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Effects of temperature and surface water availability on spatiotemporal dynamics of stream salamanders using pattern-oriented modelling

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ABSTRACT

Ecological models are powerful tools for generating predictions about the viability of populations of endangered species, especially in landscapes where they may be subject to complex, cross-scale disturbances. Spatially explicit, individual-based approaches are particularly promising due to their ability to simulate the effect of landscape level changes in habitat on individual-level behaviour, thus predicting possible emergent responses from the bottom up. We apply this approach to modelling the movement behaviour and the complex life cycles of two species of stream-dwelling salamanders (the Allegheny Mountain Dusky Salamander, *Desmognathus ochrophaeus*, and the Northern Spring Salamander, *Gyrinophilus porphyriticus*) in response to a spatially and temporally varying environment. Despite the poor state of ecological knowledge about these species, our model provides reasonable predictions about life cycle, as well as the density and distribution of salamanders. When tested with a dynamic, drought prone environment, the model predicts viability levels that are biologically plausible. By simulating the cross-scale interactions between organisms and their environment, individual-based models such as we have developed here provide a new tool for *in silico* investigations of the expected impacts of varying landscape scenarios and environmental changes.

1. Introduction

Over the past decade, ecological models combining individual-based approaches and landscape process-based approaches have emerged as powerful tools in conservation, management and planning (Grimm and Railsback, 2005; Stillman and Goss-Custard, 2010; McClain et al., 2012; Metcalfe et al., 2012). By considering individual variation, entire life cycles, interactions between individuals and variations in the immediate environment, a well-constructed "hybrid" model of this sort has promise for making improved predictions about the local viability of species in response to land use changes or landscape-scale environmental processes. However, this potential comes with a cost. Such models generally need extensive, precise knowledge about individual behaviour, life cycle and environmental requirements that is often not available.

To offset a lack of detailed biological knowledge, a pattern-oriented modelling (POM) approach can be used (Latombe et al., 2011; Topping et al., 2012). The underlying premise of POM is that non-random biological patterns contain information on the mechanisms from which they emerge. Patterns can thus be used to guide model design and parameterisation through a cyclic process of trial and error (Grimm and Railsback, 2005; Kramer-Schadt et al., 2007; Latombe et al., 2011). This approach is especially appealing in that a model able to reproduce a series of pre-identified biological patterns will most likely also capture the essential aspects of a species' ecology (Tyre et al., 2007) and therefore, be able to generate reliable, testable predictions about the species' local resilience as well as indicate directions for further observation or experimentation (Grimm et al., 2005).

The problem of a lack of data is especially relevant for amphibians, in general, and salamanders in particular (Petranka, 1998). Most amphibians remain poorly characterized ecologically

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yet many are threatened by intricate, cross-scale disturbances to their habitats (Wake and Vredenburg, 2008). Amphibians are ectotherms, which means that ambient temperature has significant impact on these species' physiological, metabolic and life-history traits compared to endotherms such as birds and mammals (Carey and Alexander, 2003). In addition, amphibians are dependent upon the availability of moisture and can become extremely vulnerable to changes in the water table, runoff, hydroperiod and/or discharge activity from springs (Alvo and Bonin, 2003). This is particularly true for stream-dwelling species (Davic and Welsh, 2004). The development of a pattern-oriented model may have great value in aid of amphibian conservation insofar as it may better predict, *in silico*, the persistence, population dynamics and behaviour of these animals. In this context, a pattern-oriented approach would seem relevant for developing an ecological model for stream salamanders.

We aimed to build a model that would be realistic enough to reproduce patterns of life cycle, density and distribution so as to predict the persistence of certain stream salamanders in response to dynamic biological and environmental processes in their environment. Our purpose was to answer two types of questions (1) what could be the impacts of temperature variations on salamander life cycle? and (2) what could be the impacts of water availability on individual distribution? Predictions concerning individuals are then raised to the population level in order to evaluate the impacts of alternative environmental scenarios on the local viability of the species concerned. We also desired a model that required minimal and easily accessible environmental data in order to work and that was generally configurable so that it could potentially be applicable to a variety of similar species. For this work, we selected two salamander species, the Allegheny Mountain Dusky Salamander, *Desmognathus ochrophaeus*, and the Spring Salamander, *Gyrinophilus porphyriticus* (family Plethodontidae), for which enough data were available to provide usable patterns for calibration. Though broadly sympatric, these species differ substantially in terms of life cycle characteristics and population density (Petranka, 1998). Depending on the model outputs, these species, as case studies, promised to provide good indications about the model's transferability to any of the 40+ species of surface stream-dwelling salamanders in the genera *Desmognathus*, *Gyrinophilus*, *Eurycea* and *Rhyacotriton* in North America.

