

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).

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 $N \times N$ 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 sub-models 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).

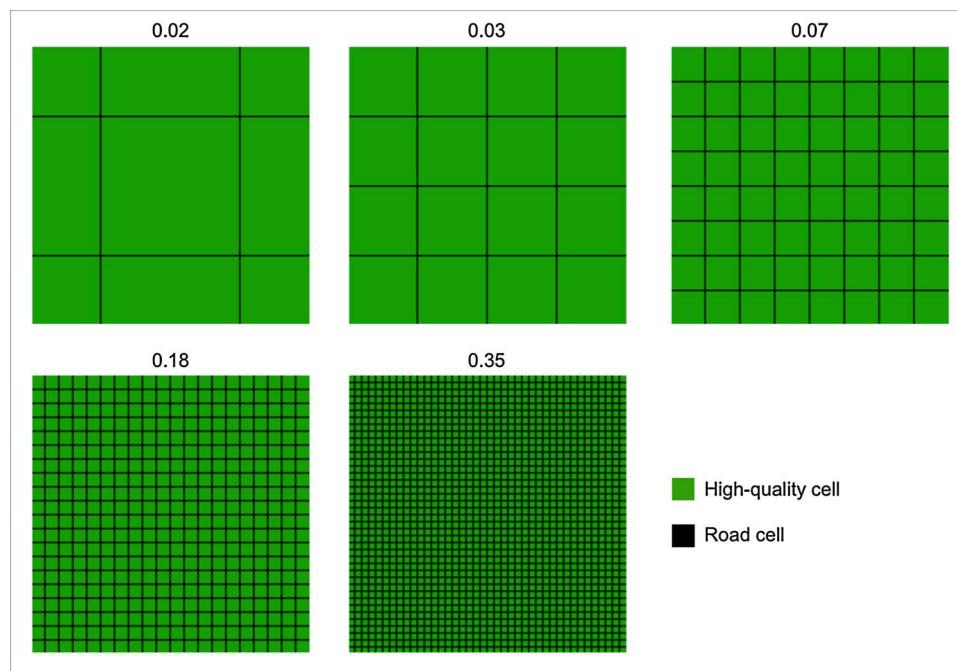


Fig. 1. Landscape configurations used in simulations. Each landscape is a grid of 200×200 cells composed of high-quality habitat cells, and road cells. Numbers on top of each panel indicate the proportion of road cells in each landscape.

Table 1
Model parameters and values used in the simulations.

Parameter	Value	
	1st set of simulations	2nd set of simulations
Landscape size ($N \times N$)	200×200 cells	
Initial population size	10 individuals	
Number of replicates	100	
Number of time steps	1000	
Fecundity (b_i)	2	
Survival probability (s)	0.4	
Dispersal distance (d)	5 or 50 cells	
Road mortality, Road avoidance (m_{RM}, p_{RA})	(0.0, 0.0); (0.0, 1.0); (1.0, 0.0)	varied from 0 to 1 in steps of 0.1
Proportion of road cells in the landscape	0.02, 0.03, 0.07, 0.18, 0.35	0.07, 0.35

2.1.4.4. Sensing. During dispersal, juveniles evaluate cell type (road versus non-road cell) and occupancy.

2.1.4.5. Interaction. Juveniles do not disperse through cells that are already occupied.

2.1.4.6. Stochasticity. Stochasticity was incorporated in several processes (reproduction, natural mortality, dispersal of juveniles); see Section 2.1.7 for details.

2.1.4.7. Observation. For each model run, we recorded population size at the end of each simulation and averaged population size across replicates. We calculated the probability of extinction as the proportion of replicates in which populations went extinct before the end of the simulation.

2.1.5. Initialization

The model starts by settling an initial population of females at breeding age in the landscape. After the initial population is created, each simulation time step consists of the events described in Section 2.1.7 (Submodels). In all simulations, the initial population size was 10 individuals, set at random in the landscape. See Table 1 for the

remaining parameter values used in the simulations and Fig. 3 for a representation of the settlement of the initial population in the landscape and of the colonization of the landscape.

2.1.6. Input data

The model does not import data of driving environmental variables.

2.1.7. Submodels

2.1.7.1. Reproduction. Females reproduce after one year and once they have established their home range. The number of female juveniles that a breeding female produces follows a Poisson distribution with mean equal to its fecundity b_i .

2.1.7.2. Natural mortality. Adults and juveniles die with probability $(1 - s)$. When an individual dies it is removed from the population and its home range cell is made available for dispersing individuals.

