Appropriate resolution in time and model structure for population viability analysis: Insights from a butterfly metapopulation

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ABSTRACT

The importance of a careful choice of the appropriate scale for studying ecological phenomena has been stressed repeatedly. However, issues of spatial scale in metapopulation dynamics received much more attention compared to temporal scale. Moreover, multiple calls were made to carefully choose the appropriate model structure for Population Viability Analysis (PVA). We assessed the effect of using coarser resolution in time and model structure on population dynamics. For this purpose, we compared outcomes of two PVA models differing in their time step: daily individual-based model (dIBM) and yearly stage-based model (ySBM), loaded with empirical data on a well-known metapopulation of the butterfly *Boloria eunomia*. Both models included the same environmental drivers of population dynamics that were previously identified as being the most important for this species. Under temperature change scenarios, both models yielded the same qualitative scenario ranking, but they quite substantially differed quantitatively with dIBM being more pessimistic in absolute viability measures. We showed that these differences stemmed from inter-individual heterogeneity in dIBM allowing for phenological shifts of individual appearance. We conclude that a finer temporal resolution and an individual-based model structure allow capturing the essential mechanisms necessary to go beyond mere PVA scenario ranking. We encourage researchers to carefully chose the temporal resolution and structure of their model aiming at (1) depicting the processes important for (meta)population dynamics of the species and (2) implementing the environmental change scenarios expected for their study system in the future, using the temporal resolution at which such changes are predicted to operate.

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1. Introduction

Ecology focuses on understanding the patterns that arise from the processes acting on multiple temporal and spatial scales (Levin, 1992). Our understanding of the process depends on the scale at which it is studied, and different inferences are made as one looks at the same phenomenon at different scales. The scale concept covers both the extent and the grain (resolution) of space and/or time (Turner et al., 1989; but some authors use a more restrictive definition, where scale equals extent, e.g. Wiens, 1989). There is no single correct scale for studying the phenomena, and it is essential to understand what information is lost or acquired as one moves from one scale to the other (Levin, 1992). In this light, multiple calls

were made to conduct both empirical and modeling experiments at several temporal and spatial scales and using varying grains (Addicott et al., 1987; Turner et al., 1989; Wiens, 1989). Yet, usually empirical ecological studies are confined to only one scale that is often smaller than the scales relevant for understanding the pattern due to practical constraints or ethical issues (Jarvis, 1995). Nevertheless, predictions on large temporal and spatial scales are a must under global human-induced alteration of the environment (Turner et al., 1989). Up-scaling is therefore often needed, but is complicated by non-linearity in the response at different scales and heterogeneity in phenomena underlying the processes (Chesson, 2009; Jarvis, 1995; Turner et al., 1989).

A scale transition theory was developed (Bergström et al., 2006; Chesson, 2009) and successfully used to up-scale demographic processes from the small scale of experiments to real-world phenomena (Bergström et al., 2006; Englund and Leonardsson, 2008; Melbourne and Chesson, 2006). It exploits a series of

analytical approximations to up-scale the processes to larger spatial (Englund and Leonardsson, 2008; Melbourne and Chesson, 2006) and temporal extents (Chesson, 2009). However, analytical solutions are not always available. For such cases usage of individual-based models (IBMs) was suggested (Levin, 1992), and successfully tested, e.g. for the spatial scale problem of the death rate in a coral reef fish (Vance et al., 2010), for scaling up animal movement behavior (Morales and Ellner, 2002) or for deriving population level consequences from individual interactions (Griebeler, 2011; Johst et al., 2008, 2013).

Metapopulation dynamics can be considered as a pattern that emerges as a result of processes that take place on a range of smaller spatial and shorter temporal scales (Levin, 1992; Wiens, 1989). The spatial aspect of metapopulation functioning received a fair share of attention as Population Viability Analysis (PVA) models evolved from patch occupancy models (Sjögren-Gulve and Hanski, 2000) and aggregated analytical formula for metapopulation lifetime (Drechsler and Johst, 2010), via structured population models (Akcakaya, 2000; Schtickzelle and Baguette, 2009), to individual-based models (Grimm and Railsback, 2005; Huston et al., 1988). The spatial resolution increased gradually along this continuum, with the grain of studies becoming finer and more details being incorporated on the landscape description and individual's movement.

However, much less attention was paid to the temporal dimension of population dynamics. Only a few empirical (e.g. Carpenter, 1989) and modeling studies (e.g. Chesson, 2009) exist, and they are mostly concerned with studying coexistence in two- or multispecies predator–prey systems. Fahrig (1992) demonstrated with a theoretical simulation model that the temporal scale might be of a higher importance to the population persistence than its spatial counterpart.

