Ecological Modelling 375 (2018) 45–53

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Population persistence in landscapes fragmented by roads: Disentangling isolation, mortality, and the effect of dispersal

Ana Ceia-Hasse[a,b,c,d,*], Laetitia M. Navarro[a,b], Luís Borda-de-Água[c,d], Henrique M. Pereira[a,b,c,d]

[a] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
[b] Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany
[c] Infraestruturas de Portugal Biodiversity Chair, CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal
[d] CEABN/InBio, Centro de Ecologia Aplicada "Professor Baeta Neves", Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal

ARTICLE INFO

Keywords:
Extinction
Abundance
Barrier effect
Mortality
Roads
Individual-based model

ABSTRACT

Linear infrastructures, one of several forms of land-use, are a major driver of biodiversity loss. Roads impact populations at many levels, with direct road mortality and barrier effect contributing to decreased population abundance, higher isolation and subdivision, and therefore to increased extinction risk. In this paper, we compared the effect of road mortality and of the barrier effect on population isolation, persistence and size, and assessed the interaction of these effects with dispersal. We used a spatially explicit, process-based model of population dynamics in landscapes fragmented by varying levels of road density. We modelled a barrier effect independently from road mortality by varying the probability with which individuals avoid crossing roads. Both road mortality and the barrier effect caused population isolation. While road mortality alone had stronger negative effects than the barrier effect without extra mortality, the latter also resulted in decreased population size. Yet, road avoidance could, in some cases, rescue populations from extinction. Populations with a large dispersal distance were more negatively affected as road mortality increased. However, when there was no road mortality they maintained larger sizes than populations with a short dispersal distance. Our results highlight the much higher relative importance of road mortality than the barrier effect for population size and persistence, and the importance of assessing relevant species traits for effective long-term transportation planning and conservation management. Our model can be used in species-specific situations and with real landscape configurations in applications such as conservation planning.

1. Introduction

The current biodiversity crisis is mainly driven by land-use change (Pereira et al., 2012; Maxwell et al., 2016). Roads, one of many forms of land-use, cause major impacts on populations. As the road network is predicted to strongly increase in the coming years (van der Ree et al., 2015), it is crucial to assess its impact on populations, in order to apply suitable mitigation measures, and improve conservation and road planning.

Roads cause habitat loss and fragmentation, and decrease habitat quality. Roads also cause direct mortality through wildlife collisions with vehicles, and act as a barrier to movement (van der Ree et al., 2015). These direct and indirect impacts of roads can contribute to population isolation and subdivision, to decreases in population abundance, and therefore can increase population extinction risk (van der Ree et al., 2015; Ascensão et al., 2016), although there are also positive effects for some species (e.g., see Rytwinski and Fahrig, 2012, 2013).

Species traits can also influence population-level responses to land-use change (Pereira and Daily, 2006), and should be considered when assessing the effects of roads. Specifically, dispersal has been identified as an important factor but its influence on population persistence is still not fully understood. For example, while the role of dispersal is beneficial in metapopulation models (e.g., Hanski, 1998), because more patches can be colonized if dispersal is large, in source-sink models or reaction-diffusion models (e.g., Skellam, 1951; Pulliam, 1988) dispersal affects populations negatively, because it can lead to colonization of habitats where population growth rates are negative (sink habitats) (Pereira and Borda-de-Água, 2013). Moreover, dispersal can be associated with increased mortality risk (e.g., Nathan et al., 2012), with some studies suggesting there is an optimal intermediate dispersal rate

* Corresponding author at: German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.
E-mail addresses: ana.ceia_hasse@idiv.de (A. Ceia-Hasse), laetitia.navarro@idiv.de (L.M. Navarro), lbagua@cibio.up.pt (L. Borda-de-Água), hpereira@idiv.de (H.M. Pereira).

https://doi.org/10.1016/j.ecolmodel.2018.01.021
Received 5 December 2016; Received in revised form 4 January 2018; Accepted 6 January 2018
0304-3800/

for persistence in disturbed habitats (Casagrandi and Gatto, 1999).

The detrimental effect of dispersal in disturbed habitats is supported by several empirical studies (e.g., fragmented forests: Gibbs, 1998; Van Houtan et al., 2007). In the specific case of roads, a higher mobility has been related to negative effects of roads in mammal and bird species (Rytwinski and Fahrig, 2012). Furthermore, using a theoretical approach, Borda-de-Água et al. (2011) predicted that the larger the mean dispersal distance in a population, the larger would be the minimum area necessary for this population to persist in a landscape fragmented by roads.

In this paper we focus on dispersal movement as the process whereby individuals leave their initial location, move across a more or less suitable environment, and settle in a new location (Clobert et al., 2012; Matthysen, 2012). Our model does not currently include other types of movement (such as daily movements).

