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Rapid assessment of metapopulation viability under climate and land-use change

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ABSTRACT

In order to predict species response to climate and land-use change, numerically fast and easily applicable assessment tools for species survival are required. We present a set of formulae to calculate the mean lifetime of a metapopulation in a spatially heterogeneous and dynamic landscape subject to habitat patch diminution, loss and/or spatial shift of the habitat network. The formulae require as inputs (i) information about the number, location and size of the habitat patches for several time steps to quantify landscape dynamics in terms of patch destruction, diminution or shifting rates and (ii) data on species traits such as their vulnerability to environmental variation and their dispersal ability to quantify local colonisation and extinction rates. We validate the formulae with a spatially explicit simulation. The analysis is complemented by a protocol for the easy use of the approach and practical application examples. A software implementation is available on request from the authors.

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1. Introduction

The habitats of many species are undergoing permanent change. They may increase or decrease in size, quality and number and they may shift in space. The drivers of such landscape dynamics may be anthropogenic or natural.

Anthropogenic drivers include land use changes and human-induced climate changes. Climate change may lead to geographic range shifting of species because their suitable habitat (e.g., in terms of suitable temperature and/or precipitation ranges) may shift in latitudinal (e.g., northwards) or altitudinal directions (e.g., upward in elevation) (Walther et al., 2002; Chen, 2011; Bellard et al., 2012). Global meta-analyses documented significant range shifts averaging 6.1 km per decade towards the poles or metres per decade upward (Parmesan and Yohe, 2003). These range shifts vary greatly across species. For Finnish butterflies, for example, an average range shift northwards of about 60 km has been observed during two observational periods (1992–1996 and 2000–2004), where small shifts were observed, e.g., for *Pyrgus alveus* (5 km) and large shifts, e.g., for *Celastrina argiolus* (355 km) (Pöyry et al., 2009). Range shifts to higher elevations have been reported by Chen et al. (2011) with an observed median rate of 11 m per decade and variation in shifting rates among different taxonomic groups from

zero for birds to about 100 m for arthropods. This high variation in range shifts may be caused, amongst others, by additional drivers interacting with climate change.

Human land use as the second important anthropogenic driver (Parmesan and Yohe, 2003) may lead to ongoing destruction and recreation of habitats for species or to habitat loss (Walther et al., 2002; Parmesan and Yohe, 2003; Travis, 2003; Chen 2011). For instance, the heath fritillary butterfly (*Melitaea athalia*) in woodland in England depends on the creation of woodland clearings and is thus affected by rotational cutting (Hodgson et al., 2009). Moreover, agricultural intensification and accompanied habitat loss are thought to be important drivers of bee declines (Potts et al., 2010).

Besides these anthropogenic drivers, natural drivers of landscape dynamics exist as well. For example, due to land uplift on the east coast of Sweden along a line of about 50 km over several decades (Sjögren, 1991), small ponds which serve as habitats for a pool frog species *(Rana lessonae)* change in size and quality, and new ponds are created close to the coastline such that the whole pond system shifts (Hanski, 1999).

Natural and the different kinds of anthropogenic drivers can interact causing additional threats to biodiversity (Travis 2003; Bellard et al., 2012). Anthropogenic drivers can modify natural dynamics or they can add to already existing anthropogenic and natural drivers. This may result in changed landscape dynamics such as habitat shifting or modified shift speeds, in a decline in quality and/or number of habitat patches, or in a combination of all

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these kinds of landscape dynamics. These alterations can be so severe that many species cannot track or resist them (Hodgson et al., 2012; Best et al., 2007; Dytham et al., 2014). The question arises which species have a high and which have a low survival probability (Bellard et al., 2012). Thus, modelling approaches which are able to consider these different kinds of landscape dynamics both separately and in combination are badly needed.

Simulation and analytical models have been developed to analyse the survival of species in patchy and dynamic landscapes. Patchy landscapes can be modelled as habitat networks in which the habitat patches are separated by hostile space (matrix). The dynamics of species reproducing in the patches and dispersing between them are called metapopulation dynamics. Corresponding simulation models are computationally intensive so their use in those cases where many parameter combinations have to be analysed in a fast manner (e.g., to identify optimal land-use patterns or perform comprehensive sensitivity analysis) is limited.

Here we focus on analytical models for metapopulations in dynamic landscapes for which only few examples exist in the literature (Oborny et al., 2007; Gyllenberg and Hanski, 1997; Hanski, 1999; Johnson, 2000; Keymer et al., 2000; Amarasekare and Possingham, 2001; Hastings, 2003; DeWoody et al., 2005; Cornell and Ovaskainen, 2008; Drechsler and Johst, 2010). All these analytical models consider only landscapes with stationary dynamics, i.e., although habitat patches are destroyed and recreated and/or change in quality, there is no deterministic temporal trend in the number of patches or the distribution of patch sizes and qualities, and the region in which the patches are located is constant. Therefore, these models do not allow considering non-stationary landscape dynamics where habitat networks shift in space and/or habitat patches diminish in number and/or sizes. However, such non-stationary network changes become increasingly important for biodiversity in the face of climate change (Travis, 2003; Best et al., 2007; Dytham et al., 2014; Hodgson et al., 2012).

