaluated at \mathbf{X}_0 is thus key to understanding the early spatial patterns of species spread,
161 and can thus be useful – at least from a qualitative perspective – to study the geography of
162 aquatic invasions in riverine ecosystems.

163 **3 Results**

164 **A spatially explicit persistence criterion**

As detailed in Appendix S2, the stability switch of the extinction equilibrium corresponds to
the condition $\det(\mathbf{I}_n - \mathbf{J}^*) = 0$, where \mathbf{J}^* is a matrix of size n , deducible from the $2n$ -sized

Jacobian \mathbf{J} of (1), defined as

$$\begin{aligned} \mathbf{J}^* = & R_0 \mathbf{I}_n + \frac{1}{\mu_Y + \gamma} \sum_{h=1}^{N_Y} l_h (\mathbf{P}_h^T - \mathbf{I}_n) + \frac{1}{\mu_A} \sum_{k=1}^{N_A} m_k (\mathbf{Q}_k^T - \mathbf{I}_n) + \\ & - \frac{1}{\mu_A(\mu_Y + \gamma)} \sum_{h=1}^{N_Y} l_h (\mathbf{P}_h^T - \mathbf{I}_n) \sum_{k=1}^{N_A} m_k (\mathbf{Q}_k^T - \mathbf{I}_n) . \end{aligned} \quad (2)$$

165 In the previous expression, $R_0 = \nu\gamma/\mu_A/(\mu_Y + \gamma)$ is the quantity controlling population
 166 persistence in a non-spatial setting and can be interpreted as the average number of daughters
 167 successfully reaching maturity generated by one mother during her entire lifetime. The
 168 condition for an isolated population to persist is thus $R_0 > 1$. In the presence of dispersal,
 169 instead, metapopulation persistence is determined by the dominant eigenvalue $\lambda_{max}(\mathbf{J}^*)$.
 170 Specifically, the persistence-extinction boundary (i.e. the curve or surface in the system
 171 parameter space that separates parameter combinations corresponding to metapopulation
 172 extinction from those corresponding to persistence; Casagrandi & Gatto, 1999) is given by
 173 the condition

$$E_0 = \lambda_{max}(\mathbf{J}^*) > 1 . \quad (3)$$

174 In other words, the occasional introduction of some individuals in some network nodes results
 175 in a successful colonization if (and only if) $E_0 > 1$. In this case, the assumption of strong
 176 connectivity made above implies that persistence is granted in all the network nodes.

177 Criterion (3), shows that not only local demographic processes (first term in the right-
 178 hand side of eq. (2)), but also average net immigration from connected sites (second and
 179 third terms) is relevant to the persistence of riverine metapopulations. It also shows that the
 180 intertwining between different dispersal pathways may have nontrivial effects on metapop-
 181 ulation persistence or extinction (last term in the right-hand side of eq. (2)). As a matter
 182 of fact, the persistence condition is based on the dominant eigenvalue of \mathbf{J}^* , which is not
 183 simply deducible from R_0 and the eigenvalues of matrices \mathbf{P}_h and \mathbf{Q}_k . Note that, close to the

184 persistence-extinction boundary, E_0 also sets a timescale for metapopulation dynamics and,
185 in particular, for metapopulation extinction (see again Appendix S2). Criterion (3) can be
186 extended to account for spatial heterogeneities in the model parameters whenever relevant
187 for the underlying ecological processes (Appendix S3).

188 **The role of network structure and dispersal pathways**

189 As a basic test case to study persistence in a river network, we have analyzed a population in
190 which adults are sessile and juveniles are subject to drift/operate along-stream dispersal ($l_1 >$
191 0 , $l_h = 0$ for any $h > 1$, $m_k = 0$ for any k , $\mathbf{P}_1 = \mathbf{F}$, with \mathbf{F} being the hydrological connection
192 matrix; see Appendix S1). Fig. 2a (gray lines) shows that high values of along-stream
193 dispersal and bias are always detrimental to species persistence, and that network topology
194 remarkably influences the fate of the metapopulation. Specifically, more complex networks
195 (Peano, OCN) favor metapopulation persistence compared to simpler geometries (lattice)
196 with the same backbone length. Quite interestingly, the largest relative differences emerging
197 from the three contrasting topologies are found for high dispersal rates and low values of
198 the transport bias. In these conditions, along-stream movement is significantly influenced
199 by geomorphological dispersion, i.e. by the intertwining of hydrodynamic dispersion within
200 individual reaches and the morphology of the network structure (Rinaldo *et al.*, 1991).