Not only the temporal aspect of metapopulation functioning was understudied, but often the need to use appropriate temporal resolution when studying heterogeneous and non-linear processes in PVA models was completely overlooked. For example, most PVAs on butterfly species belong to structured population models (Schtickzelle and Baguette, 2009) and use a yearly population growth rate to project the population size into the future. However, much finer temporal resolution, on the order of days, would seem more appropriate to describe the ecology of butterflies. Indeed, most of butterfly life stages span the period of days (typically, tens of days; Bink, 1992), and extreme environmental conditions acting on the scale of days can be highly detrimental to the survival of individuals (high temperature: Mercader and Scriber, 2008; Petersen et al., 2000; Scriber et al., 2002, submergence: Joy and Pullin, 1997; Webb and Pullin, 1998, droughts: Gibbs et al., 2012) and/or their fitness (via effect on morphology, growth and survival over later life stages: Gibbs et al., 2012; Mercader and Scriber, 2008; Petersen et al., 2000; Scriber et al., 2002). Furthermore, usually measurements are taken and observations are made on a daily scale: for example Capture-Mark-Recapture studies (e.g. Haddad et al., 2008; Schtickzelle et al., 2002) or laboratory studies on the survival of individuals in different life stages (e.g. Petersen et al., 2000; Radchuk et al., 2013b). Clark et al. (2011) suggested that analysis of data on higher scales than those at which the process operates may lead to very misleading and controversial conclusions. In this light, a bias or partial distortion in the predictions of butterfly population viability could be expected due to the discrepancy between the scales at which ecological processes governing butterfly population dynamics operate and are measured on the one hand, and are currently depicted using PVA models on the other hand.

Model structures used in PVA differ in their temporal and spatial resolution. In general, individual-based models (IBMs) tend to have a finer temporal and spatial resolution compared to more aggregated stage-based models, which, in turn, usually have finer spatial resolution compared to patch occupancy models (Akcakaya, 2000; Huston et al., 1988). The temporal and spatial scales used by such types of models are inevitably linked to different levels of biological organization: while the focus of a stage-based model is a cohort of organisms characterized by the same stage/age, an IBM is focusing on depicting unique individuals, and a patch occupancy model considers a population as the finest entity in the model. Therefore, the appropriate temporal resolution will be different for the modeled level of biological organization.

In this study, we investigated the impact of temporal resolution and the level of biological organization on the predictions delivered by a PVA model. To this end we assessed the effect of using a coarser resolution in time and model structure by comparing two PVA models developed for a well-studied species, the bog fritillary butterfly *Boloria eunomia* (Baguette et al., 2011 and references therein): an individual-based model with daily time step vs. a stage-based model with yearly time step. The processes in both models are driven by temperature and several habitat quality descriptors, since these environmental factors were shown to be important and sufficient for an efficient depiction of the studied system (Radchuk et al., 2013a). The two models were compared in terms of model fit to the observed field data, viability predictions under current environmental conditions, and viability predictions under temperature change conditions. With the model comparison under temperature change scenarios we did not aim at identifying which model made better predictions, since this would require knowing how the environment and the population will actually change in the future. Rather, we show how the different temporal resolution and model structure used in the two models led to differences in viability predictions and reveal the underlying reasons for such discrepancies.

2. Methods

2.1. Study species and system

B. eunomia is a univoltine butterfly species inhabiting peat bogs and wet meadows. It is highly specialized: *Persicaria bistorta* is at the same time its single host plant, providing larval food, and its single nectar plant, used by adults. Adults are on the wing from end of May till beginning of July. Females lay clutches of 2–20 eggs that hatch 12 days later on average (Schtickzelle, 2003). Young instar caterpillars cease their activity after approximately 20 days by entering into diapause, in which they overwinter. In the mid-April caterpillars terminate diapause, resume feeding and growth for several weeks, after which they pupate. We studied the metapopulation of the species consisting of 20 habitat patches in the Fange de Pisserotte peat bog nature reserve, located in Ardenne region of Belgium (50°13′N 5°4′E, area = 28.92 ha, Fig. 1).

2.2. Model descriptions

The purpose of the yearly stage-based model (ySBM) and the daily individual-based model (dIBM) is to investigate how temperature change will affect the population dynamics of *B. eunomia* over the next 100 years. The two models differ by two main features: ySBM considers a set of identical individuals and represents their fate on a generation (yearly) basis; dIBM considers unique individuals and represents their fate on a daily basis. We designed the dIBM with the goal of increasing the temporal resolution while keeping changes made to model structure to a minimum: the only state variable that differentiates individuals in dIBM in addition to those used in ySBM (life stage and sex) is their age. Both models were developed and documented according to the TRACE