2.1.7.3. Dispersal of juveniles. In our model adults do not move, and do not get killed by direct road mortality. Only juveniles disperse. Each juvenile disperses a fixed number of cells from its mother cell. A dispersal step is always to one of the four neighboring cells (von Neumann neighborhood), and is composed of the following events (Fig. 2b): (1) the individual evaluates whether its four neighboring cells are occupied or free, and does not disperse to occupied cells; (2) the individual evaluates whether the free neighboring cells correspond to roads or not, and can avoid dispersing through road cells with probability p_{RA} ; (3) if the individual disperses through a road cell, sink dispersal mortality (road mortality) is applied with probability m_{RM} . The dispersal process is not stopped when the individual finds a first suitable empty cell; instead it continues until the individual either dies (due to road mortality), or disperses over his dispersal distance, d . An individual is allowed to move back to a cell it has previously visited. Therefore, two neighboring unoccupied cells are sufficient for an individual to survive over any number of dispersal steps. Moreover, each juvenile disperses from its mother cell, but given natural mortality that cell may be freed, and in that case it can be occupied by a juvenile. The default probability of dispersing to any neighboring cell is 1. However, if all four neighboring cells are occupied, and since

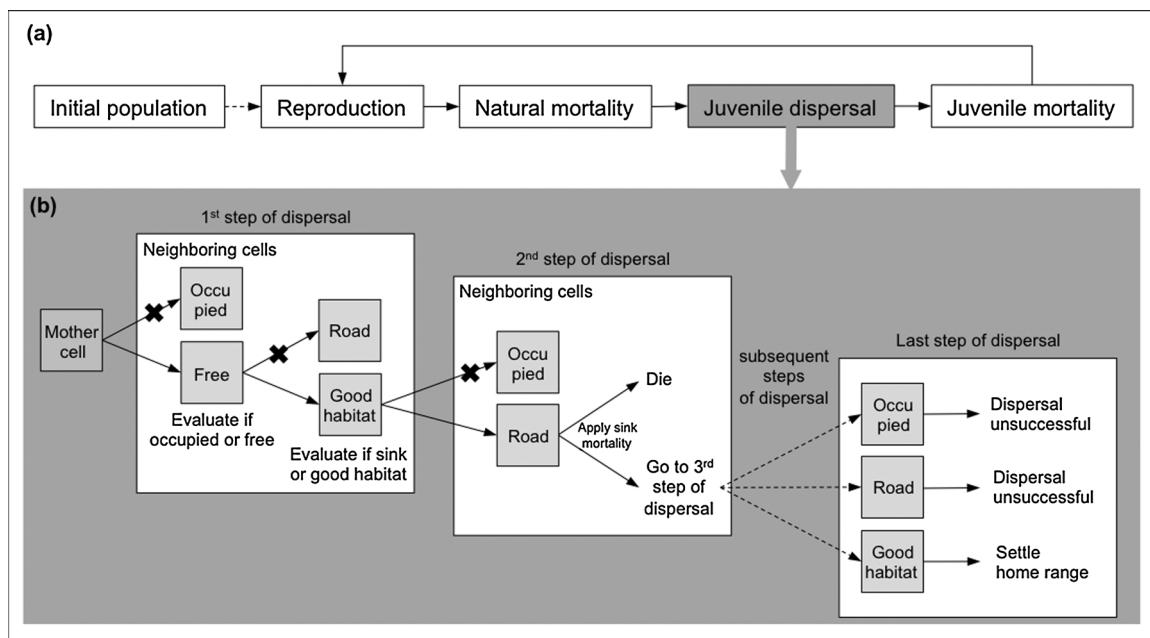


Fig. 2. Scheme of the model. (a) Schematic representation of the complete model simulation steps. (b) Schematic representation of juvenile dispersal. The x in (b) indicate that the individual does not disperse to occupied cells, and that it will disperse to a good habitat cell over a road cell.

individuals do not disperse to occupied cells, then the individual cannot move and dispersal is unsuccessful. If the cell in which the individual is at the end of dispersal is a road, dispersal is also unsuccessful. If dispersal is successful, the individual can settle a home range. In this

study, we set the home range size to one cell and only one individual can establish its home range in each cell.