201

Figure 2 about here

202 Changes in the flow regime can obviously affect the persistence of metapopulation dispers-
203 ing through water pathways. Fig. 2b (gray lines) shows that the metapopulations that cannot
204 compensate higher bias of aquatic dispersal with higher natality are doomed to extinction
205 – i.e. that downstream drift reduces metapopulation capacity (*sensu* Hanski & Ovaskainen,
206 2002). Close to the persistence-extinction boundary the dynamics of the metapopulation
207 is very slow, because $E_0 \approx 1$ (and $\lambda_{max}(\mathbf{J}) \approx 0$). Therefore, extinctions may occur over

208 long (yet still ecological) timescales depending on the distance from the bifurcation curve
209 characterized by $E_0 = 1$. This delay generates an extinction debt (*sensu* Tilman *et al.*,
210 1994). As an example, the model predicts extinction for all the parameter settings lying
211 below the persistence-extinction boundaries in Fig. 2b – yet in the light-gray-shaded regions
212 metapopulation extinction will take more than 10 years, approximately corresponding to
213 10 generation times for the population under study (see again Appendix S2).

214 To analyze how different dispersal pathways can influence metapopulation persistence,
215 we have studied populations in which juveniles disperse not only along the hydrological
216 network but also overland ($l_1 > 0$, $l_2 > 0$, $l_h = 0$ for any $h > 2$, $m_k = 0$ for any k ,
217 $\mathbf{P}_1 = \mathbf{F}$, $\mathbf{P}_2 = \mathbf{G}$, with \mathbf{G} being the connection matrix describing overland isotropic dispersal
218 with characteristic dispersal length D ; see Appendix S1). Figs. 2a and 2b (black lines)
219 show that overland dispersal can remarkably benefit riverine metapopulation persistence,
220 in particular for high values of the bias of along-stream dispersal. Under these conditions,
221 corresponding in fact to advection-dominated environments, overland dispersal can provide
222 riverine populations with an effective mean of upstream propagation, thus mitigating the
223 downstream drift imposed to offspring and juveniles by passive hydrological transport. These
224 results hold qualitatively for all the considered network topologies (not necessarily riverine;
225 see Appendix S4 for some examples of 2-D lattice geometries). However, it is apparent that
226 topological complexity and the multiplicity of dispersal pathways operate synergistically (last
227 term in eq. (2)), thus greatly favoring the persistence of metapopulation inhabiting complex
228 river networks (Fig. 2c). The effects of this synergism are very robust not only to changes
229 of the demographic rates, but also to variations in the exploitation of different dispersal
230 pathways in relation to specific life histories (Appendix S5).

231 One might wonder whether enhanced persistence due to the superimposition of different
232 dispersal pathways is simply due to higher overall (i.e. along-stream + overland) dispersal.
233 We have thus repeated some of the analyses above considering different dispersal strategies,

234 defined as the combination of overland and aquatic dispersal operated by a population.
235 Specifically, we assume that a fraction ϕ of the total movement rate K is allocated to overland
236 movement, while the remaining fraction $1 - \phi$ is allocated to water-mediated dispersal.
237 Fig. 2d reports a systematic exploration of the parameter space (K, ϕ) , each point of which
238 represents a different dispersal strategy, and shows that even relatively small fractions of
239 total movement rate allocated to overland dispersal are sufficient to guarantee persistence.
240 The exploitation of alternative dispersal pathways (specifically, of overland dispersal) can
241 thus remarkably affect the fate of a population subject to downstream drift in a riverine
242 ecosystem.

