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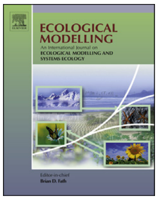

Assessing how uncertainty and stochasticity affect the dispersal of fish in river networks

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ABSTRACT

Species dispersal and population dynamics determine the spatio-temporal patterns of species spread and thus, species invasions and recolonization following habitat restorations. However, the effects of stochasticity and spatial habitat heterogeneity on species spread are poorly understood.

By coupling a fish dispersal model and a population growth model in GIS, we simulated the spread of a model fish species (*Salmo trutta*) over five years in river networks of varying habitat heterogeneity. Replicated model runs and a sampling-based sensitivity analysis allowed us to disentangle the uncertainty in the rate of spread related to (i) specific model input parameters and (ii) stochasticity inherent to the dispersal process.

Our results revealed the spread of the model species being particularly sensitive to the choice of parameters determining fish dispersal (e.g. fish size) and less to demographic parameters (e.g. reproductive rate). Moreover, the spread of fish is strongly affected by stochasticity inherent to dispersal and the availability and spatial arrangement of suitable habitats patches. Stochastic effects cause considerable variations in the predictability of up to 120% of the median dispersal distance whereof 52% is solely attributed to stochasticity inherent to dispersal decisions.

Our findings demonstrate that process-based models combining individual dispersal, population dynamics and spatial habitat heterogeneity as well as carefully selected model input parameters are crucial for reasonably simulating the spread of fishes in river networks. Moreover, we suggest considering stochasticity inherent to dispersal in models of species spread as this contributes to a considerable variation in the predictability of movement distances.

1. Introduction

Species dispersal is a key factor in ecology determining the spatio-temporal colonization patterns of habitats (Bullock et al., 2002). Current research in biological dispersal is mainly concentrated around three realms in conservation ecology: (i) the invasion of non-native species (e.g. Lockwood et al., 2007), (ii) the recolonization following habitat restoration (e.g. Albanese et al., 2009; Sundermann et al., 2011), and (iii) more recently, the movement of species to track climate-driven shifts of species' habitats (e.g. Harsch et al., 2017; Radinger et al., 2017). Invasion biological studies typically focus on how fast non-native species spread and invade new environments, whereas in restoration ecology and climate change research species dispersal is viewed as a limiting factor that delays or prevents the successful (re)colonization of restored or shifted habitats. Despite opposing views, both fields are mainly concerned about the rate of species spread, its governing factors and its realization in heterogeneous environments causing spatio-temporal variability and stochasticity.

Riverine ecosystems are considered as heterogeneous networks with typical discontinuous patterns of alternating patches of differently suitable habitats. Their spatial habitat heterogeneity is driven by global and regional factors (e.g. climate and land use) that interact with finer-scale factors like specific hydro- and geomorphological conditions, the flow regime, physical in-stream features and local hydraulics (McCluney et al., 2014; Thorp et al., 2006). The specific arrangement of suitable habitat patches provides habitat connectivity by means of dispersal, i.e. so-called stepping stones (Saura et al., 2014), and thus determines if and how fast species spread or invade new habitats (Hastings et al., 2005). It is of particular interest for fish species conservation and river management if and how environmental heterogeneity interacts with dispersal and population dynamics and thus promotes or hampers species spread. However, to which extent the spatial arrangement of suit-

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able habitat patches affects the spread of fishes in dendritic river systems is largely unknown.

In their review of models of the spread of invasive species, Hastings et al. (2005) emphasize the importance of integrating theoretical and empirical approaches and of considering spatial heterogeneity to determine underlying processes that control species' spread rates. Moreover, they suggest further improvements by including uncertainty and stochasticity inherent to natural systems and to conduct sensitivity analysis of dispersal models (Hastings et al., 2005). Therefore, we propose a sensitivity/uncertainty analysis of a coupled dispersal-population growth model for river fish based on a geographic information system (GIS). Such a modelling framework allows identifying the critical aspects of the dispersal process by simultaneously considering realistic spatial configurations of habitat patches in dendritic river networks and varying model input parameters describing dispersal patterns and demographic processes.

In addition, species dispersal is typically affected by inherent stochasticity caused by dispersal decisions made by individuals. For example, Melbourne and Hastings (2009) found that the inherent stochasticity caused by individual's decisions to move or stay caused considerable variability in the rate of population spread in flour beetles (*Tribolium castaneum*), and thus indicates fundamental limitations of the predictability of the spread of organisms. However, the extent to which stochasticity inherent to species dispersal interacts with the spatial heterogeneity of habitats and how this affects the spread of fish in river networks has not yet been studied.