2.1.7.4. Juvenile density-dependent mortality.

Following unsuccessful

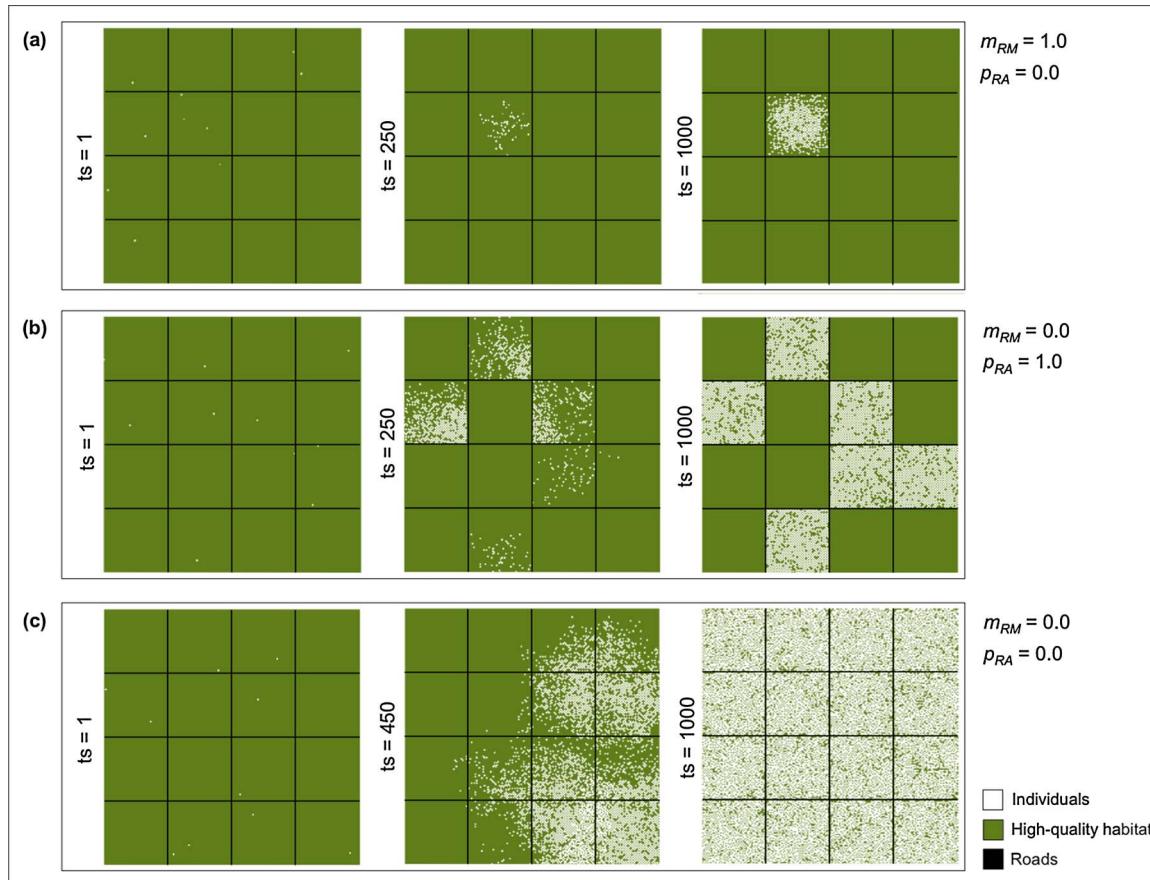


Fig. 3. Representation of the colonization of the landscape by a population under different combinations of values of road mortality probability (m_{RM}) and of road avoidance probability (p_{RA}), in different time steps (ts) of a model run. In the example shown, the dispersal distance is set to 50 cells (i.e. large dispersal) and the proportion of road cells in the landscape is 0.03.

dispersal, juveniles that did not establish their home range are removed from the population.

2.2. Simulations

We created five landscapes of 200×200 cells with perpendicular roads, each with a different proportion of road cells (Fig. 1, Table 1). We used two dispersal distances: short (5 cells), and large (50 cells), the latter of which we deemed reasonable considering the total size of the grid (40,000 cells). We modelled a barrier effect independently from sink mortality by varying the probability with which individuals do not cross roads while dispersing.

We performed two sets of simulations. In the first set of simulations, we assessed the effect of different extreme scenarios of road mortality and of road avoidance in landscapes with different proportions of road cells: (i) road mortality probability was one and there was no road avoidance; (ii) road avoidance probability was one and there was no road mortality; (iii) road mortality and road avoidance probabilities were both zero, for each dispersal distance and each road density. To assess the combined effects of road mortality and of road avoidance, in the second set of simulations we varied road mortality and road avoidance probabilities both at the same time independently from 0 to 1 in steps of 0.1 (i.e., using all combinations possible), for each dispersal distance (Table 1).

In all simulations, we used fixed values of the remaining parameters (Table 1), simulating the dynamics of hypothetical animal populations in hypothetical landscapes, because our main objective was to obtain general predictions on the differential effects of road mortality versus a barrier effect that did not introduce additional mortality (due to road avoidance behavior or physical structures such as fences), under different levels of dispersal.

We ran each simulation for 1000 time steps, to ensure that population size did not vary by more than 10% between consecutive simulation time steps, for at least the last 10 simulation time steps, and ran 100 replicates for each combination of values of parameters (Table 1).

Our computer program was extensively debugged, thus we are confident that the program is reproducing accurately the intended model. Being an individual-based model computer simulation, we performed our simulations under a set of assumptions that we deemed reasonable, and we tested them for a wide range of parameter values, obtaining the expected results.

Our model takes as input the model parameters and a two-dimensional matrix with the landscape. It produces a file containing the location of the home range of each adult in the landscape at each time step, and the population age structure at each time step. To apply the model to other species and landscape configurations, users can choose the values of the parameters specific to the species or population of interest, and a matrix with the desired landscape configuration.

3. Results

In our simulations, isolation occurred due to road mortality or to road avoidance (Fig. 3). With complete road mortality and no avoidance (Fig. 3a), or with complete avoidance and no road mortality (Fig. 3b), the landscape was only partially occupied. In contrast, when there was no mortality and no avoidance (Fig. 3c), the whole landscape was occupied.

When there was no road mortality and no road avoidance, the probability of extinction was higher and the population size was smaller at higher road densities, suggesting an effect due to habitat loss (Fig. 4). Nevertheless, with no road mortality and no road avoidance, the probability of extinction was zero or close to zero, even with high road density (Fig. 4a); and the population size was considerably larger than with either complete road avoidance, or complete road mortality (Fig. 4b). These results suggest that in such cases there was an effect of road avoidance or of road mortality, respectively.

The probability of extinction was higher and the population size was smaller when there was road mortality alone, than when there was road avoidance alone, except at the highest road density (Fig. 4). However, population size was much smaller at all road densities when there was road avoidance than in the case with no road avoidance and no road mortality (Fig. 4b).