In the present paper we develop an analytical modelling approach to calculate the mean lifetime of a metapopulation in non-stationary dynamic landscapes. It is based on the modelling approach by Drechsler and Johst (2010) which allows determining the mean lifetime of a metapopulation in a stationary dynamic landscape where patches are destroyed and created elsewhere in the landscape at certain rates. This formula is enhanced to consider landscapes with non-stationary dynamics of three types: (1) the habitat network may shift in space (i.e., patches are destroyed at one margin of the network and are created at another one), (2) there may be temporal trends in the sizes or qualities of the patches, and (3) the number of habitat patches may decline (i.e., even if new patches are created in the course of the dynamics more patches are destroyed on average). All three types of landscape dynamics may interact. To consider such non-stationary landscape dynamics we extend the concept of spatial connectivity to one of spatio-temporal connectivity (Hanski, 1999) and make use of population viability theory (Grimm and Wissel, 2004).

The paper is structured as follows. In the Methods section we briefly present the analytical modelling approach by Drechsler and Johst (2010) and extend it in three directions: (i) a shifting habitat network where patches are destroyed on one end of the region and added to the other so that the region moves through space, (ii) patch diminution where the sizes of the patches decrease over time while patch locations are constant over time, (iii) permanent patch loss where patch destruction is without patch recreation so that the number of patches declines over time while locations of extant patches are constant over time. Finally, we combine all these three types of landscape dynamics. The Material and Methods section and the Results section contain the comparison of the new analytical modelling approach

with a simulation model. We show that errors of the approach are tolerable if certain conditions are fulfilled. In the Application section we then present a protocol and two example applications of the modelling approach. The paper concludes with a discussion of the results of the three types of landscape dynamics and of the applicability and implications of the new analytical approach.

2. Material and methods

2.1. Mean metapopulation lifetime in a dynamic landscape of fixed network area and with fixed number of habitat patches

Drechsler and Johst (2010) estimate the mean lifetime of a metapopulation in a dynamic landscape with N (termed N_{dyn} in that paper) habitat patches. The region is fixed but the habitat patches are destroyed and recreated elsewhere in the region at certain rates. Their formulae are an extension of a Markov model of local extinction and recolonisation processes of a metapopulation in a static habitat network (Frank and Wissel, 2002; Frank, 2004). The hostile space (matrix) between the habitat patches allows for dispersal between the patches but not for reproduction. Patches are destroyed at rate μ and recreated in the same region so that the number of patches N is constant. The sizes A_i ($i = 1, \ldots, N$) of the patches may differ. Local populations go extinct at rates (Hanski et al., 2000)

$$e_i = \varepsilon A_i^{-\eta} \tag{1}$$

and individuals emigrate from local populations at rates $n_i \sim A_i^b$. The ratio of n_i and the number of immigrants required for the successful establishment of a local population in an empty patch is denoted as the colonisation rate

$$c_i = m A_i^b. \tag{2}$$

An aggregated colonisation rate is formed as the power mean of the patch specific colonisation rates c_i (Eq. (2))

$$\bar{c} = \left(\frac{1}{N}\sum_{i=1}^{N} c_i^{\eta/b}\right)^{b/\eta}, \tag{3}$$

an aggregated local extinction rate in the absence of patch destruction by the geometric mean of the patch specific extinction rates e_i (Eq. (1))

$$\tilde{e} = \prod_{i=1}^{N}(e_i)^{1/N}. \tag{4}$$

If patches are destroyed at rate μ the corresponding geometric mean of the aggregated local extinction rate becomes

$$\tilde{e}_{dyn} = \prod_{i=1}^{N}(e_i + \mu)^{1/N} \tag{5}$$

The geometric mean of the ratios of colonisation and extinction rates

$$\gamma = \prod_{i=1}^{N}(c_i/e_i)^{1/N} \tag{6}$$

measures the mean number of individuals emigrating during the average lifetime of a local population, divided by the number of immigrants required for the successful colonisation of an empty patch. Thus, it is related to the dispersal propensity of a species and equals the well-known colonisation-extinction ratio c/e introduced by Levins (1970) for static homogenous networks with colonisation rate c and local extinction rate e.

Habitat patch sizes may differ so that the local extinction rates e_i and colonisation rates c_i generally differ among the patches. We