Direct road mortality introduces an additional source of mortality besides natural mortality. In addition, roads can also act as a barrier that does not introduce additional mortality, when the animals do not cross the roads. This barrier effect can be due to physical structures (such as fences) or to road avoidance behavior (e.g., Jaeger and Fahrig, 2004; Grilo et al., 2012), and for simplicity in this paper we refer to it simply as barrier effect. Although this can rescue individuals from road mortality to some extent, the negative consequences of habitat loss and fragmentation may be higher when such barrier effect is present, since road avoidance can lead to population isolation and to higher exposure to demographic and environmental stochasticity (Rytwinski and Fahrig, 2012; Ascensão et al., 2016). Moreover, the effects of road mortality and of road avoidance can be confounded and are still to be properly disentangled. For example, reduced population abundance near roads may be due to direct road mortality, or due to road avoidance behavior (e.g., Fahrig et al., 1995).

Although there is evidence that the effects of roads on population abundance are in general negative (Rytwinski and Fahrig, 2015), the impact of roads on population persistence has not been so commonly addressed (but see, for example Borda-de-Água et al., 2014 and Ceia-Hasse et al., 2017).

The key issue addressed in this paper was to disentangle the influence of an additional source of mortality (direct road mortality) versus the influence of a barrier effect to movement that does not introduce such additional mortality on population isolation, persistence and size, as well as the influence of dispersal, in fragmented landscapes. We addressed this using roads. We use a spatially explicit, process-based model of population dynamics. Our questions were: (1) What is the importance of road mortality versus isolation, for population persistence and size in landscapes fragmented by roads?; (2) How does dispersal influence the size and the persistence of populations under varying levels of road mortality and of a barrier effect?

2. Materials and methods

We used an individual-based toy model of population dynamics to perform a theoretical study on the effects of road mortality, barrier effect and dispersal on population isolation, size and persistence of a virtual species. Our study is not based on any empirical data and thus is more appropriately considered under the virtual ecology rationale (e.g., Grimm, 1999; Zurell et al., 2010).

2.1. Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing agent-based models (Grimm et al., 2006, 2010). The model was implemented as an ANSI C++ program, which can be downloaded from https://github.com/anaceiahasse/landsim.

2.1.1. Purpose

The purpose of the model is to simulate population dynamics in fragmented landscapes. Specifically, in this study, the model simulated population dynamics in landscapes fragmented by roads, with special emphasis on the effects of road mortality, of a barrier effect without mortality, and on the influence of dispersal distance.

2.1.2. Entities, state variables, and scales

The entities of the model are the landscape and the individuals, i.e., the model keeps track of the features of the landscape and of the female population (the model only considers female individuals for simplicity).

The landscape is a two-dimensional grid of N x N square cells with reflecting boundaries. An alternative approach to deal with edge effects would have been to consider periodic boundary conditions (i.e., torus geometry) instead of reflecting boundaries. However, given a dispersal step size of only one cell and the large size of the grid, both approaches can lead to similar outcomes. Each cell of the landscape is assigned to one of n possible types with values varying between 0 and 1. In the present case, each cell belongs to one of two possible types, "high-quality" habitat (non-road) or "road", with values of "1″ and "0″, respectively. We generated several landscapes with different proportions of road cells, where roads were placed perpendicularly to one another (Fig. 1, Table 1). We used simple hypothetical regular road networks because our main objective was to disentangle the effects of sink mortality versus those of a barrier effect that does not introduce additional mortality. Sink mortality here corresponds to road mortality, and it is the probability that an individual dies when crossing a road (see Section 2.1.7.3 below). Our goal was to derive general principles that can be the basis to understanding and model more specific or complex cases.

Individuals are characterized by the following state variables: age, developmental stage (juvenile or adult), position in the landscape; and by the following attributes: fecundity, age at first breeding, natural survival probability, home range size, dispersal distance, road mortality probability, road avoidance probability (Table 1).

2.1.3. Process overview and scheduling

Each simulation time step consists of the following sequential events (Fig. 2, Table 1): reproduction; natural mortality; dispersal of juveniles; juvenile density-dependent mortality. Section 2.1.7 describes the submodels implementing these processes. Juveniles that establish a home range are inserted into the adult population at the end of each simulation time step, thereby updating population size and landscape cell availability for the following time step. At the beginning of each simulation time step, the age of each individual is updated (increased by 1), and the sequential steps listed above ensue.

2.1.4. Design concepts

2.1.4.1. Basic principles. Roads can contribute to population isolation, decreased size and increased extinction risk through direct mortality and barrier effects (e.g., van der Ree et al., 2015; Ascensão et al., 2016). Dispersal can also influence how roads impact populations (e.g., Borda-de-Água et al., 2011; Rytwinski and Fahrig, 2012). The model allows assessing the relative importance of these factors for population isolation, persistence and size, which is not yet fully understood.

2.1.4.2. Emergence. Population dynamics emerges from the model (i.e. from the set of rules defined, parameter values used and landscape configuration).

2.1.4.3. Adaptation. Juveniles choose the direction in which they disperse according to cell type (road versus high-quality habitat cell) and occupancy (they may avoid dispersing into road cells with a given probability and they do not disperse to occupied cells, respectively).