When assessing the combined effects of road mortality and of road avoidance for different dispersal distances at the highest road density, the probability of extinction increased and the population size decreased with increasing road mortality (horizontal lines in Fig. 5). For a constant value of road mortality (vertical lines in Fig. 5), probability of extinction decreased and population size increased with increasing road avoidance. However, at this road density, the good habitat patches delimited by roads were small (16 cells), and populations went extinct when road avoidance was complete, even without road mortality.

The role of dispersal varied with road mortality. The probability of extinction increased and the population size decreased much faster with increasing road mortality for the large than for the short dispersal distance. However, when there was no road mortality, the probability of extinction was higher (Fig. 5a) and the population size was smaller (Fig. 5b) for the short dispersal distance.

Similar patterns were observed when assessing these effects at a lower road density (proportion of road cells in the landscape = 0.07; Fig. S1 in Appendix). However, they were less obvious than in the case of high road density, especially for the short dispersal distance: the probability of extinction was low, and the population sizes varied less. Nevertheless, population size strongly decreased with complete road avoidance, or with complete road mortality, for both dispersal distances, as in the case of high road density (Fig. 5).

Note that for the short dispersal distance and also for most of the large dispersal distance simulations in Fig. S1, while the probability of population extinction is close to zero, the population size is low, both when road mortality is one, and when road avoidance is one. This is because many individuals die on roads (when road mortality is one), or the population can only occupy part of the landscape (when road avoidance is one).

4. Discussion

Our results allow to make inferences about the differential effects of sink mortality versus those of a barrier effect without additional mortality, and the role of dispersal, on population persistence, isolation and size, which were the goals of this study. While habitat amount was kept constant when road mortality probability and road avoidance probability were varied with a same road density, it should nevertheless be taken into account that by generating landscapes with habitats and roads as grid cells, and by using a regular road network pattern, landscapes with higher road densities have lower total habitat amount and smaller habitat patches. In this sense, there were three effects present (i.e., road mortality, road avoidance, and habitat amount change).

4.1. Importance of road mortality versus a barrier effect without mortality for population persistence and size

Road mortality alone had a stronger negative effect on the probability of persistence and on population size than road avoidance alone. Road avoidance could also in some cases rescue populations under low to moderate road mortality from extinction, as suggested by other authors, since road avoidance decreases the probability that individuals cross roads, therefore reducing mortality caused by collision with vehicles (Jaeger and Fahrig, 2004; Rytwinski and Fahrig, 2013). Previous studies also suggest that the genetic effects of road mortality are stronger than those of the barrier effect without road mortality (e.g., Jackson and Fahrig, 2011; Ascensão et al., 2013).

In our simulations, population isolation occurred both when there was road mortality, or when there was a barrier effect without

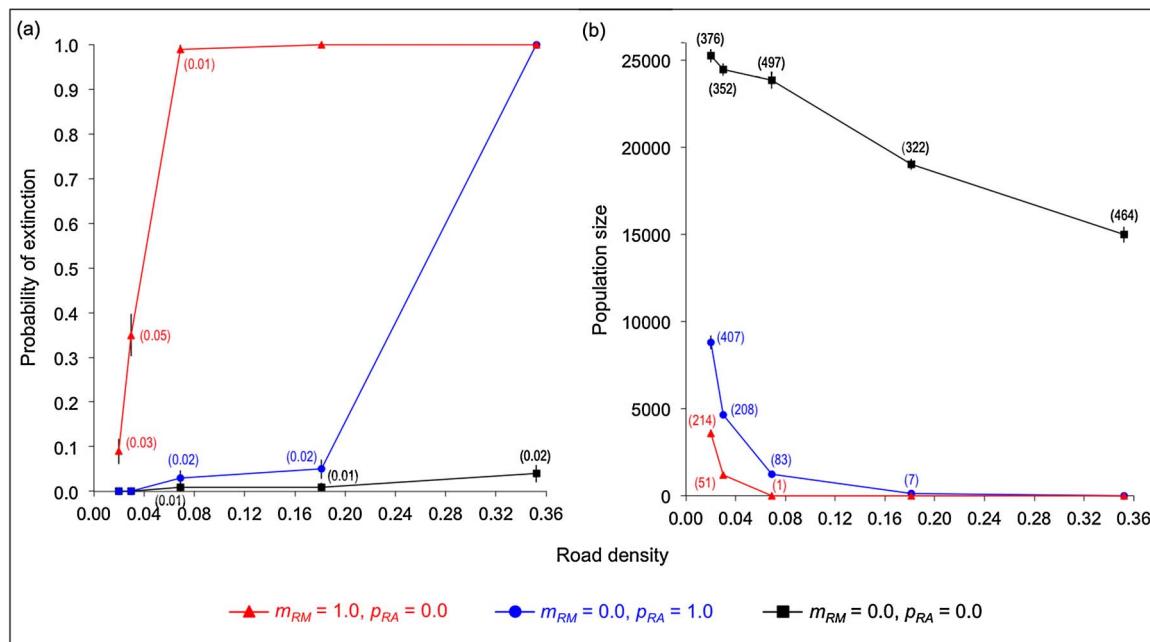


Fig. 4. Probability of population extinction (a) and population size (b) for the different proportions of road cells in the landscape, for different combinations of values of road mortality probability (m_{RM}) and of road avoidance probability (p_{RA}). Results shown are for the large dispersal distance (50 cells). Error bars correspond to the standard error of the mean, whose values are indicated in brackets (when different from zero).

additional mortality. Populations persisted even when road avoidance was very high, provided that the road mortality was low to moderate. Only complete road avoidance led populations to extinction, when road density was the highest. In those cases, individuals were isolated within the small patches of good habitat that were bounded by roads, and the resulting small populations exhibited an increased extinction risk due to demographic stochasticity (Lande, 1993).

