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Behind the scenes of population viability modeling: Predicting butterfly metapopulation dynamics under climate change

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ABSTRACT

Studies explaining the choice of model structure for population viability analysis (PVA) are rare and no such study exists for butterfly species, a focal group for conservation. Here, we describe in detail the development of a model to predict population viability of a glacial relict butterfly species, *Boloria eunomia*, under climate change. We compared four alternative formulations of an individual-based model, differing in the environmental factors acting on the survival of immature life stages: temperature (only temperature impact), weather (temperature, precipitation, and sunshine), temperature and parasitism, and weather and parasitism. Following pattern-oriented modeling, four observed patterns were used to contrast these models: one qualitative (response of population size to habitat parameters) and three quantitative ones describing population dynamics during eight years (mean and variability of population size, and magnitude of the temporal autocorrelation in yearly population growth rates). The four model formulations were not equally able to depict population dynamics under current environmental conditions; the model including only temperature was selected as the most parsimonious model sufficiently well reproducing the empirical patterns. We used all four model formulations to test a range of climate change scenarios that were characterized by changes in both mean and variability of the weather variables. All models predicted adverse effects of climate change and resulted in the same ranking of mean climate change scenarios. However, models differed in their absolute values of population viability measures, underlining the need to explicitly choose the most appropriate model formulation and avoid arbitrary usage of environmental drivers in a model. We conclude that further applications of pattern-oriented modeling to butterfly and other species are likely to help in identifying the key factors impacting the viability of certain taxa, which, ultimately, will aid and speed up informed management decisions for endangered species under climate change.

1. Introduction

Ecological models have high potential to support environmental decision making, but their impact on real decisions often is limited (Schmolke et al., 2010). One main reason for this is inappropriate communication not only of the model itself (Grimm et al., 2006) but also of its underlying rationale. Unless decision makers know and understand why a certain model structure was chosen, they tend to perceive model structure as being chosen ad hoc and therefore have doubts whether the model is a good enough representation of its real counterpart. Therefore, in their recent guidelines for Good Modeling Practice, Schmolke et al. (2010) recommend that the choice of model structure should be justified, for example by documenting that alternative representations of a certain process have been tested against certain data sets or observed patterns.

Different model types are applied in conservation biology to a diverse set of purposes: e.g. statistical models to understand the impact of different factors on ecological phenomena (Turlure et al., 2010; WallisDeVries, 2004), species-distribution models to predict the future distribution of species (Elith et al., 2006; Martin et al., 2012), and population viability analysis (PVA) to develop management plans for species conservation (Ferson and Burgman, 2000). However, PVA models that provide clear and well organized

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justification of their model structure are rare (Pe'er et al., 2013). Exceptions are mostly individual-based models (IBMs), e.g. Wiegand et al. (1998), Sable and Rose (2008), Groeneveld et al. (2009) and Railsback and Johnson (2011). But to the best of our knowledge none of the PVA models developed for butterflies includes clear justification of the chosen structure. We therefore contrast four alternative IBMs that differ in their number and type of environmental factors driving population dynamics of a glacial relict butterfly by comparing their output to a set of observed patterns.

Most existing butterfly PVAs are based on matrix models using yearly population growth rate to predict future population dynamics (Schtickzelle and Baguette, 2009). Yearly population growth rate in such cases implicitly incorporates all the environmental factors acting on population dynamics, precluding the assessment of the impact that each separate environmental factor has on the population viability. Such models are therefore too aggregated to be able to disentangle the impacts of diverse environmental factors. Only a few individual-based models exist for butterfly populations (Cormont et al., 2012; Griebeler and Seitz, 2002; McIntire et al., 2007), but none of them has attempted to contrast alternative environmental drivers.

Basically, the structure of any model is defined by its purpose, which consequently determines the processes and factors to be considered (Grimm and Railsback, 2005). So, what are the key factors indispensable for modeling the dynamics of a butterfly population? Temperature was claimed a "dominant abiotic factor" affecting herbivorous insects, and, particularly, butterflies (Bale et al., 2002). Indeed, a vast realm of studies demonstrate that temperature affects multiple levels of butterfly ecology: behavior (Koda and Nakamura, 2010), survival (Koda and Nakamura, 2010; Radchuk et al., 2013), phenotypic plasticity (de Jong et al., 2010), and phenology (Hodgson et al., 2011; Roy and Sparks, 2000).