243 **Persistence of an amphibian metapopulation in a river system**

244 The framework presented above can be adapted to study the persistence of a real metapopu-
245 lation in a river network. As a proof of concept, here we study the fate of a metapopulation
246 of stream salamanders in the Shenandoah river network (Virginia, US; Fig. 3a). Model (1)
247 has been parameterized with demographic (Organ, 1961) and dispersal (Campbell Grant
248 *et al.*, 2010) data relative to the salamander species *Desmognathus fuscus* and *D. monticola*
249 *cola* (technical details in Appendix S6). The juveniles of these two amphibian species can
250 move both along stream corridors and overland, while larvae and adults are almost sessile.
251 Quite interestingly, juveniles' along-stream dispersal is known to be biased towards upstream
252 sites in the river network. Despite the ongoing decline of amphibian abundances worldwide,
253 populations of stream salamanders in Eastern North America are reportedly stable – an
254 observation that has been linked to their ability to exploit multiple dispersal pathways (see
255 again Campbell Grant *et al.*, 2010).

256 Our analysis shows that if the cost of dispersal (here defined as the fraction of individuals
257 that disperse outside their suitable habitat) is negligible, both along-stream (low ϵ_s) and
258 overland (low ϵ_o), then the salamander metapopulation is predicted to persist ($E_0 \gg 1$).

259 However, for increasing values of the cost of dispersal (possibly due to the alteration of the
260 habitat template), the metapopulation can cross the persistence-extinction boundary, and
261 can thus be doomed to extinction (Fig. 3b). It is also possible to test the sensitivity of E_0
262 to changes of the model parameters. Besides expected positive [negative] effects of increased
263 natality ν [mortality μ_Y and μ_A] on E_0 , increasing levels of overland dispersal l_2 can promote
264 metapopulation persistence (as suggested by Campbell Grant *et al.*, 2010), provided that the
265 cost of overland movement is lower than that of along-stream dispersal. E_0 can actually peak
266 for intermediate values of the overland dispersal rate (as in Fig. 3c), a result that mirrors the
267 intermediate dispersal principle of metapopulation ecology (e.g. Casagrandi & Gatto, 1999,
268 2006).

269 Figure 3 about here

270 **The geography of riverine biological invasions**

271 The dominant eigenvector of the linearized model nearby extinction is a synthetic spatial
272 indicator of the initial spread of a riverine population, not only in theoretical settings (as in
273 Appendix S7) but also in real applications, as it turns out by adapting model (1) to qual-
274 itatively describe two paradigmatic examples of biological invasion recorded in the MMRS
275 (Fig. 4a). Here we report the results for the first example only (the zebra mussel colonization
276 of the MMRS; technical details in Appendix S8), while the second example (the Asian carp
277 invasion of the MMRS) is discussed in Appendix S9.

278 The zebra mussel (*Dreissena polymorpha*), a freshwater bivalve native to Eurasia, invaded
279 the Great Lakes region in the late 1980's and rapidly spread across North America inland
280 waters (e.g. Strayer, 2009, see also panels b and c of Fig. 4). The main vectors of species
281 dispersal during the early phase of the invasion were hydrological transport of larvae (the
282 so-called 'veligers') and long-distance port-to-port veliger dispersal because of inland com-

283 mercial navigation (Mari *et al.*, 2011). The veligers may in fact be shipped within the ballast
284 water of commercial vessels, thus allowing the species to disperse over very long distances
285 and to colonize stretches of the river network that could not have been reached otherwise.