Habitat fragmentation impairs species persistence and ecosystem functions. Moreover, the several effects of fragmentation are interlinked and can operate over long time scales (Haddad et al., 2015). In our analysis, population sizes were negatively affected when road avoidance was complete regardless of the road density, even if there was no road mortality. Population sizes were much smaller when compared to the cases with no road avoidance (and no road mortality). This may influence population persistence in the long-term, especially if other factors of disturbance come into play. For example, we did not vary habitat quality (all non-road cells had maximum habitat quality), because our aim was to obtain general predictions on the differential effects of road mortality versus those of a barrier effect without mortality. However, habitat quality can influence how roads affect populations (e.g., Grilo et al., 2014) and therefore the habitat quality of the non-road cells could be varied in more detailed studies, for example by including species-specific information on habitat preferences.

Moreover, although not included explicitly in our analysis, traffic volume is also important to consider when assessing the effects of roads on populations and in landscape connectivity studies, since traffic intensity may influence both road mortality and road avoidance, and thus population persistence (Jaeger et al., 2006; Jaeger, 2007; Charry and Jones, 2009; van Langevelde and Jaarsma, 2009; van Strien and Grêt-Regamey, 2016). Several studies suggest that road mortality may be higher at intermediate traffic volumes than high traffic volumes, because at higher traffic volumes road avoidance will be higher for many species (e.g., Seiler 2005; Grilo et al., 2015).

However, the focus of our analysis was on comparing the effects of road mortality vs. those of a barrier that does not introduce additional mortality, which can be due to road avoidance behavior but also due to physical structures such as fences (e.g., Jaeger and Fahrig, 2004; Grilo

et al., 2012). Hence we modeled these directly as the probability of an individual dying on a road while crossing it, and the probability of an individual not crossing a road, regardless of the cause (e.g., road surface avoidance behavior, road avoidance due to traffic, fences), and therefore we did not consider traffic volume explicitly.

Additionally, while in our simulations individuals only evaluated their immediate neighboring cells in each step of dispersal, some species avoid roads from a distance (e.g., Jaeger et al., 2005), which may exacerbate the effects of habitat loss and fragmentation. Including microevolution in our individual-based model, which is fundamental to capture the response of organisms to changing conditions (Grimm and Berger, 2016), would also allow analysing eco-evolutionary responses to fragmentation (Haddad et al., 2015).

4.2. Influence of dispersal distance on population persistence and size

The role of dispersal distance varied depending on the values of road mortality. In fragmented landscapes, as was the case in all our simulations since roads were always present, populations with a larger dispersal distance showed a lower probability of extinction and maintained larger sizes, provided an additional source of mortality due to roads was not present. However, a large dispersal distance was detrimental for population size and persistence as road mortality increased.

We used fixed dispersal distances in our simulations. However, dispersal distance is usually stochastic (e.g., Nathan et al., 2012), and therefore it would not only be interesting but also add realism to the model by implementing dispersal kernels to determine dispersal distances (e.g., Austerlitz et al., 2004; Chipperfield et al., 2011), instead of using fixed dispersal distances.

Furthermore, in our simulations, dispersing individuals only evaluated their immediate four neighboring cells in each dispersal step, which can be considered as a biased random walk (e.g., Turchin 1998). While this has been a common choice to model movement with an orientation component (e.g., Börger et al., 2008), expanding the perceptive range of dispersing individuals would increase the realism and facilitate the transferability of the model to concrete situations.