2. Methods

2.1. Modelling approach

A spatially-explicit, individual-based model of stream salamander habitat occupancy and survival was developed using a pattern-oriented approach and inverse modelling (Grimm and Railsback, 2005, 2012; Kramer-Schadt et al., 2007). Based on a modelling objective, which in this case is to predict the persistence of a salamander population in response to changes in the hydrology of the streams in which they live, and cognizance of knowledge limitations such as incomplete data, the model is structured and its parameters refined until it accurately reproduces a set of empirical patterns carefully pre-selected by the modeller. Patterns are defined as any non-random behaviour of the modelled system and may include individual movement patterns, spatial distributions of individuals, or non-random population dynamics such as predator-prey cycles. The selected patterns, in addition to the modelling objective, guide the choice of model structure (i.e. which entities, processes and variables should be included in the model). Once the model structure is defined (Fig. 1), the patterns are used to select appropriate submodels for the processes represented in the model and to calibrate the parameters for these submodels (Supplementary information Figs. S1 and S2). The basic premise of pattern-oriented modelling is that if the model is able to reproduce the selected patterns, then it has likely represented the mechanisms that generate those patterns (Grimm and Railsback, 2012). The robustness of this assumption increases with the number of patterns reproduced by the model. When the model is able to simultaneously reproduce faithfully all the selected patterns, the modelling process stops.

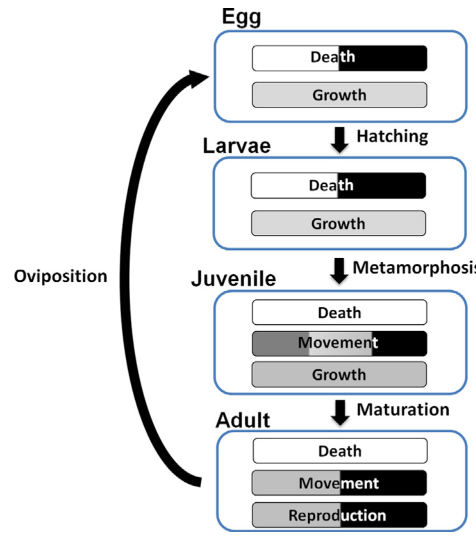

Fig. 1. Summary flowchart of the spatially-explicit, individual-based model of stream salamander populations, indicating the four distinct life cycle stages of the salamanders and their modelled biological functions. The biological functions can be random (white), influenced by water content (black), by temperature (light grey) and/or density (dark grey).

2.2. Patterns for model development

The selected patterns must reflect the modelling objective, be supported by empirical observations as strongly as possible and should be independent of site-specific conditions, database flaws or measurement artefacts (Grimm and Railsback, 2005). We identified seven patterns of life history and habitat use in *D. ochrophaeus* and *G. porphyriticus* to form the basis for constructing the model. Five of these patterns are related to the salamanders' life cycles (hereafter called the individual level patterns). The two other patterns are the density and habitat selection of individuals on the landscape (hereafter called the population level patterns) (Table 1). All seven of these patterns emerge from individual-level rules and are assessed by averaging the life-cycles and movement behaviour of all individuals in a simulation. The individual level patterns were used to parameterise a growth sub-model and life-stage transition functions (see Section 2.3). Values for these patterns to calibrate the model were taken from published observations in the literature on the two salamander species (Table 1). The two population-level patterns were used to select and calibrate movement submodels for the two species.

2.3. Model description

This model description follows the ODD (Overview, Design Concepts, Details) protocol (Grimm et al., 2006, 2010) that has been widely adopted for communicating individual and agent-based models.

2.3.1. Purpose

The explicit purpose of the model is to predict (1) the impacts of temperature variations on salamander life cycle and (2) the