286 **Figure 4 about here**

287 We have parameterized model (1) to describe zebra mussel invasion dynamics (Casagrandi
288 *et al.*, 2007; Mari *et al.*, 2009, 2011), namely by considering sessile adults and a juvenile stage
289 during which veligers can undergo dispersal through hydrological transport and port-to-port
290 relocation (described by a port-to-port connectivity matrix $\mathbf{\Gamma}$ with characteristic dispersal
291 distance Δ ; see Appendix S8). The resulting value of $E_0 \gg 1$ implies that the zebra mussel
292 can persist and spread in the MMRS (as indeed observed; note that a high value of E_0
293 corresponds to a great risk of invasion). The dominant eigenvector of the linearized model
294 computed under these hypotheses turns out to be a satisfactory qualitative indicator of the
295 risk of mussel spread in the early phase of the invasion (Fig. 4d). Interestingly, the dominant
296 eigenvector of matrix \mathbf{J} correctly predicts the widespread occurrence of zebra mussel colonies
297 throughout the MMRS, not only in the Upper and Lower Mississippi, but also in the lower
298 course of the Missouri river, as well as in the Ohio river – i.e. in the rivers where most
299 of the largest MMRS commercial ports are located (see also Fig. 2a in Mari *et al.*, 2011).
300 Numerical experiments suggest that the dominant eigenvector of matrix \mathbf{J} is also rather a
301 robust descriptor of the spatial patterns of early population spread, even in the presence of
302 non-negligible uncertainty in the model parameters (see again Appendix S7).

303 **4 Discussion**

304 In this work we have proposed a novel way to determine conditions for population persistence
305 and spread in a river network. Our study has shown that metapopulation persistence is

306 determined by complex interactions between network geometry and dispersal mechanisms –
307 among which along-stream movement plays a prominent role in fluvial settings. In particular,
308 we have shown that a dendritic geometry does enhance metapopulation persistence in a river
309 network. This result echoes recent theoretical and experimental findings that have linked
310 dendritic topologies to long species persistence times and high local biodiversity (e.g. when
311 compared to 2-D landscapes; Bertuzzo *et al.*, 2011; Carrara *et al.*, 2012; Suweis *et al.*, 2012;
312 Altermatt, 2013). Our work has also formally confirmed that overland dispersal can favor
313 metapopulation persistence, especially (but not only) for species subject to hydrological
314 drift. Moreover, extra-range dispersal, i.e. the movement of organisms from the current
315 range to a new area of suitable habitat (e.g. Wilson *et al.*, 2009), is expected to influence
316 both metapopulation persistence and spatiotemporal invasion patterns, as indeed found in
317 the zebra mussel invasion of the MMRS. We can thus conclude that diffusive dispersal,
318 landscape geometry, and exploitation of multiple dispersal pathways may offer a multifaceted
319 solution of the ‘drift paradox’ for riverine populations. More in general, our work shows that
320 these ingredients are key to understanding metapopulation persistence in realistic (or even
321 real) landscapes.

322 Although derived in the context of river systems, the persistence criterion proposed in
323 this work can be adapted to populations living in different ecosystems, possibly character-
324 ized by high levels of spatial complexity. As an example, an interesting application would
325 be the analysis of 2-D lattice geometries, which would allow to address the study of per-
326 sistence conditions for terrestrial metapopulations. Preliminary explorations (Appendix S4)
327 confirm that, also in 2-D lattices, metapopulation persistence is deeply related to the con-
328 nectivity of the underlying environmental matrix, as well as to the dispersal mechanisms
329 relevant to the metapopulation. The flexibility of our tools is essentially granted by the
330 multi-layer network framework (Mari *et al.*, 2011), which generalizes previous network-based
331 approaches in metapopulation ecology (e.g. Hanski & Ovaskainen, 2000) and allows a hier-

332 archical description of the interactions between ecological and spatial dynamics at different
333 level of organizational complexity. In addition, our mathematical framework can be readily
334 applied to real case studies whenever there is sufficient information on the focal species to: i)
335 formalize a demographic model for its local-scale dynamics; ii) identify the underlying envi-
336 ronmental matrix constituting its habitat (such as river stretches in a fluvial system, patches
337 in a fragmented forest, etc.); iii) sort out its main dispersal pathways (e.g. Appendices 6,
338 8 and 9). In the absence of detailed information on the dynamics of the focal population
339 (which is often the case for endangered species), scaling relations could assist in the defini-
340 tion of its demographic parameters (Marquet *et al.*, 2005). The model can then guide the
341 analysis of persistence conditions for metapopulations living in realistic ecosystems, possibly
342 subject to habitat alterations.