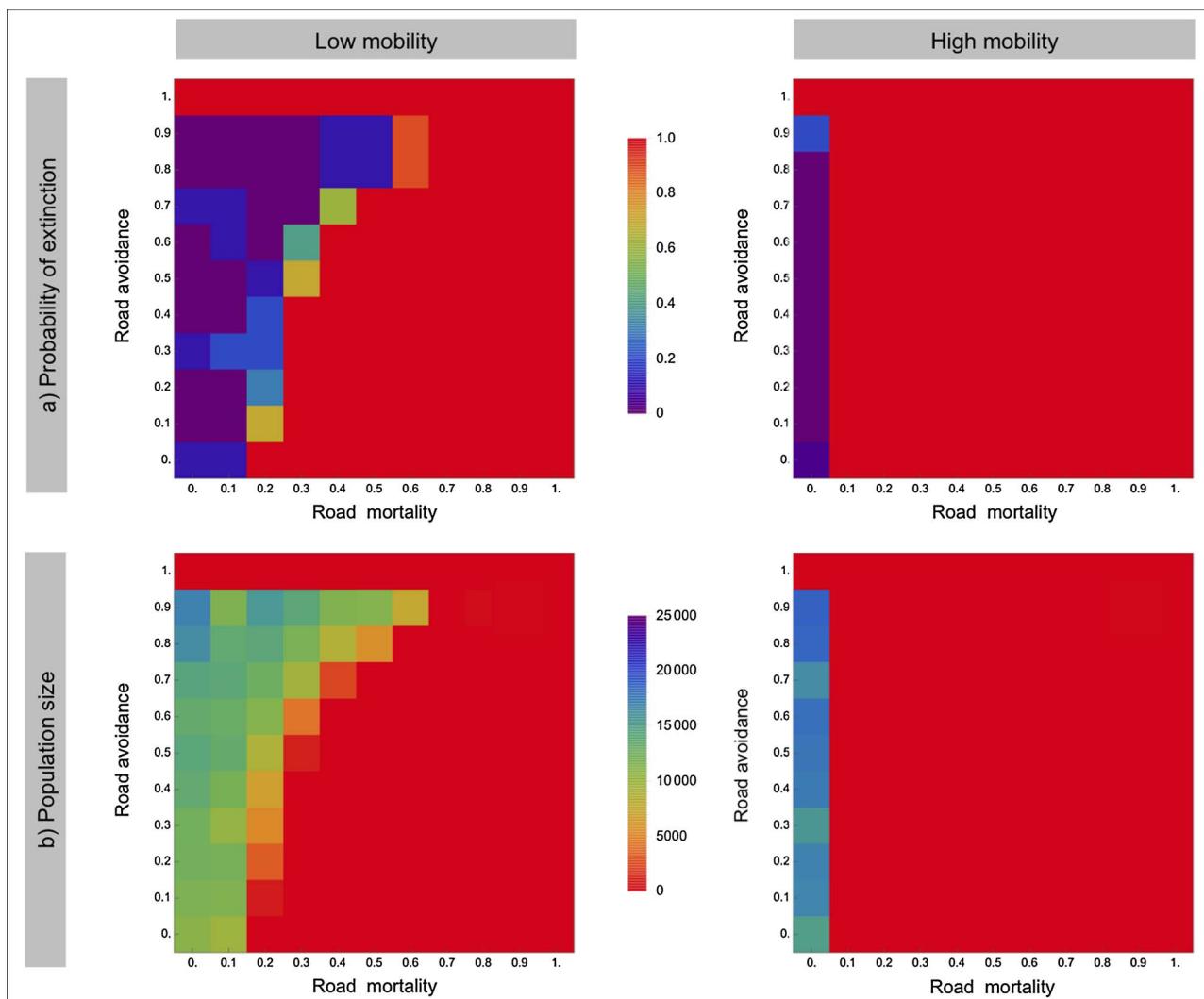


Fig. 5. Probability of population extinction (a) and population size (b) as a function of road mortality and road avoidance, for different dispersal distances (Low mobility = 5 cells; High mobility = 50 cells) in the landscape with the highest proportion of road cells in the landscape (0.35).

4.3. Limitations

The type of movement (juvenile dispersal) considered in our paper can have a large influence on individual fitness and population structure (Matthysen, 2012). However, our model does not currently include other types of movement (such as daily movements), and thus adults do not get killed due to road mortality. This is a simplification, because in real contexts animals will encounter roads during other types of movement as well. Therefore, it would be important to include such types of movement in the analysis.

Furthermore, in our model each juvenile disperses over a fixed number of cells, which implies that individuals may end their dispersal movement on a road (or right of way). This could correspond to situations where there are no other options for dispersal, e.g., all neighboring areas already occupied or corresponding to unsuitable habitat, but it should be considered as a simplification of real cases.

We used two dispersal distances in our simulations because we wanted to ensure that we were comparing the roles of contrasting dispersal distances, i.e., a short vs. a large dispersal distance. Including a wider range of dispersal distances could help further understand the role of dispersal in these fragmented landscapes, as some studies suggest there is an optimal intermediate dispersal rate for persistence in disturbed habitats (Casagrandi and Gatto, 1999).

We used a virtual species and simple hypothetical regular road

networks because our main goal was to disentangle the effects of road mortality versus those of a barrier effect without such mortality. However, this implies that our results hold for the virtual species in the regular road network used.

4.4. Conclusions and future research directions

Our results highlight the much higher relative importance of road mortality than the barrier effect (without road mortality), and of assessing relevant species traits such as dispersal distance. We emphasize three results of our study: first, that even though population persistence was not impaired when road avoidance was complete (except when suitable habitat patches became too small to sustain viable populations), population size was considerably decreased, which is important to consider in long-term conservation management; secondly, that a large dispersal distance is not necessarily always detrimental for population size and persistence in fragmented landscapes if mortality in unsuitable habitats is low, which calls for further investigation; and thirdly, that population isolation occurred in extreme cases (i.e., complete road mortality or a complete barrier effect without road mortality). These may be especially important for species expected (Rytwinski and Fahrig, 2013) or observed (e.g., some snakes and turtles; Shepard et al., 2008) to avoid roads, and for species for which road avoidance increases with increasing traffic volume (e.g., carnivores and

ungulates; Dyer et al., 2002; Alexander et al., 2005; Leblond et al., 2013).