Diffusion-reaction models (i.e. the Fisher-Kolmogorov equation; Fisher, 1937; Kolmogorov et al., 1937) are commonly used to describe species' spread. These mathematical models describe the propagation of traveling waves by two components, (i) a diffusion term related to the dispersal ability of a species and (ii) population growth accounting for recruitment 'along the road' (Holmes et al., 1994). While recruitment has long been studied in fisheries ecology (Ricker, 1954) and recruitment models are increasingly used for river fish (e.g. Ayllón et al., 2012; Nicola et al., 2008), the development and use of fish dispersal models is rather young. Recently, Radinger et al. (2014) introduced a fish dispersal model (FIDIMO) for river networks. Consequently, these new developments allow for coupled mechanistic models of fish dispersal and population growth, thus, following Kolmogorov et al.'s (1937) principle idea.

In this study we coupled the fish dispersal model FIDIMO with a density-dependent recruitment model while accounting for uncertainty and variability of the input parameters. We specifically aimed to analyse how uncertainty related to the parameters describing (i) fish dispersal, (ii) population growth and (iii) the configuration of suitable habitats, as well as stochasticity inherent to the model, interact and how these affect predicted dispersal distances.

We hypothesized that (i) a mechanistic, coupled dispersal-population growth model is a valuable tool to investigate species spread in dendritic river networks, (ii) species-specific dispersal abilities and spatial configuration of habitats jointly govern species spread, (iii) and dispersal is stochastically determined by varying realizations of individual dispersal probabilities.

2. Materials and methods

2.1. Coupled dispersal model

A step-wise, coupled model chain that includes fish dispersal and population growth was used to simulate species' spread from starting points within a river network (Fig. 1). The main steps comprise (i) the calculation of fish dispersal from a source population based on a probabilistic dispersal kernel, (ii) the transformation of dispersal probabilities to fish counts (realization of dispersal events) and (iii) the modelling of density-dependent population growth based on the number of specimen arriving at a cell. These three modelling steps simulating dispersal and population growth were calculated in a loop for five discrete yearly time steps ($t_0 \ldots t_5$). The output of a time step t was used as input for the subsequent time step t_{+1}. Specifications of the single modelling steps and the model parameterization are described in the following.

2.1.1. Probabilistic fish dispersal

The open source GRASS GIS (GRASS Development Team, 2012) model FIDIMO (Radinger et al., 2014) served to simulate fish dispersal in river networks. FIDIMO calculates the probability of spread for single raster grid cells of a river network based on a leptokurtic (double-Gaussian) dispersal kernel:

$$f(x) = p \times \frac{1}{\sqrt{2\pi\sigma_{stat}^2}} \times e^{-\frac{(x-\mu)^2}{2\sigma_{stat}^2}} + (1-p) \times \frac{1}{\sqrt{2\pi\sigma_{mob}^2}} \times e^{-\frac{(x-\mu)^2}{2\sigma_{mob}^2}}$$

where σ_{stat} describes the mean movement distance of the stationary component, σ_{mob} describes the mean movement distance of the mobile component and p describes the share of the stationary component of the population. For the parameterization of the dispersal kernel, FIDIMO obtains σ_{stat} and σ_{mob} from a multiple regression model on fish length L, aspect ratio of the caudal fin AR, stream order SO (stream size) and time T (Radinger and Wolter, 2014). The share of the stationary component was set to a mean value of 0.67 for cells that contained fewer individuals than the carrying capacity (cf. Table 1). To account for density dependence of dispersal, the share of the stationary component, p, decreased exponentially with increasing density in the source cell, if density exceeded the carrying capacity (for details see Appendix A in Supplementary material). To model the effect of habitat quality on dispersal (i.e. habitat attractiveness, AH) the probability of dispersal between two cells was weighted by the ratio between the habitat quality in the source cell and the target cell (for details see Appendix A in Supplementary material).

For the first initial time step at t_0 (model initialization) the most downstream cell in the model network was considered as source cell with a starting abundance of 50 individuals spreading into the upstream river network (Fig. 1).

2.1.2. Transformation of dispersal probabilities into fish counts

Population dynamic models are either based on abundance or biomass of fish populations. Thus, the dispersal probabilities have to be transformed into discrete fish counts. This was achieved by allocating the total number of fish in each source cell at time step t to the target cells at time step t_{+1} using a multinomial distribution to discretize the dispersal probability map. Specifically, we applied the multinomial distribution function (*numpy.random.multinomial)* of the software Scientific Python (Jones et al., 2001), which is implemented as a multivariate generalization of the binomial distribution. The applied function introduces model stochasticity (reflecting the inherent stochasticity of fish dispersal) by generating random counts based on the multinomial distribution and for a given dispersal probability (i.e. weighted random number). Accordingly, a greater integer number of the initially available fish was (randomly) generated and assigned to cells with higher dispersal probability (i.e. closer to the source, better habitat quality) while low-probability cells received fewer specimens.

2.1.3. Population growth model

The discrete output of the fish dispersal model is subsequently used as input for a cell-wise calculation of a population dynamic model. Specifically, we applied a discrete version of