343 Human activities represent a main driver for such alterations. Damming, for instance,
344 is usually cited as a primary threat to the integrity of riverine habitats (see e.g. Allan &
345 Castillo, 2007). From an ecological perspective, one of the main effects of damming (in
346 addition to changes of water quality and assemblage composition) is that of reducing along-
347 stream dispersal and migration, especially in the upstream direction. This would in turn
348 entail a highly biased hydrological dispersal. Our analysis has shown that increasing bias
349 could reduce metapopulation capacity (Hanski & Ovaskainen, 2002), i.e. it could doom to
350 extinction species that rely on aquatic dispersal and that cannot compensate higher drift
351 with higher natality. In contrast, species that can disperse overland at some specific life
352 stage are predicted to be more resilient to environmental changes, such as alterations of the
353 flow regime or habitat fragmentation. Extinction debts and average times to metapopulation
354 extinction (also known as relaxation times; see e.g. Tilman *et al.*, 1994; Hanski & Ovaskainen,
355 2002; Kuussaari *et al.*, 2009; Hylander & Ehrlén, 2013) can also be quantified through the
356 analysis of persistence-extinction boundaries.

357 The presented framework could obviously be made even more realistic in many respects.

358 In its present form, for instance, it does not account for the possible temporal variability of
359 the environmental conditions which, however, has already been proposed – along with spatial
360 heterogeneity – as an important factor for population persistence in advective environments
361 (e.g. Speirs & Gurney, 2001; Lutscher *et al.*, 2006; Lutscher & Seo, 2011). Incorporating
362 spatial heterogeneity in the model parameters is relatively straightforward and does bear
363 major changes to our derivation of persistence conditions – although the algebra required is
364 rather involved (Appendix S3). On the contrary, adding seasonal variability would demand
365 a considerably more elaborated mathematical treatment, possibly relying on Floquet (e.g.
366 Klausmeier, 2008) or Lyapunov exponents (e.g. Ferrière & Gatto, 1995). Another aspect
367 that certainly deserves future investigations is demographic stochasticity, that has already
368 been shown to play an important role for metapopulations dynamics close to the extinction
369 threshold (e.g. Casagrandi & Gatto, 1999, 2006).

370 Despite its limitations, the theoretical framework used to derive persistence conditions
371 (i.e. the stability analysis of an ordinary differential equation network model) can be applied
372 to study other ecological problems. We envisage that similar persistence criteria could in
373 fact be usefully applied to design natural reserves aimed at preserving ecologically important
374 species, as already proposed for marine protected areas (White *et al.*, 2010; Aiken & Navar-
375 rete, 2011) and fragmented landscapes (Hanski & Ovaskainen, 2000). In these cases, too,
376 metapopulation persistence can be established by properly accounting for the relevant spatial
377 interactions and studying the conditions under which the extinction equilibrium changes its
378 stability properties. Eigenvector analysis could then assist in designing spatially-calibrated
379 conservation efforts. In an even broader perspective, extending our framework to interacting
380 functional groups would allow to study persistence of aquatic metacommunities (rather than
381 metapopulations). With functional diversity being tightly related to ecosystem functioning
382 and services (Naeem *et al.*, 2012), achieving a better understanding of how we can preserve
383 it through suitably targeted actions would certainly represent a major accomplishment for

384 current conservation ecology.

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Table 1: Mathematical symbols used in the text and their definitions.