Finally, our model can stimulate other studies, either theoretical or empirical. Our results hold for the virtual species in the regular road network used, but our model can be applied to species-specific situations, by using the specific trait values of the species or population of interest. Information on model parameter values (initial population size, fecundity, age at first breeding, survival probability, home range size, dispersal distance, road mortality, or road avoidance) can be obtained from published databases, individual studies, or derived from related or ecologically similar species, and using allometric relationships (e.g., Jones et al., 2009; Borda-de-Águia et al., 2014; Salguero-Gómez et al., 2016; Ceia-Hasse et al., 2017). For example, data on population density can be used to determine the initial population size. Data availability is usually higher for vertebrates and within these for mammals, followed by birds. This is also true for data on road mortality, and especially on road avoidance behavior, for which species-specific information is lacking for many species (Rytwinski and Fahrig, 2012).

Furthermore, although we used only simple hypothetical regular road networks in our simulations, the modelled landscape can represent real landscapes with real road configurations, and can hence also be used to evaluate the impact of different mitigation options for increasing population persistence, in environmental impact assessments, and for conservation planning.

Acknowledgments

We thank the anonymous reviewers and the editor for their helpful comments that contributed to considerably improve our paper. This work was supported by the DFG - German Research Foundation, by FEDER through the Operational Programme for Competitiveness Factors – COMPETE (POCI-01-0145-FEDER-006821) and by FCT - Foundation for Science and Technology (UID/BIA/50027/2013). ACH, LBA and HMP were funded by the Infraestruturas de Portugal Biodiversity Chair.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2018.01.021>.

References

- Alexander, S.M., Waters, N.M., Paquet, P.C., 2005. Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. *Can. Geogr. Géographie Can.* 49, 321–331.
- Ascensão, F., Clevenger, A., Santos-Reis, M., Urbano, P., Jackson, N., 2013. Wildlife–vehicle collision mitigation is partial fencing the answer? An agent-based model approach. *Ecol. Model.* 257, 36–43.
- Ascensão, F., Mata, C., Malo, J., Ruiz-Capillas, P., Silva, C., Silva, A., Santos-Reis, M., Fernandes, C., 2016. Disentangle the causes of the road barrier effect in small mammals through genetic patterns. *PLoS One* 11, e0151500.
- Austerlitz, F., Dick, C., Dutech, C., Klein, E., Oddou-Muratorio, S., Smouse, P., Sork, V., 2004. Using genetic markers to estimate the pollen dispersal curve. *Mol. Ecol.* 13, 937–954.
- Borda-de-Águia, L., Grilo, C., Pereira, H.M., 2014. Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. *Ecol. Model.* 276, 29–37.
- Borda-de-Águia, L., Navarro, L., Gavinhos, C., Pereira, H.M., 2011. Spatio-temporal impacts of roads on the persistence of populations: analytic and numerical approaches. *Landscape Ecol.* 26, 253–265.
- Börger, L., Dalziel, B.D., Fryxell, J.M., 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.* 11, 637–650.
- Casagrandi, R., Gatto, M., 1999. A mesoscale approach to extinction risk in fragmented habitats. *Nature* 400, 560–562.
- Ceia-Hasse, A., Borda-de-Águia, L., Grilo, C., Pereira, H.M., 2017. Global exposure of carnivores to roads. *Glob. Ecol. Biogeogr.* 26, 592–600.
- Charry, B., Jones, J., 2009. Traffic volume as a primary road characteristic impacting wildlife: a tool for land use and transportation planning. In: Wagner, P.J., Nelson, D., Murray, E. (Eds.), *Proceedings of the 2009 International Conference on Ecology and Transportation*, pp. 159–172.
- Chipperfield, J., Holland, E., Dytham, C., Thomas, C., Hovestadt, T., 2011. On the approximation of continuous dispersal kernels in discrete-space models. *Methods Ecol. Evol.* 2, 668–681.
- Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. (Eds.), 2012. *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Can. J. Zool.* (80), 839–845.
- Fahrig, L., Pedlar, J., Pope, S., Taylor, P., Wegner, J., 1995. Effect of road traffic on amphibian density. *Biol. Conserv.* (74), 177–182.
- Gibbs, J.P., 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecol.* 13, 263–268.
- Grilo, C., Reto, D., Filipe, J., Ascensão, F., Revilla, E., 2014. Understanding the mechanisms behind road effects: linking occurrence with road mortality in owls. *Anim. Conserv.* 17, 555–564.
- Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., Costa, M., Bernardo, J., Reto, D., Lourenço, R., Santos-Reis, M., Revilla, E., 2012. Individual spatial responses towards roads: implications for mortality risk. *PLoS One* 7, e43811.
- Grilo, C., Smith, D.J., Klar, N., 2015. Carnivores: struggling for survival in road landscapes. In: van der Ree, R., Smith, D.J., Grilo, C. (Eds.), *Handbook of Road Ecology*. John Wiley & Sons, Ltd, Chichester, UK, pp. 300–312.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned, and what could we learn in the future? *Ecol. Model.* 115, 129–148.
- Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. *Ecol. Model.* 198, 115–126.
- Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. *Ecol. Model.* 221, 2760–2768.
- Grimm, V., Berger, U., 2016. Structural realism, emergence, and predictions in next-generation ecological modelling: synthesis from a special issue. *Ecol. Model.* 326, 177–187.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townsend, J.R., 2015. Habitat fragmentation and its lasting impact on earth's ecosystems. *Sci. Adv.* 1, e1500052.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Jackson, N.D., Fahrig, L., 2011. Relative effects of road mortality and decreased connectivity on population genetic diversity. *Biol. Conserv.* 144, 3143–3148.
- Jaeger, J., 2007. Effects of the configuration of road networks on landscape connectivity. In: Irwin, C.L., Nelson, D., McDermott, K.P. (Eds.), *Proceedings of the 2007 International Conference on Ecology and Transportation*, pp. 267–280.
- Jaeger, J., Fahrig, L., Ewald, K., 2006. Does the configuration of road networks influence the degree to which roads affect wildlife populations? In: Irwin, C.L., Garrett, P., McDermott, K.P. (Eds.), *Proceedings of the 2005 International Conference on Ecology and Transportation*, pp. 151–163.
- Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., von Toschanowitz, K.T., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecol. Model.* 185, 329–348.
- Jaeger, J.A.G., Fahrig, L., 2004. Effects of road fencing on population persistence. *Conserv. Biol.* 18, 1651–1657.
- Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Scherst, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M., Purvis, A., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90, 2648.
- Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142, 911–927.
- Leblond, M., Dussault, C., Ouellet, J.-P., 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. *J. Zool.* 289, 32–40.
- Matthysen, E., 2012. Multicausality of dispersal: a review. In: Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. (Eds.), *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK, pp. 3–18.
- Maxwell, S., Fuller, R., Brooks, T., Watson, J., 2016. Biodiversity: the ravages of guns, nets and bulldozers. *Nature* 536, 143–145.
- Nathan, R., Klein, E., Robledo-Arnuncio, J., Revilla, E., 2012. Dispersal kernels: review. In: Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. (Eds.), *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK, pp. 187–210.
- Pereira, H.M., Borda-de-Águia, L., 2013. Modelling biodiversity dynamics in countryside and native habitats. *Encyclopedia of Biodiversity*. Elsevier, New York, pp. 321–328.
- Pereira, H.M., Daily, G.C., 2006. Modeling biodiversity dynamics in countryside landscapes. *Ecology* 87, 1877–1885.
- Pereira, H.M., Navarro, L.M., Martins, I.S., 2012. Global biodiversity change: the bad, the good, and the unknown. *Annu. Rev. Environ. Resour.* 37, 25–50.
- Pulliam, H.R., 1988. Sources, sinks, and population regulation. *Am. Nat.* 132, 652–661.
- Rytwinski, T., Fahrig, L., 2015. The impacts of roads and traffic on terrestrial animal populations. In: van Der Ree, R., Smith, D.J., Grilo, C. (Eds.), *Handbook of Road Ecology*. John Wiley & Sons, Ltd, Chichester, UK, pp. 237–246.

