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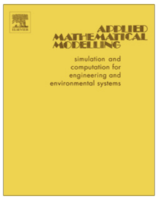

Spatially continuous modeling approach for population persistence in road-fragmented landscapes

Nataša Bojković [a,*], Vladimir Božin [b], Marijana Petrović [a], Ivan Anić [b]

[a] Faculty of Transport and Traffic Engineering, University of Belgrade, Serbia
[b] Faculty of Mathematics, University of Belgrade, Serbia

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ABSTRACT

The paper addresses the characteristics of landscape fragmentation caused by roads and their consequences on movement/dispersal and persistence of species. We propose a mathematical model, sufficiently general to enable inclusion of the effects of fragmentation by roads, assuming that the continuity of habitats across road-fragmented landscapes cannot be strictly defined. The mathematical formalization of the colonization–extinction dynamics is given, respecting the fact that both inter-patch and intra-patch processes matter in road-fragmented landscapes. Using the technique of integral operators, we define a population persistence capacity, indicating at what point the landscape is prone to be functionally disconnected for the species of interest. Population persistence capacity derived from the model, responds monotonically to fragmentation processes. The explicit inequalities relating population persistence capacity to other relevant fragmentation metrics are established.

1. Introduction

Landscape fragmentation resulting from human activities is a process leading to progressive, usually irreversible degradation of habitat, thereby acknowledged as a serious threat to population viability. Fragmentation divides contiguous landscapes into smaller patches - areas containing resources needed by one or more species of interest [1,2]. As patches become more isolated over time, ecological processes are disrupted and population is exposed to an increasing risk of extinction. Together with other forms of human land-use and landscape alteration (agriculture, urban zones and other built-up areas), transport infrastructure is one of the leading causes of habitat fragmentation. Due to high network density and growing traffic volumes, road infrastructure has come to the forefront in terms of its impacts on population persistence [3,4].

Roads act as a barrier and affect the populations directly by obliterating the landscapes in their path [5]. The consequences are complex and depend on the characteristics and properties of the species as well, primarily in terms of their mobility/dispersal, area requirements or dependence on a certain type of habitat [6]. Additionally, the area of a roadless habitat may be several times the home range of some species, but only a fraction of the home range of the other ones. Road-fragmented habitats create disconnected resource networks, non-permeable or semi-permeable landscapes and most critically, isolated populations.

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* Corresponding author at: Vojvode Stepe 305 (room 005), 11 000 Belgrade, Serbia. Tel.: +381 63366114; fax: +381 11 3096704.
E-mail address: nbojkovic@yahoo.com (N. Bojković).

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The topology of road networks determines the size and locations of un-fragmented sites - patches, all of which may designate the persistence of living beings and their habitats.

This article provides a new modeling approach that accommodates for varying permeability of barriers between patches. The paper starts with a brief theoretical background on modeling the effects of fragmentation caused by roads. Next, we give the description and mathematical formalization of the derived model and define the population persistence capacity, which denotes the threshold for the persistence of species. After that, we examine the response of population persistence capacity to fragmentation processes. In addition, we compare it to other well established fragmentation metrics - effective mesh size [7,8] and metapopulation persistence capacity [9].

2. Background of the study

Along with an analysis of population processes in fragmented landscapes, a number of ecological/fragmentation metrics have been proposed in the scientific literature. They have been developed using mathematical models of various complexity.

When it comes to landscape fragmentation caused by roads, the effective mesh size (m_{eff}) proposed by Jaeger [7] is probably the most suitable for practical application. Such is the one recently included in EEA – TERM 2011 indicators (European Environment Agency - Transport indicators tracking progress towards environmental targets in Europe). The definition of this metric is based on the probability that two points chosen randomly in a region are connected, i.e. are located in the same roadless area - patch. In that way, it indicates the ability of individuals to move freely without encountering road barriers. As Jaeger et al. [10] suggest, the m_{eff} can be intuitively interpreted as a measure of persistence, since the probability of individuals to encounter each other is the "prerequisite for reproduction and thus for the persistence of a species in a region and for genetic exchange in a metapopulation as well". Besides formal and intuitive interpretations, effective mesh size is characterized by important mathematical properties. These are related to the reaction to fragmentation processes like perforation, dissection and attrition of habitats, as investigated in [7]. Concerning road network, the refined version called "topology-sensitive effective mesh size" is sensitive to spatial arrangement of transportation routes [8]. It, for example, expresses differences between bundled and evenly distributed routes; gridded patterns vs. parallel configuration, etc.

To relate the landscape pattern to ecological processes and predict population persistence, the spatially explicit population models (SEPMs) are often used [11]. In road-fragmented landscapes, these simulation models may include movements across roads (successful or resulting with traffic mortality), road avoidance and movements without encountering the roads. Concerning spatial patterns of roads, simulation models have shown that the effects of road density on the viability of wildlife populations can reach the level above which populations are prone to extinction [4]. Nevertheless, it should be noted that SEPMs, although widely exploited and undoubtedly useful for road fragmentation problems, are burdened with immense data requirements and problems with parameterization [12], which often results in significant uncertainty (for comprehensive discussion see [13]).

Another modeling approach for investigating and predicting the effects of landscape fragmentation on population persistence is using spatially realistic version of metapopulation modeling. The model is realistic in the sense that it includes the biologically significant processes, colonization and extinction, and it can be parameterized with data from real metapopulations [14–21]. This approach derives a metric that depends on landscape characteristics, called metapopulation capacity. If its value is above a threshold depending on species characteristics, persistence condition is fulfilled. As such, metapopulation capacity indicates the potential of the landscape to support persistence of species.

The basis for the application of metapopulation concept is that when a landscape is fragmented, a system of subpopulations inhabiting different habitat patches is formed and a population can be considered as a metapopulation. Further, the patches are located close enough to permit migration of species, but are capable to support independent local dynamics as well [22,23]. The backbone of the theory is the Levins metapopulation concept [24]. which uses the extinction and colonization probabilities to determine the fraction of occupied patches in a landscape. The model assumes an infinitely large network of discrete patches of equal size and equal connectivity. The 'spatially realistic' metapopulation model (hereafter referred as SRM) which originated from the Levins model, explicitly takes the area and locations/connectivity of habitat patches into account. Colonization rate is distance dependent, while extinction rate is dependent on patch area which is the surrogate for population size [9,25,26].

The model describes the rate of change in the probability of patch A_i being occupied (given by p_i) (Eq. (1)).

$$\frac{dp_i}{dt} = c_i[1 - p_i(t)] - e_i p_i(t). \tag{1}$$

Extinction rate for species in patch A_i with an area $|A_i|$ is area dependent and expressed as

$$e_i = \frac{e}{|A_i|}. \tag{2}$$

The colonization rate of patch A_i is expressed as

$$c_i = c\sum_{j\neq i} e^{-\alpha d_{ij}}|A_j|p_j(t) = c\sum_{j\neq i} M_{ij}p_j(t). \tag{3}$$