Symbol	Definition
	<u>State variables</u>
Y_i	Abundance of juveniles in node i
A_i	Abundance of adults in node i
	<u>Network geometry</u>
n	Number of nodes in the network
n_b	Number of nodes in the network backbone
L_b	Length of the network backbone
	<u>Demographic parameters</u>
\mathcal{M}_Y	Density-dependent mortality rate of juveniles
μ_Y	Mortality rate of adults at low population density
\mathcal{M}_A	Density-dependent mortality rate of adults
μ_A	Mortality rate of adults at low population density
\mathcal{N}	Density-dependent natality rate
ν	Natality rate at low population density
γ	Rate at which juveniles reach maturity
	<u>Dispersal parameters</u>
N_Y	Number of dispersal pathways available to juveniles
l_h	Dispersal rate of juveniles along the h -th pathway
\mathbf{P}_h	Connectivity matrix for the h -th juveniles' dispersal pathway
N_A	Number of dispersal pathways available to adult individuals
m_k	Dispersal rate of adults along the k -th pathway
\mathbf{Q}_k	Connectivity matrix for the k -th adults' dispersal pathway
	<u>Persistence criterion</u>
\mathbf{X}_0	Extinction equilibrium
\mathbf{I}_n	Identity matrix of size n
R_0	Reproduction number
\mathbf{J}	Jacobian matrix of size $2n$ associated with model (1) (Appendix S2)
\mathbf{J}^*	Matrix of size n deducible from \mathbf{J} (Appendix S2)
E_0	Dominant eigenvalue of matrix \mathbf{J}^* (Appendix S2)
	<u>Figure 2</u>
l_1	Juveniles' along-stream dispersal rate
\mathbf{F}	Hydrological connectivity matrix (Appendix S1)
b	Bias of along-stream dispersal (Appendix S1)
l_2	Juveniles' overland dispersal rate
\mathbf{G}	Connectivity matrix for overland dispersal (Appendix S1)
D	Average distance of the overland dispersal kernel (Appendix S1)
K	Total movement rate
ϕ	Fraction of the total movement rate allocated to overland dispersal
	<u>Case studies</u>
\mathbf{N}	Connectivity matrix for salamanders' overland dispersal (Appendix S6)
ϵ_s	Cost of salamanders' along-stream dispersal (Appendix S6)
ϵ_o	Cost of salamanders' overland dispersal (Appendix S6)
$\mathbf{\Gamma}$	Port-to-port veligers' connectivity matrix (Appendix S8)
Δ	Average distance of veligers' port-to-port dispersal (Appendix S8)

554 Figure legends

555 **Figure 1.** Schematic representation of the model metapopulation and theoretical river
556 networks used in numerical analyses. (a) A hypothetical sketch of our multi-layer network
557 model (1); hydrological connections (in the example involving juveniles only) are in light gray,
558 while overland connections (in the example adults only) are represented as dashed arrows.
559 (b–d) Different river network topologies; the backbone of each hydrological network has the
560 same number of nodes ($n_b = 33$) and the same arbitrary length ($L_b = 33$) independently of
561 topology, and is indicated by the white-filled nodes (the southmost node being the network
562 outlet).

563 **Figure 2.** Persistence conditions for populations with sessile adults and juveniles dispersing
564 via water and overland. Metapopulation persists for parameter combinations below (a)
565 [above (b–d)] the persistence-extinction boundaries ($E_0 = 1$ contour lines, gray and black
566 curves). All rates in year⁻¹. (a) Effect of aquatic dispersal parameters without (gray, $l_2 = 0$)
567 [with (black, $l_2 = 5$)] overland dispersal. (b) Effect of transport and demographic parameters
568 in an OCN without (gray) [with (black)] overland dispersal; gray-shaded areas indicate
569 extinction debts longer than 10 years. (c) Effect of overland dispersal parameters ($l_1 = 400$,
570 $b = 0.9$). (d) Effect of dispersal strategies ($l_1 = (1 - \phi)K$, $b = 0.8$, $l_2 = \phi K$, with $K = l_1 + l_2$).
571 Other parameters: $\nu = 25$, $\gamma = 1$, $\mu_A = 1$, $\mu_Y = 5$, $\mathbf{P}_1 = \mathbf{F}$, $\mathbf{P}_2 = \mathbf{G}$, $D = 0.1$, $l_h = 0$ for
572 any $h > 2$, $m_k = 0$ for any k .

573 **Figure 3.** Persistence of stream salamanders in the Shenandoah river network (Virginia,
574 US). (a) River network geometry; inset: *Desmognathus monticola* (from USGS). (b) Effect
575 of dispersal cost on population persistence. (c) Sensitivity of E_0 to variations of the model
576 parameters. Parameters: $\nu = 3.9$ juveniles adult⁻¹ year⁻¹, $\gamma = 0.25$, $\mu_Y = 0.40$, $\mu_A = 0.92$,
577 $l_1 = 1.58$, $\mathbf{P}_1 = \mathbf{F}$, $b = -0.49$, $l_2 = 1.04$, $\mathbf{P}_2 = \mathbf{N}$, $l_h = 0$ for $h > 2$, $m_k = 0$ for any k . All
578 rates in year⁻¹. See Appendix S6 for details on the parameterization of the model.