- Rytwinski, T., Fahrig, L., 2013. Why are some animal populations unaffected or positively affected by roads? *Oecologia* 173, 1143–1156.
- Rytwinski, T., Fahrig, L., 2012. Do species life history traits explain population responses to roads? A meta-analysis. *Biol. Conserv.* 147, 87–98.
- Salguero-Gómez, R., Jones, O.R., Archer, C.R., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y.M., Che-Castaldo, J., Hodgson, D., Scheuerlein, A., Caswell, H., Vaupel, J.W., 2016. COMADRE: a global data base of animal demography. *J. Anim. Ecol.* 85, 371–384.
- Seiler, A., 2005. Predicting locations of moose–vehicle collisions in Sweden. *J. Appl. Ecol.* 42, 371–382.
- Shepard, D.B., Kuhns, A.R., Dreslik, M.J., Phillips, C.A., 2008. Roads as barriers to animal movement in fragmented landscapes. *Anim. Conserv.* 11, 288–296.
- Skellam, J.G., 1951. Random dispersal in theoretical populations. *Bull. Math. Biol.* 53, 135–165.
- Turchin, P., 1998. Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants, Weimar and Now. Sinauer, pp. 13.
- van der Ree, R., Smith, D.J., Grilo, C., 2015. The ecological effects of linear infrastructure and traffic. In: van Der Ree, R., Smith, D.J., Grilo, C. (Eds.), *Handbook of Road Ecology*. John Wiley & Sons, Ltd, Chichester, UK, pp. 1–9.
- Van Houtan, K.S., Pimm, S.L., Halley, J.M., Bierregaard, R.O.J., Lovejoy, T.E., 2007. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecol. Lett.* 10, 219–229.
- van Langevelde, F., Jaarsma, C., 2009. Modeling the effect of traffic calming on local animal population persistence. *Ecol. Soc.* 14, 39.
- van Strien, M., Grêt-Regamey, A., 2016. How is habitat connectivity affected by settlement and road network configurations? Results from simulating coupled habitat and human networks. *Ecol. Model.* 342, 186–198.
- Zurell, D., Berger, U., Cabral, J.S., Jeitsch, F., Meynard, C.N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B., Grimm, V., 2010. The virtual ecologist approach: simulating data and observers. *Oikos* 119, 22–635.