However, other environmental variables, despite being less well studied, have also been shown to play a role. Joy and Pullin (1997, 1999) demonstrate that flooding has drastic impacts on the survival rates of overwintering larvae of *Coenonympha tullia*. Heavy rainfall negatively affects the survival of larval and pupal stages in several butterfly species (*Acraea acerata*: Azerefegne et al., 2001, *Boloria eunomia*: Schtickzelle and Baguette, 2004, *Pararge aegeria*: Gibbs et al., 2011). Droughts were shown to detrimentally affect several aspects of *P. aegeria* life history: survival of immature life stage, adult mass, wing loading and fecundity (Gibbs et al., 2012). Additionally, sunshine stimulates adults activity resulting in higher number of realized movements (Cormont et al., 2010). Moreover, even the same environmental factor can impact different life stages differentially (Petersen et al., 2000; Radchuk et al., 2013).

In addition to abiotic factors, interactions with other species can also have profound effects on population dynamics. For example, *Maculinea* butterflies spend the biggest part of their life cycles in a *Myrmica* ant nest and are fed by ants (Thomas and Elmes, 1998), which leads to strong coupling of butterfly and ant population dynamics. Moreover, parasitoids play a crucial role in regulating the population dynamics of their hosts (Choutt, 2011; Johst et al., 2006; Klapwijk et al., 2010). Therefore, if possible, multiple environmental factors affecting butterfly population dynamics and viability should be tested to identify those that are essential enough to be kept in the model.

Pattern-oriented modeling (POM) is a general modeling strategy (Grimm et al., 2005; Wiegand et al., 2003) based on the explicit selection among alternative representations of the processes to be included in the model (Grimm and Railsback, 2005; Railsback and Grimm, 2012). In POM, a set of patterns observed at different scales and levels of aggregation is used as criteria to select the "best" process representation. POM is increasingly used and has helped already in many cases to optimize model structure and communication for different taxa (e.g. Railsback and Johnson, 2011 for the black-throated blue warbler, Piou and Prévost, 2012 for Atlantic salmon, Rossmanith et al., 2007 for the Lesser Spotted Woodpecker, Swanack et al., 2009 for Houston toad; for more examples, see Grimm and Railsback, 2012; Railsback and Grimm, 2012). Yet, to our best knowledge, POM has not been applied for modeling population dynamics of butterfly species.

The bog fritillary butterfly *B. eunomia* has been used as a model organism in ecology and conservation biology for the past 20 years and is one of the best studied butterfly species in the realm of (meta)population biology (e.g. Baguette et al., 2011; Schtickzelle et al., 2006 and references therein). The ecology of this species makes it well suited for being used as an example in this context: the duration and survival of almost all life stages are affected by temperature (Radchuk et al., 2013); other abiotic variables (sunshine and precipitation) also impact the survival of some life stages (pupae and larvae: Schtickzelle, 2003; Schtickzelle and Baguette, 2004); *B. eunomia* larvae are subject to parasitism by a specialist wasp, *Cotesia eunomiae* (Choutt et al., 2011). Moreover, *B. eunomia* is a glacial relict species whose habitat in Belgium is separated by thousands of kilometers from the potential habitat northwards, making this species vulnerable to climate change (Nève et al., 1996; Schtickzelle, 2003). Hence, PVA models aiming at assessing the viability of the populations in Belgium under potential impacts of climate change are of high importance.

We developed four formulations of an IBM differing in the factors affecting the survival of individuals: (1) temperature (temperature affecting the survival of all immature stages); (2) weather (temperature affecting the survival of egg and overwintering larval stages, and sunshine and precipitation affecting the others); (3) temperature and parasitism (with temperature effects as in (1) and parasitism affecting overwintering larvae), and (4) weather and parasitism (with weather effects as in (2) and parasitism affecting overwintering larvae). We chose the model formulation that best matched four observed population-level patterns as the most suitable for predicting the future fate of *B. eunomia* population. However, to quantify the uncertainty related to the choice of the model formulation, we used all four models to predict population viability under several climate change scenarios, reflecting the change in both average and variability of weather variables over the next 100 years (Belgian National climate commission, 2010; Schär et al., 2004; Scherrer et al., 2005), and demonstrated that arbitrary model formulations strongly alter population viability estimates.

2. Methods

2.1. Study species and system

The bog fritillary butterfly *B. eunomia* is a glacial relict specialist of peat bogs and wet meadows and listed as "vulnerable" in the European Red List (van Swaay et al., 2006). It is highly food specialized, because only one plant species, the bistort *Persicaria bistorta*, is used as a nectar plant by adults and a host plant for larval food. *B. eunomia* is univoltine and individuals go through the following stages: egg, larva (which diapauses during the winter), pupa, and adult. We studied the patchy population of this species inhabiting Pisserotte peat bog nature reserve, located in Ardenne region of Belgium (50°13′N 5°4′E; Fig. 1).

2.2. Model description

We developed four model formulations: *Temperature* with temperature affecting the survival of all immature stages; *Weather* with temperature affecting the survival of egg and overwintering