579 **Figure 4.** Zebra mussel invasion of the MMRS. (a) River network geometry and localization
580 in the conterminous USA. (b) Fraction of hydrological units (DTAs) invaded by *D. polymor-*
581 *pha* (inset, from USGS). (c) Spatial occurrence of zebra mussels during the initial phase of
582 the invasion (red in b). (d) Normalized components (adult individuals) of the dominant
583 eigenvector of \mathbf{J} . Parameters: $\nu = 10^6$ larvae adult $^{-1}$ year $^{-1}$, $\gamma = 26$, $\mu_Y = 120$, $\mu_A = 0.33$,
584 $l_1 = 180$, $\mathbf{P}_1 = \mathbf{F}$, $b = 0.8$, $l_2 = 3.6$, $\mathbf{P}_2 = \mathbf{\Gamma}$, $\Delta = 0.2$, $l_h = 0$ for $h > 2$, $m_k = 0$ for any k .
585 All rates in year $^{-1}$. Parameters have been chosen to reproduce the basic timescales of zebra
586 mussels' lifecycle (Appendix S8).

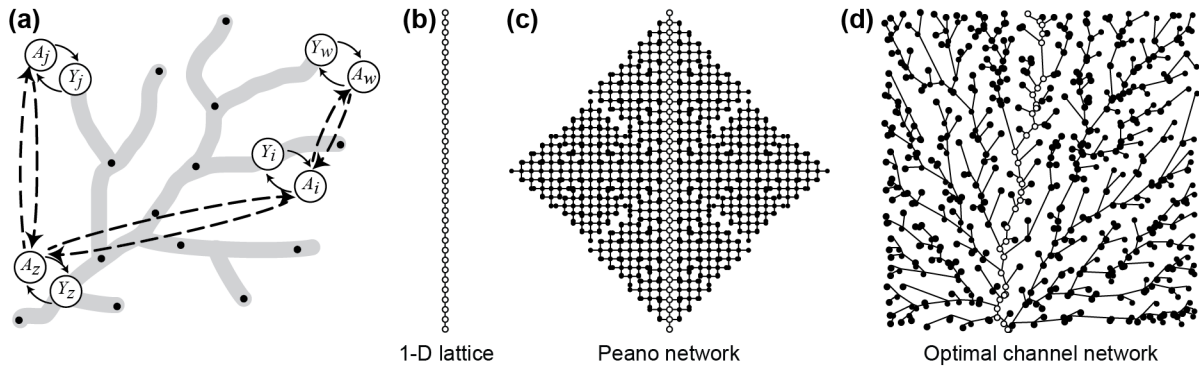


Figure 1:

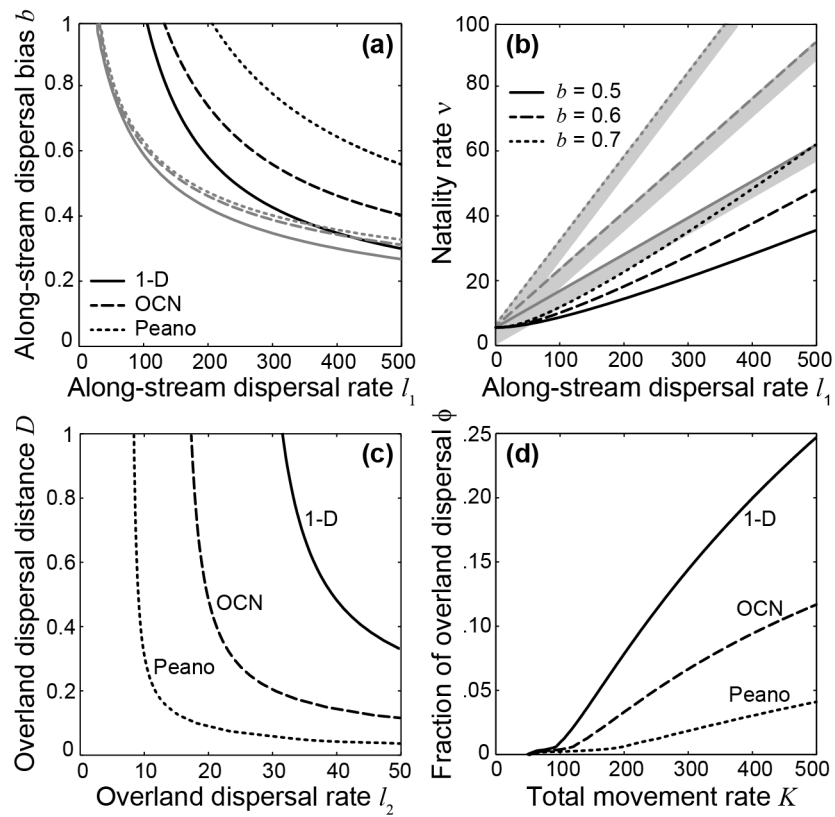


Figure 2:

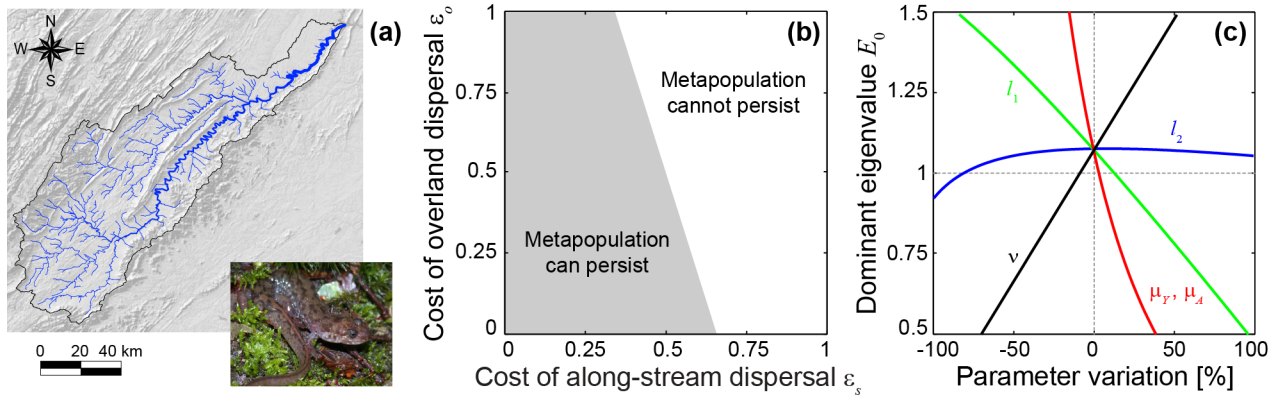


Figure 3:

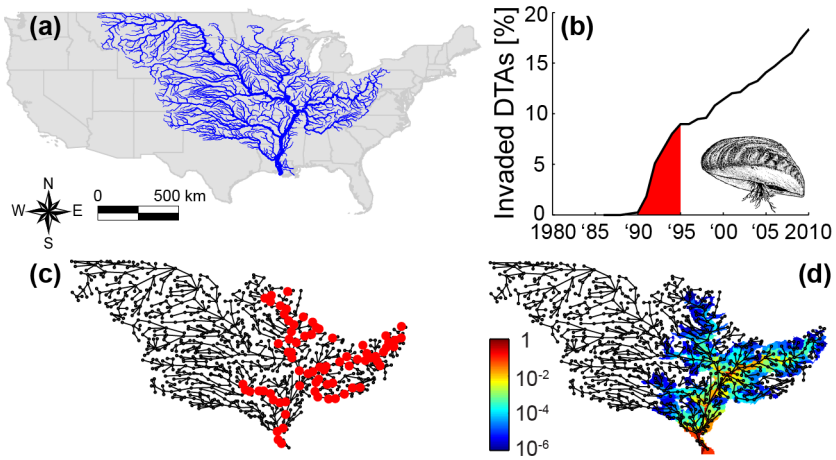


Figure 4: