Process-based models of biodiversity response to global change

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Summary

The present biodiversity crisis is unmatched. Despite increasing efforts from society to slow biodiversity loss, the status of biodiversity is projected to continue to decline. Improving our ability to understand and predict biodiversity responses to environmental change is fundamental to conserve biodiversity and inform conservation policies. Projections of change are essential for conservation planning, but more broadly they are needed to manage ecosystem services and functions.

The aims of this thesis were to develop modeling frameworks that contribute to better understand and predict biodiversity responses to environmental change. Process-based models are emphasized, and where possible, the integration with other approaches, using the integration of process-based models with macroecology, by incorporating different types of information, or by combining those with other types of models. The issues addressed were population persistence in fragmented landscapes (chapter 2), vulnerability to land-use change (chapter 3), and range shifts in response to climate change (chapter 4).

Chapter 2 of this thesis investigated factors driving population isolation, persistence and size in fragmented landscapes, using a spatially explicit individual-based model of population dynamics. Direct road mortality and road avoidance contribute to decreased population abundance, to population isolation and subdivision, and therefore to increased population extinction risk. Species traits such as dispersal have also been suggested to influence population responses to land-use change. However, the relative importance of these factors on the persistence of populations is still not fully understood. Chapter 2 assessed the effect of road mortality and of road avoidance, and their interaction with dispersal, on population isolation, persistence and size, in landscapes fragmented by varying levels of road density. Both road mortality and road avoidance caused population isolation, but road mortality alone had stronger negative effects than road avoidance alone. However, road avoidance also resulted in decreased population size, highlighting the importance of knowing both the levels of road mortality and of road avoidance for effective long-term conservation management. Populations with large dispersal distances were more negatively affected as road mortality increased, but maintained larger sizes than populations with a short dispersal distance when there was no road mortality. When road avoidance was complete, populations either went extinct, or maintained small sizes, suggesting that at least a small amount of dispersal is needed for population persistence. The model presented in chapter 2 can be adapted to species-specific situations and to represent real landscape configurations, and in this sense it can also be used in environmental impact assessments, and for conservation planning.

Chapter 3 of this thesis developed a spatially explicit modeling framework that combines a mechanistic population model with life history data, biogeographic data, and land-use data. This framework was used to assess the exposure of biodiversity to a major threat, the road infrastructure, and to map hotspots of road impact on biodiversity globally. Roads cause major impacts on populations, and

the road network is projected to expand in the coming years. However, studies evaluating the impact of roads on population persistence are still not common, center on a small number of species, and upscale, at best, to national levels. Assessments on larger scales, and across species, were never conducted. The evaluation performed in chapter 3 used a simple, spatially explicit demographic reaction-diffusion model that describes population dynamics and the dispersal of individuals. The framework was applied to a particularly vulnerable group - terrestrial mammalian carnivore species, and predicted that species are affected in regions with medium to high road density, but also in regions with relatively low road density. Hotspots of road impact were predicted for North America and Asia. Approximately one-third of the species expected to be more exposed to roads has not been identified by IUCN as threatened by roads. These species belong to families Felidae, Ursidae, Mustelidae, Canidae and Procyonidae. The approach presented in chapter 3 can be applied at different spatial scales and to evaluate the effects of road network development, as well as to identify species requiring specific mitigation or restoration measures.

Using different types of models under a common modeling framework may reduce uncertainty in projections of biodiversity response to environmental change. However, this approach is not generally adopted. This gap was addressed in chapter 4, using a physiologically inspired model of extinction to assess climate change induced range shifts for three reptile species in Europe, projected by phenomenological species distribution models. Climate change is a major driver of biodiversity change and is affecting the distribution and phenology of organisms. Agreement between model projections varied between species and depended on whether or not dispersal ability was considered. Under this approach, the reliability of predictions is greatest where the predictions of the different types of models converge. Both current high temperatures and significant future temperature increases characterize the sites where this convergence occurs, suggesting they may become hotspots of local extinctions for one of the species analysed, *Lacerta lepida*. In contrast, high temperatures during the breeding period in the future were not projected to impair population persistence for the other two species analysed, *Iberolacerta monticola* and *Hemidactylus turcicus*, indicating it may not be the most limiting factor for these species. By highlighting areas where high temperatures in the future may hinder (or allow) population persistence, the type of analysis performed in chapter 4 of this thesis can be an asset for conservation planning, such as the design of reserves or habitat restoration efforts.

Summing up, this thesis presents several modeling frameworks that contribute to: i) clarifying how population persistence may be affected by different factors in fragmented landscapes using an individual-based model of population dynamics that can be adapted to different contexts (chapter 2); ii) moving from a descriptive towards a mechanistic, more biologically sound evaluation of threats - in this case, the road infrastructure, by bringing together process-based models that explicitly link extrinsic factors of threat and intrinsic species traits (chapter 3); iii) improving projections of biodiversity response to environmental change, specifically range shifts in response to climate change, by applying process-based and phenomenological models under a common modeling framework (chapter 4).

Chapter 1. Introduction

1.1. Biodiversity change, and environmental change

The current biodiversity crisis is unparalleled (Pereira et al. 2012). The status of biodiversity is projected to continue declining even though society's efforts to decelerate this trend have been increasing (Tittensor et al. 2014). Biodiversity loss is driven by environmental change, which in turn is mainly driven by anthropogenic pressures (e.g., Brotons et al. 2016). Global environmental change includes habitat change, climate change, overexploitation, pollution, exotic species, and disease (Millennium Ecosystem Assessment 2005, Pereira et al. 2010, 2012).

Biodiversity responses to global environmental change include species extinctions, loss of genetic diversity, and changes in the abundance and in the distribution of species (Pereira et al. 2010, 2012). These responses therefore occur at different organizational levels, i.e., from the individual to the ecosystem or biome, and in space (e.g., range shifts), in time (e.g., changes in the onset of reproduction events), or in self (e.g., physiological adjustments) (Bellard et al. 2012).

How biodiversity responds to environmental change will depend on the nature, magnitude, and rate of those changes, and on eco-evolutionary processes such as demography, dispersal, physiology, or adaptation (Thuiller et al. 2013). Moreover, the impact of environmental changes on biodiversity will also be influenced by where biodiversity is, and where those environmental changes occur (Pimm et al. 2014).

1.2. Modeling biodiversity responses to environmental change

To conserve biodiversity and inform conservation policies, it is essential to better understand and predict biodiversity responses to environmental change. The impacts of environmental change on biodiversity and ecosystems, and on ecosystem services and human well-being, can be assessed through models (Brotons et al. 2016). Modeling also enables policy makers to evaluate the consequences of scenarios of change and of policy options (Pereira et al. 2010, Akçakaya et al. 2016), rendering modeling an important scientific tool to support decision making (Brotons et al. 2016).

Projections of change are essential for conservation planning (Thuiller 2007), but their accuracy needs to be improved to sustain ecosystem services and functions (Millennium Ecosystem Assessment 2005). Moreover, the uncertainty level in projections of biodiversity change is greater than had been previously acknowledged (Pereira et al. 2010).

The impacts of global environmental change on biodiversity can be estimated through a large variety of modeling approaches, at different levels of biological organization (from individuals to ecosystems), and at different scales (from the local to the global scale) (Brotons et al. 2016). The complexity and degree of formalization of models varies from expert-based models to quantitative models, which can be broadly categorized into phenomenological models, or process-based models (e.g., Pereira et al. 2010, Dormann et al. 2012).

This thesis focuses on process-based models. Process-based models are based explicitly on mathematical representations of processes or mechanisms (Pereira and Borda-de-Água 2013), determining the mechanistic interactions between the growth or fitness of an organism and its environment, using theoretical inferences, experiments, or both (Araújo 2009).

Examples of process-based models include source-sink models (e.g., Skellam 1951, Pulliam 1988), or metapopulation analysis (e.g., Hanski 1998). Source-sink models describe the dynamics of populations occupying several habitats within a landscape, and the movement of individuals between those habitats, where the population growth rate can be positive (source habitats), or negative (sink habitats). Metapopulation models consider a population that occupies several habitat patches within a matrix that is used only for dispersal, and analyses patch extinction and colonization rates (Pereira and Borda-de-Água 2013).

Process-based models also include physiological mechanistic models, which can infer range constraints and model potential distributions by establishing an explicit link between the energy and water requirements of an organism, and environmental availability (e.g., Kearney and Porter 2009, Kearney et al. 2010).

The aims of this thesis were to develop modeling frameworks that contribute to better understand and predict biodiversity responses to environmental change, and that could be applied to different circumstances, through the use of process-based models that integrate different types of information, or by combining them with other types of models. Specifically, the issues addressed were population persistence in fragmented landscapes (chapter 2), vulnerability to land-use change (chapter 3), and range shifts in response to climate change (chapter 4).

Chapter 2 assessed the importance of road mortality, of road avoidance, and of dispersal, for population isolation, persistence and size in landscapes fragmented by roads. This was done through an individual-based model of population dynamics. However, it may not be practical to perform simulations for many species, and for large spatial scales, with such an approach. In fact, process-based models have been mainly applied to a relatively small number of species, and to local scales (Pereira and Borda-de-Água 2013).

It is desirable to develop frameworks that allow the application of process-based models at a scale that is relevant for macroecological studies. In this sense, in chapter 3 a process-based model integrating different types of information (species traits, biogeography, and land-use data) was applied for a large number of species and at a large spatial scale, to assess species vulnerability to land-use change.

Specifically, chapter 3 assessed the exposure of terrestrial mammalian carnivore species to roads at the global level.

Process-based models can also be relevant for macroecology in reducing uncertainty in projections of biodiversity response to global environmental change, by applying them in combination with other types of models. This was addressed in chapter 4 of this thesis, where a process-based, physiologically inspired model of extinction was used to assess climate change induced range shifts projected by phenomenological species distribution models for reptile species.

1.3. Population persistence in fragmented landscapes

Land-use change is one of the main drivers of biodiversity loss (Pereira et al. 2012). Roads, one of many forms of land-use change, cause habitat loss, fragmentation, and decreased quality. As the road network is projected to expand in the coming years (van der Ree et al. 2015), it is essential to assess and predict its impacts on populations, in order to apply suitable mitigation measures, and improve conservation and road planning.

Roads also cause direct mortality through wildlife collisions with vehicles, and act as a barrier to movement, with several species showing road avoidance behavior (e.g., Jaeger and Fahrig 2004, Grilo et al. 2012). While road avoidance can rescue individuals from road mortality, the effects of habitat loss and fragmentation may be higher for species showing this type of response to roads (Rytwinski and Fahrig 2012). 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).

These direct and indirect impacts of roads can decrease population abundance, isolate and subdivide populations, and therefore can increase population extinction risk (van der Ree et al. 2015, Ascenção et al. 2016).

Population-level responses to land-use change can also be influenced by species traits (Pereira and Daily 2006), which should be considered when assessing the effects of roads. Specifically, dispersal has been recognized as an important factor but its effect on population persistence is still not fully understood. For example, in metapopulation models (e.g., Hanski 1998) the role of dispersal is beneficial, because more patches can be colonized if dispersal is large. In contrast, in source-sink models or reaction-diffusion models (e.g., Skellam 1951, Pulliam 1988) a large dispersal is disadvantageous, because it can occur into habitats where population growth rates are negative (sink habitats) (Pereira and Borda-de-Água 2013).

Several empirical studies have suggested that dispersal has a negative effect in disturbed habitats (e.g., Gibbs 1998, Van Houtan et al. 2007). In the case of roads, a higher mobility has been related with negative effects of roads in mammal and bird species (Rytwinski and Fahrig 2012). Borda-de-Água et al. (2011) predicted that the minimum area necessary for a population to persist in a landscape fragmented by roads would increase with the mean dispersal distance.

The effects of roads on population abundance are in general negative and relatively well studied (Rytwinski and Fahrig 2015). However, the impact of roads on population persistence has not been so commonly addressed (but see, for example, Borda-de-Água et al. 2014). Additionally, disentangling the factors that drive population isolation, and their effects on population persistence and size, as well as the influence of dispersal, still needs further investigation. In this thesis these issues were addressed in chapter 2 by using a spatially explicit, process-based model of population dynamics.

1.4. Vulnerability to land-use change

Several models have been used to estimate the impacts of land-use change on biodiversity. For example, the species-area relationship, which predicts the number of species as a function of area, has been applied to a wide variety of taxa at different scales (for a review see, for example, Drakare et al. 2006). The PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project is modeling how biodiversity responds to human activities (e.g., Newbold et al. 2015), using a database that contains spatial data from around the world on local terrestrial biodiversity, together with type and intensity of anthropogenic pressures (Hudson et al. 2014). The GLOBIO3 model uses mean species abundance to assess past, present and future responses of biodiversity to environmental drivers, including fragmentation or infrastructure development, at different spatial scales (Alkemade et al. 2009).

Roads cause major impacts on populations, and the road network is projected to expand in the coming years (van der Ree et al. 2015). The effect of roads on animal populations has been studied at the local and regional scales, focusing on behavioral and physiological responses to roads (Grilo et al. 2012, Navarro-Castilla et al. 2014), the effect of road noise and pollution (Hopkins et al. 2013, McClure et al. 2013), and projections of population declines and loss of genetic diversity (Jackson and Fahrig 2011). However, studies that assess the impact of roads on population persistence remain uncommon. Moreover, they upscale, at best, to national levels, focusing on a limited number of species (e.g., Beaudry et al. 2008). Assessments on larger scales up to global, and across species, have never been conducted (but see Torres et al. 2016).

This thesis assessed the exposure of terrestrial mammalian carnivore species to the road infrastructure, and mapped hotspots of road impact globally. This was done by developing a spatially explicit modeling framework that combines a mechanistic population model (Skellam 1951) with life history data, biogeographic data, and land-use data (chapter 3). Mammalian carnivores may be especially vulnerable to human-induced environmental changes due to their life history traits, such as relatively high mobility and low reproductive rates (Grilo et al. 2015). Moreover, they are important for maintaining ecosystem function, structure and resilience (Ripple et al. 2014).

This assessment used a simple, spatially explicit demographic reaction-diffusion model describing population dynamics and the dispersal of individuals (Skellam 1951; see also Cantrell & Cosner, 2003). This model can be used to simulate source-sink dynamics (Pulliam 1988) of populations occupying several habitats within a landscape, where the population growth rate can be positive in favourable habitats (source habitats), or negative in unfavourable habitats (sink habitats; e.g., roads) (Pereira and Borda-de-Água 2013). It has been used to assess species vulnerability to land-use change (Pereira et al. 2004, Pereira and Daily 2006), and to develop metrics to analyse the impact of road networks on population persistence (Borda de Água et al. 2011). These metrics predict how road density and patch size affect population viability in landscapes fragmented by roads. In particular, the model shows that the minimum patch size necessary for a population to persist increases with population mean dispersal distance, and decreases with intrinsic population growth rate (Borda de Água et al. 2011).

Despite not taking into account several factors that influence how populations are affected by roads - e.g. the behaviour of species, type of road, traffic intensity and habitat loss (Jaeger and Fahrig 2004, Jaeger et al. 2005), the framework developed in chapter 3 of this thesis opens the way for similar global mechanistic assessments of other threats.

1.5. Range shifts in response to climate change

Besides process-based models, another class of quantitative models that can be used to estimate the impacts of environmental change on biodiversity are phenomenological models (Pereira et al. 2010, Dormann et al. 2012). Phenomenological models relate observable variables, but in contrast with process-based models, do not postulate the mechanisms that underlie those relations (Pereira and Borda-de-Água 2013, Brotons et al. 2016). For example, the species-area relationship predicts changes in the number of species as a function of changes in area (e.g., Drakare et al. 2006), without explicitly stating the processes that lead to the relation between the two (Pereira and Borda-de-Água 2013). Bioclimatic envelope models are also phenomenological models that establish statistical relationships between current species distributions and environmental variables, to project the future distribution of a species under projected environmental change (Heikkinen et al. 2006, Zimmermann et al. 2010).

When comparing process-based with phenomenological models, one of the main advantages of phenomenological models is their relative simplicity (Morin and Thuiller 2009). Process-based models require more parameters, and more natural history and physiological knowledge, than phenomenological models (Thuiller 2007, Pereira and Borda-de-Água 2013). Phenomenological models can capture ecological processes implicitly (Elith et al. 2010), but may fail to predict range dynamics accurately

(Buckley et al. 2010). Process-based models are expected to be more robust under new environmental conditions, but their success depends on the identification of the key limiting processes (Elith et al. 2010).

One such model, that defines the interaction between organisms and their environment based on theoretical inferences (Araújo 2009), is the model proposed by Sinervo et al. (2010). Climate change is one of the major drivers of biodiversity change (Bellard et al. 2012) and is affecting the distribution and phenology of organisms (Parmesan 2006). Using a simple, spatially explicit physiologically inspired model of extinction, Sinervo et al. (2010) predicted extinction rates for reptiles due to climate warming. This model assumes that restriction in activity due to hot weather during the breeding period of lizards may lead to population extinction by constraining foraging, and therefore the accumulation of the amount of energy that is necessary for reproduction and population growth or stability (Sinervo et al. 2010). Reptiles are an excellent model system for explicitly incorporating such thermal constraints when modeling range shifts in response to climate change, because being ectothermic their physiology and distribution are more directly influenced by environmental temperature than in endothermic vertebrates (Buckley et al. 2012).

Several authors have suggested that using different types of models provides independent lines of evidence that may confer accuracy to projections where these converge (Hijmans and Graham 2006, Kearney and Porter 2009, Morin and Thuiller 2009). This approach has been used to predict range shifts in response to climate change for plants (Hijmans and Graham 2006, Morin and Thuiller 2009) and several animal groups (e.g., lizards: Buckley et al. 2010, mammals: Kearney et al. 2010, butterflies: Buckley et al. 2010, 2011), as well as for invasive species (Elith et al. 2010). However, this procedure is still not commonly undertaken (Leadley et al. 2010). This thesis addressed this gap in chapter 4 by combining two types of models with the aim of improving projections of change. The modeling approach consisted of using the physiologically inspired model of extinction of Sinervo et al. (2010) to assess phenomenological species distribution model projections of reptile range shifts, in response to climate change.

1.6. Outline of the thesis

The research presented in this thesis is summarized in Fig. 1. In chapter 2, factors driving population isolation, persistence and size in landscapes fragmented by roads were investigated using a spatially explicit individual-based model of population dynamics. This model keeps track of the features of the landscape and of the number of females in the population. Different sets of simulations were performed, where the probabilities of road mortality and of road avoidance, as well as the magnitude of dispersal distance were varied, in several theoretical landscapes with different road densities. Population isolation, size and persistence were compared between simulations performed with different combinations of values of parameters. This model can be used to represent species-specific situations, and real road configurations or other types of fragmented landscapes. The work presented in this chapter is currently a manuscript: Ceia Hasse A., Navarro L., Borda-de-Água L., Pereira H.M., Population persistence in fragmented landscapes: disentangling isolation, road mortality, and the effect of dispersal.

Chapter 3 performed a multispecies evaluation to assess which terrestrial mammalian carnivore species are more exposed to roads at the global level, as well as where within their range those species are most at risk. Species exposure to roads was ranked by first estimating for each species the maximum road density and the minimum patch size beyond which populations are expected to go extinct. These metrics were then compared with the road density and the habitat fragment sizes that are observed within each species range, which were obtained by intersecting global road density with each species range. This framework can be applied at different spatial scales and to evaluate the effects of road network development, as well as to identify species requiring specific mitigation or restoration measures. The work presented in this chapter is provisonally accepted for publication pending minor corrrections revision in Global Ecology and Biogeography as: Ceia Hasse A., Borda-de-Água L., Grilo C., Pereira H.M., Global exposure of carnivores to roads.

In chapter 4, the outputs of a simple spatially explicit physiologically inspired model of extinction that predicted extinction rates for reptiles due to climate warming were integrated with the projections of phenomenological species distribution models to assess climate-change induced range shifts of three reptile species for the coming decades in Europe. The two types of models were integrated by mapping and quantifying agreement and disagreement between their projections. Under this framework, the reliability of predictions is greatest where the predictions of the models converge. The relationships between climate change and projected range shifts were also analyzed, illustrating how this approach can contribute to a better understanding of the constraints underlying species range limits. The work presented in this chapter was published as: Ceia Hasse A., Sinervo B., Vicente L., Pereira H.M. (2014) Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. Ecography 37: 679-688.

Chapter 5 provides a synthesis and discussion of the main results obtained from the previous chapters, and considers implications for future research.

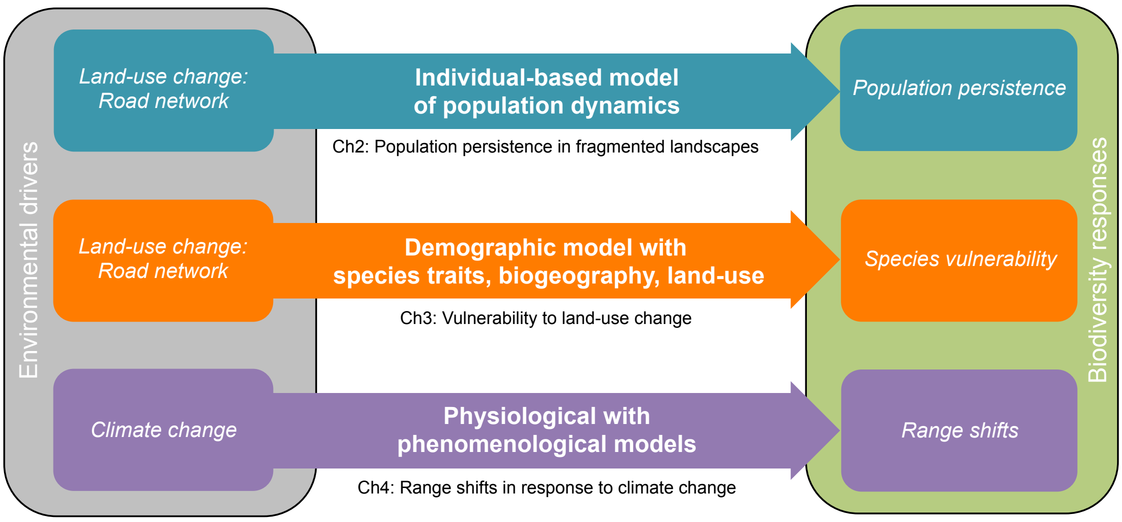

Fig. 1. Structure of the thesis. This thesis developed several approaches to model biodiversity responses to environmental change, using process-based models integrating different types of information, or in combination with phenomenological models. The types of modeling approaches used, the environmental driver considered and the biodiversity response modeled in each chapter are indicated.

1.7. References

Akçakaya HR, Pereira HM, Canziani GA, Mbow C, Mori A, Palomo MG, Soberon J, Thuiller W, Yachi S (2016) Improving the rigour and usefulness of scenarios and models through ongoing evaluation and refinement. In: Ferrier S, Ninan KN, Leadley P, Alkemade R, Acosta LA, Akçakaya HR, Brotons L, Cheung WWL, Christensen V, Harhash KA, Kabubo-Mariara J, Lundquist C, Obersteiner M, Pereira H, Peterson G, Pichs-Madruga R, Ravindranath N, Rondinini C, Wintle BA (Eds.) IPBES, 2016: Methodological assessment of scenarios and models of biodiversity and ecosystem services. Secretariat of the Intergovernmental Platform for Biodiversity and Ecosystem Services, Bonn, Germany.

Alkemade R, Van Oorschot M, Miles L, Nellemann C, Bakkenes M, ten Brink B (2009) GLOBIO3: A Framework to Investigate Options for Reducing Global Terrestrial Biodiversity Loss. Ecosystems 12: 374-390.

Araújo MB (2009) Climate change and spatial conservation planning. In: Moilanen A, Wilson KA, Possingham H (Eds.) Spatial conservation prioritization: quantitative methods and computational tools. Oxford University Press. Pp. 172-184.

Ascensão F, Mata C, Malo JE, Ruiz-Capillas P, Silva C, Silva AP, Santos-Reis M, Fernandes C (2016) Disentangle the Causes of the Road Barrier Effect in Small Mammals through Genetic Patterns. PLoS ONE 11: e0151500.

Beaudry F, deMaynadier PG, Hunter MLJ (2008) Identifying road mortality threat at multiple spatial scales for semi-aquatic turtles. Biological Conservation 141: 2550-2563.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecology Letters 15: 365-377.

Borda-de-Água L, Grilo C, Pereira HM (2014) Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. Ecological Modelling 276: 29-37.

Borda-de-Água L, Navarro L, Gavinhos C, Pereira HM (2011) Spatio-temporal impacts of roads on the persistence of populations: analytic and numerical approaches. Landscape Ecology 26: 253-265.

Brotons L, Christensen V, Ravindranath NH, Cao M, Chun JH, Maury O, Peri PL, Proença V, Salihoglu B (2016) Modelling impacts of drivers on biodiversity and ecosystems. In: Ferrier S, Ninan KN, Leadley P, Alkemade R, Acosta LA, Akçakaya HR, Brotons L, Cheung WWL, Christensen V, Harhash KA, Kabubo-Mariara J, Lundquist C, Obersteiner M, Pereira H, Peterson G, Pichs-Madruga R, Ravindranath N, Rondinini C, Wintle BA (Eds.) IPBES, 2016: Methodological assessment of scenarios and models of biodiversity and ecosystem services. Secretariat of the Intergovernmental Platform for Biodiversity and Ecosystem Services, Bonn, Germany.

Buckley LB, Hurlbert AH, Jetz W (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. Global Ecology and Biogeography 21: 873-885.

Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? Ecology Letters 13: 1041-1054.

Buckley LB, Waaser SA, MacLean HJ, Fox R (2011) Does including physiology improve species distribution model predictions of responses to recent climate change? Ecology 92: 2214-2221.

Cantrell RS, Cosner C (2003) Spatial ecology via reaction-diffusion equations. John Wiley & Sons, Chichester, UK.

Dormann CF, Schymanski SJ, Cabral J, Chuine I, Graham C, Hartig F, Kearney M, Morin X, Römermann C, Schröder B, Singer A (2012) Correlation and process in species distribution models: bridging a dichotomy. Journal of Biogeography 39: 2119-2131.

Drakare S, Lennon JJ, Hillebrand H (2006) The imprint of the geographical, evolutionary and ecological context on species-area relationships. Ecology Letters 9: 215-227.

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1: 330-342.

Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biological Conservation 74: 177-182.

Gibbs JP (1998) Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13: 263-268.

Grilo C, Smith DJ, Klar N (2015) Carnivores: struggling for survival in roaded landscapes. In: van Der Ree R, Smith DJ, Grilo C. (Eds.) Handbook of Road Ecology. John Wiley & Sons, Ltd, Chichester, UK. Pp. 300-312.

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.

Hanski I (1998) Metapopulation dynamics. Nature 396: 41-49.

Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30: 751-777.

Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology 12: 2272-2281.

Hopkins GR, French SS, Brodie EDJ (2013) Increased frequency and severity of developmental deformities in rough-skinned newt (*Taricha granulosa*) embryos exposed to road deicing salts (NaCl & MgCl2). Environmental Pollution 173: 264-269.

Hudson LN, Newbold T, Contu S, Hill SLL, Lysenko I, De Palma A, Phillips HRP, Senior RA, Bennett DJ, Booth H, Choimes A, Correia DLP, Day J, Echeverría-Londoño S, Garon M, Harrison MLK, Ingram DJ, Jung M, Kemp V, Kirkpatrick L, Martin CD, Pan Y, White HJ, Aben J, Abrahamczyk S, Adum GB, Aguilar-Barquero V, Aizen MA, Ancrenaz M, Arbeláez-Cortés E, Armbrecht I, Azhar B, Azpiroz AB, Baeten L, Báldi A, Banks JE, Barlow J, Batáry P, Bates AJ, Bayne EM, Beja P, Berg Å, Berry NJ, Bicknell JE, Bihn JH, Böhning-Gaese K, Boekhout T, Boutin C, Bouyer J, Brearley FQ, Brito I, Brunet J, Buczkowski G, Buscardo E, Cabra-García J, Calviño-Cancela M, Cameron SA, Cancello EM, Carrijo TF, Carvalho AL, Castro H, Castro-Luna AA, Cerda R, Cerezo A, Chauvat M, Clarke FM, Cleary DFR, Connop SP, D'Aniello B, da Silva PG, Darvill B, Dauber J, Dejean A, Diekötter T, Dominguez-Haydar Y, Dormann CF, Dumont B, Dures SG, Dynesius M, Edenius L, Elek Z, Entling MH, Farwig N, Fayle TM, Felicioli A, Felton AM, Ficetola GF, Filgueiras BKC, Fonte SJ, Fraser LH, Fukuda D, Furlani D, Ganzhorn JU, Garden JG, Gheler-Costa C, Giordani P, Giordano S, Gottschalk MS, Goulson D, Gove AD, Grogan J, Hanley ME, Hanson T, Hashim NR, Hawes JE, Hébert C, Helden AJ, Henden J-A, Hernández L, Herzog F, Higuera-Diaz D, Hilje B, Horgan FG, Horváth R, Hylander K, Isaacs-Cubides P, Ishitani M, Jacobs CT, Jaramillo VJ, Jauker B, Jonsell M, Jung TS, Kapoor V, Kati V, Katovai E, Kessler M, Knop E, Kolb A, Kőrösi Á, Lachat T, Lantschner V, Le Féon V, LeBuhn G, Légaré J-P, Letcher SG, Littlewood NA, López-Quintero CA, Louhaichi M, Lövei GL, Lucas-Borja ME, Luja VH, Maeto K, Magura T, Mallari NA, Marin-Spiotta E, Marshall EJP, Martínez E, Mayfield MM, Mikusinski G, Milder JC, Miller JR, Morales CL, Muchane MN, Muchane M, Naidoo R, Nakamura A, Naoe S, Nates-Parra G, Navarrete Gutierrez DA, Neuschulz EL, Noreika N, Norfolk O, Noriega JA, Nöske NM, O'Dea N, Oduro W, Ofori-Boateng C, Oke CO, Osgathorpe LM, Paritsis J, Parra-H A, Pelegrin N, Peres CA, Persson AS, Petanidou T, Phalan B, Philips TK, Poveda K, Power EF, Presley SJ, Proença V, Quaranta M, Quintero C, Redpath-Downing NA, Reid JL, Reis YT, Ribeiro DB, Richardson BA, Richardson MJ, Robles CA, Römbke J, Romero-Duque LP, Rosselli L, Rossiter SJ, Roulston TaH, Rousseau L, Sadler JP, Sáfián S, Saldaña-Vázquez RA, Samnegård U, Schüepp C, Schweiger O, Sedlock JL, Shahabuddin G, Sheil D, Silva FAB ,Slade EM, Smith-Pardo AH, Sodhi NS, Somarriba EJ, Sosa RA, Stout JC, Struebig MJ, Sung Y-H, Threlfall CG ,Tonietto R, Tóthmérész B, Tscharntke T, Turner EC, Tylianakis JM, Vanbergen AJ, Vassilev K, Verboven HAF, Vergara CH, Vergara PM, Verhulst J, Walker TR, Wang Y, Watling JI, Wells K, Williams CD, Willig MR, Woinarski JCZ, Wolf JHD, Woodcock BA, Yu DW, Zaitsev AS, Collen B, Ewers RM, Mace GM, Purves DW, Scharlemann JPW, Purvis A (2014) The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. Ecology and Evolution 4: 4701-4735.

Jackson ND, Fahrig L (2011) Relative effects of road mortality and decreased connectivity on population genetic diversity. Biological Conservation 144: 3143-3148.

Jaeger JAG, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, von Toschanowitz KT (2005) Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185: 329-348.

Jaeger JAG, Fahrig L (2004) Effects of road fencing on population persistence. Conservation Biology 18: 1651-1657.

Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12: 334-350.

Kearney M, Wintle BA, Porter WP (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters 3: 203-213.

Leadley PW, Pereira HM, Alkemade R, Fernandez-Manjarrés J, Proença V, Scharlemann JPW, Walpole M (2010) Biodiversity Scenarios: Projections of 21st century change in biodiversity and associated ecosystem services. Secretariat of the Convention on Biological Diversity, Montreal. 132 p.

McClure CJW, Ware HE, Carlisle J, Kaltenecker G, Barber JR (2013) An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proceedings of the Royal Society of London Series B 280: 20132290.

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC. 86 p.

Morin X, Thuiller W (2009) Comparing niche-and process based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90: 1301-1313.

Navarro-Castilla Á, Mata C, Ruiz-Capillas P, Palme R, Malo JE, Barja I (2014) Are Motorways Potential Stressors of Roadside Wood Mice (*Apodemus sylvaticus*) Populations? PLoS ONE 9: e91942.

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Börger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Díaz S, Echeverria-Londoño S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White H, Ewers RM, Mace GM, Scharlemann JPW, Purvis A (2015) Global effects of land use on local terrestrial biodiversity. Nature 520: 45-50.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37: 637-669.

Pereira HM, Borda-de-Água L (2013) Modelling biodiversity dynamics in countryside and native habitats. In: Levin SA (Ed.) Encyclopedia of Biodiversity. Elsevier, New York. Pp. 321-328.

Pereira HM, Daily GC (2006) Modeling biodiversity dynamics in countryside landscapes. Ecology 87: 1877-1885.

Pereira HM, Daily GC, Roughgarden J (2004) A framework for assessing the relative vulnerability of species to land-use change. Ecological Applications 14: 730-742.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for Global Biodiversity in the 21st Century. Science 330: 1496-1501.

Pereira HM, Navarro LM, Martins IS (2012) Global Biodiversity Change: The Bad, the Good, and the Unknown. Annual Review of Environment and Resources 37: 25-50.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science 344: 1246752.

Pulliam HR (1988) Sources, sinks, and population regulation. American Naturalist 132: 652-661.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith DW, Wallach AD, Wirsing AJ (2014) Status and Ecological Effects of the World's Largest Carnivores. Science 343: 1241484.

Rytwinski T, Fahrig L (2012) Do species life history traits explain population responses to roads? A meta-analysis. Biological Conservation 147: 87-98.

Rytwinski T, Fahrig L (2015) The Impacts of Roads and Traffic on Terrestrial Animal Populations. In: van Der Ree R, Smith DJ, Grilo C. (Eds.) Handbook of Road Ecology. John Wiley & Sons, Ltd, Chichester, UK. Pp. 237-246.

Sinervo B, Mendez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, Gadsden H, Avila L, Morando M, De La Riva I, Sepulveda P, Rocha C, Ibargüengoytía N, Puntriano C, Massot M, Lepetz V, Oksanen T, Chapple D, Bauer A, Branch W, Clobert J, Sites J (2010) Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894-899.

Skellam JG (1951) Random dispersal in theoretical populations. Bulletin of Mathematical Biology 53: 135-165.

Thuiller W (2007) Biodiversity: climate change and the ecologist. Nature 448: 550-552.

Thuiller W, Münkemüller T, Lavergne S, Mouillot D, Mouquet N, Schiffers K, Gravel D (2013) A road map for integrating eco-evolutionary processes into biodiversity models. Ecology Letters 16: 94-105.

Tittensor DP, Walpole M, Hill SLL, Boyce DG, Britten GL, Burgess ND, Butchart SHM, Leadley PW, Regan EC, Alkemade R, Baumung R, Bellard C, Bouwman L, Bowles-Newark NJ, Chenery AM, Cheung WWL, Christensen V, Cooper HD, Crowther AR, Dixon MJR, Galli A, Gaveau V, Gregory RD, Gutierrez NL, Hirsch TL, Höft R, Januchowski-Hartley SR, Karmann M, Krug CB, Leverington FJ, Loh J, Lojenga RK, Malsch K, Marques A, Morgan DHW, Mumby PJ, Newbold T, Noonan-Mooney K, Pagad SN, Parks BC, Pereira HM, Robertson T, Rondinini C, Santini L, Scharlemann JPW, Schindler S, Sumaila UR, Teh LSL, van Kolck J, Visconti P, Ye Y (2014) A mid-term analysis of progress toward international biodiversity targets. Science 346: 241-244.

Torres A, Jaeger JAG, Alonso JC (2016) Assessing large-scale wildlife responses to human infrastructure development. Proceedings of the National Academy of Sciences, 113: 8472-8477.

van der Ree R, Smith DJ, Grilo C (2015) The Ecological Effects of Linear Infrastructure and Traffic. In: van Der Ree R, Smith DJ, Grilo C. (Eds.) Handbook of Road Ecology. John Wiley & Sons, Ltd, Chichester, UK. Pp. 1-9.

Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO Jr, Lovejoy TE (2007) Dispersal of Amazonian birds in continuous and fragmented forest. Ecology Letters 10: 219-229.

Zimmermann NE, Edwards TC, Graham CH, Pearman PB, Svenning, J-C (2010) New trends in species distribution modelling. Ecography 33: 985-989.

Chapter 2. Population persistence in fragmented landscapes

The work presented in this chapter is currently a manuscript: Ceia Hasse A. [1,2,3,*], Navarro L. [1,2], Borda-de-Água L. [3,4], Pereira H.M. [1,2,3,4], Population persistence in fragmented landscapes: disentangling isolation, road mortality, and the effect of dispersal.

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2.1. ABSTRACT

Linear infrastructures, one of several forms of land-use change, are a major driver of biodiversity loss. Roads impacts populations at many levels, with direct road mortality or road avoidance contributing to decreased population abundance, isolation and subdivision, and therefore to increased extinction risk. While species traits such as dispersal have been identified as playing a role in population level responses to land-use change, the influence of these factors on population persistence is still not fully understood. In this paper we used a spatially explicit process-based model of population dynamics to assess the effect of road mortality and road avoidance, and their interaction with dispersal, on population isolation, persistence and size, in landscapes fragmented by varying levels of road density. Both road mortality and road avoidance caused population isolation. While road mortality alone had stronger negative effects than road avoidance alone, avoidance also resulted in decreased population size. Yet, road avoidance could, in some cases, rescue populations from extinction. Populations with large dispersal distances 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 importance of knowing both the levels of road mortality and of road avoidance for effective long-term conservation management. Our model can be adapted to species-specific situations and to represent real landscape configurations, and can also be used in environmental impact assessments, and for conservation planning.

Keywords: Linear infrastructures, roads, isolation, persistence, abundance, mortality, avoidance, dispersal, individual-based model

2.2. INTRODUCTION

The current biodiversity crisis is mainly driven by land-use change (Pereira et al. 2012). Roads, one of many forms of land-use change, cause major impacts on populations. As the road network is predicted to increase in the coming years (van der Ree et al. 2015), it is crucial to assess and predict 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), with several species showing road avoidance behavior (e.g., Jaeger and Fahrig 2004, Grilo et al. 2012). Although road avoidance can rescue individuals from road mortality to some extent, the negative effects of habitat loss and fragmentation may be higher for species exhibiting this type of response to roads (Rytwinski and Fahrig 2012). These direct and indirect impacts of roads can contribute to decreases in population abundance, to population isolation and subdivision, and therefore can increase population extinction risk (van der Ree et al. 2015, Ascenção 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).

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., Pulliam 1988, Skellam 1951) dispersal affects populations negatively, because it can occur into habitats where population growth rates are negative (sink habitats) (Pereira and Borda-de-Água 2013). The detrimental effect of dispersal in disturbed habitats has been further suggested by several empirical studies (e.g., Gibbs 1998, Van Houtan et al. 2007). In the specific case of roads, a higher mobility has been related with 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.

Although the effects of roads on population abundance are in general negative and relatively well studied (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). Hence, disentangling the effects of isolation *versus* mortality, and their effects on population size and persistence, as well as the influence of dispersal, still need further investigation. In this paper we address these issues by using a spatially explicit, process-based model of population dynamics. Our questions are: 1) What is the importance of road mortality *versus* isolation, for population persistence and size in landscapes fragmented by roads?; and 2) How does dispersal influence the size and the persistence of populations under varying levels of road mortality and of road avoidance?

2.3. METHODS

We used a spatially explicit individual-based model of population dynamics applied in landscapes generated with different road densities. The model keeps track of two entities: the features of the landscape and the number of females in the population. The model parameters and values used in the simulations are presented in Table 2.1.

Landscape simulations

The landscape is a two dimensional grid of N x N cells with reflecting boundaries. Each cell of the landscape is assigned to one of n possible habitats with habitat quality values varying between 0 (minimum habitat quality) and 1 (maximum habitat quality). In the present case, each cell belongs to one of two possible habitats, "good" habitat or "road", with habitat quality values of "1" and "0", respectively. We created several landscapes with different proportions of road cells (see Table 2.1), where roads were placed perpendicularly to one another.

Population dynamics model

The model starts by settling in the landscape an initial population of individuals in breeding age. Note that the model only considers female individuals. After the initial population is created, each simulation time step consists of the following sequential events (Fig. 2.1a.):

Reproduction: Females reproduce once they have established their home range and reached their breeding age. The number of female juveniles that a breeding female produces follows a Poisson distribution with mean equal to her fecundity b_i, given by, $b_i = b_0 * H(x_i,y_i)$, where b_0 is maximum annual fecundity and $H(x_i,y_i)$ is the quality of the habitat of the home range of female i.

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.

Dispersal of juveniles: Each juvenile disperses over a fixed distance from its mother cell. A dispersal step is composed of the following events (Fig. 2.1b): 1) the individual evaluates whether its four neighboring cells are occupied or free, and can avoid dispersing through occupied cells with a probability (probability of occupied cells avoidance, p_{OA}); 2) the individual evaluates whether the free neighboring cells correspond to sink habitat (roads) or not, and avoids road cells with a probability (probability of road avoidance, p_{RA}); 3) if the individual disperses through a road cell, sink dispersal mortality (road mortality) is applied with a probability (probability of road mortality, p_{RM}); Those steps are repeated until the individual either dies, or disperses over his maximum dispersal distance (d) (see Table 2.1 for the specific values of the parameters used in our simulations). If the cell in which the individual is at the end of dispersal is occupied, or it is a road, dispersal is unsuccessful. If dispersal is successful, the individual can settle a home range. In the present study, each individual has a home range size of one cell, and we assume that home ranges of different individuals do not overlap.

Juvenile density-dependent mortality: Following unsuccessful dispersal, juveniles that did not establish their home range are removed from the population.

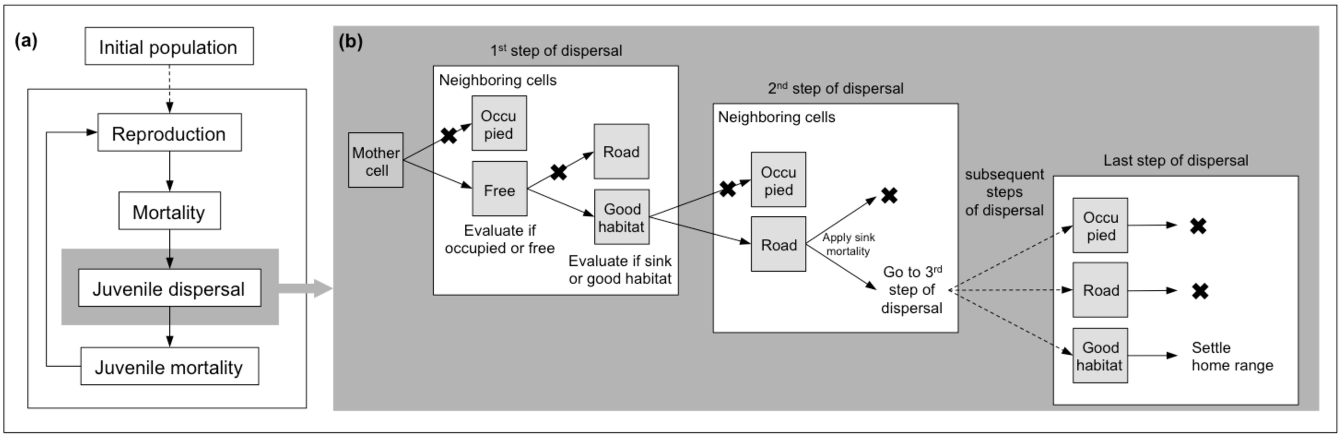


Fig. 2.1. Scheme of the model. (a) Schematic representation of the complete model simulation steps. The model starts by seeding the landscape with an initial population of females. Each simulation time step then consists of 1) reproduction of individuals in breeding age; 2) mortality of adults and juveniles; 3) dispersal of juveniles; 4) juvenile density-dependent mortality (see text for further details). (b) Schematic representation of juvenile dispersal. Juveniles evaluate neighboring cells in relation to occupancy and type of habitat while dispersing from their mother cell. In the example represented, in the first step of dispersal the individual initially evaluates which neighboring cells are occupied and which are free ("Evaluate if occupied or free"), and then chooses to disperse through a free cell of good habitat over a free cell that corresponds to a road ("Evaluate if sink or good habitat"). In the second step of dispersal, the individual chooses a road cell to disperse through (over an occupied cell), where it can suffer road dispersal mortality with a given probability ("Apply sink mortality"). In this situation the individual can either die, or continue dispersing (if it survives road mortality). In the last step of dispersal, if the individual ends up in an occupied cell, or in a road cell, it will be removed from the population. In contrast, if the individual ends up in a "good" habitat cell, it can settle a home range.

The individual-based model was implemented as an ANSI C++ program, which can be downloaded from https://github.com/anaceiahasse/landsim

Simulations

We created five landscapes with perpendicular roads, each with a different proportion of road cells (see Table 2.1). We used two dispersal distances: short (5 cells), and large (50 cells). We performed two sets of simulations. In the first set, we modeled the population size and the probability of extinction as a function of road density, for each dispersal distance, using the minimum and maximum values for road mortality and road avoidance, i.e., setting road mortality and road avoidance probabilities to 0 or to 1. To further understand how road mortality and road avoidance influenced probability of extinction and population size for either short or large dispersal distances, in the second set of simulations we varied road mortality and road avoidance independently from 0 to 1 in steps of 0.1, in two landscapes (Table 2.1).

We ran each simulation for 1000 time steps in order to allow for population size to stabilize, and ran 100 replicates for each combination of values of parameters (Table 2.1). 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.

Table 2.1. Model parameters and values used in the simulations.

Parameter	**Value**	
	1st set of simulations	**2nd set of simulations**
Landscape size (N x N)	200 x 200 cells	
Initial population size	10 individuals	
Number of replicates	100	
Number of time steps	1000	
Maximum annual fecundity (b_0)	2	
Age at first breeding	1	
Survival probability (s)	0.4	
Quality of non-road cell	1.0	
Quality of road cell	0.0	
Home range size	1 cell	
Dispersal distance (d)	5 or 50 cells	
Avoidance of occupied cells (p_{OA})	1	
Road mortality, Road avoidance (p_{RM}, p_{RA})	(0.0, 0.0); (0.0, 1.0); (1.0, 0.0)	varied from 0.0 to 1.0 in steps of 0.1
Proportion of road cells in the landscape	0.02, 0.03, 0.07, 0.18, 0.35	0.07 and 0.35

2.4. RESULTS

The probability of extinction increased and the population size decreased with increasing road density (Fig. 2.2). With no road mortality and no road avoidance, the probability of extinction was zero or close to zero, even with high road density (Fig. 2.2a) and the population size was considerably larger than with either complete road avoidance, or complete road mortality (Fig. 2.2b).

When comparing the effects of mortality and avoidance, the effects of road mortality alone were stronger than the effects of road avoidance alone. 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, regardless of the road density (Fig. 2.2). The effects of road avoidance on the probability of extinction were only seen at the highest road density, where the probability of extinction was one. On the contrary, at lower road densities and with road avoidance, the probability of extinction was zero or close to zero, independently of the dispersal distances (Fig. 2.2a). However, road avoidance affects population size at all road densities, with population size being much smaller with road avoidance than in the case with no road avoidance and no road mortality (Fig. 2.2b).

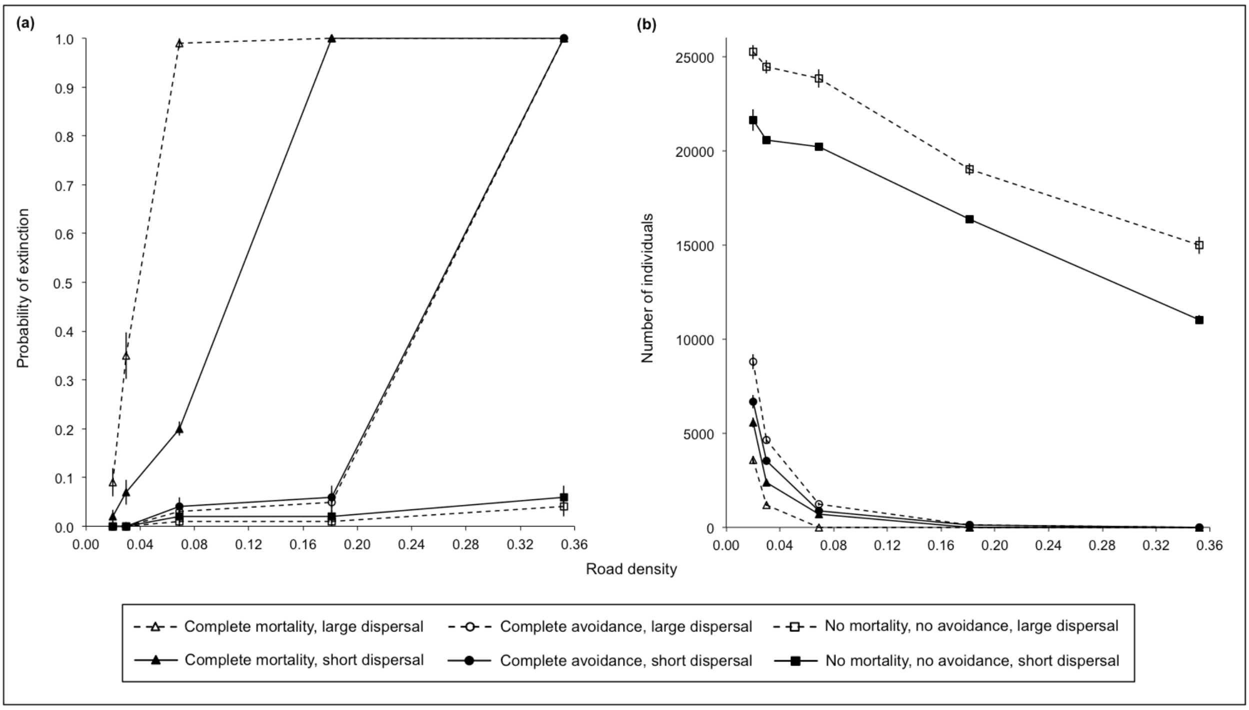


Fig. 2.2. Probability of population extinction (a) and population size (b) as a function of the proportion of road cells in the landscape, for different combinations of values of road mortality and of road avoidance and different dispersal distances. “Complete mortality” corresponds to a road mortality probability of one, and a road avoidance probability of zero. “Complete avoidance” corresponds to a road avoidance of one, and a road mortality of zero. “No mortality, no avoidance” corresponds to road mortality and road avoidance probabilities of zero. “large dispersal” corresponds to a dispersal distance of 50 cells, and “short dispersal” corresponds to a dispersal distance of 5 cells. Error bars correspond to the standard error of the mean.

Both road mortality and road avoidance caused isolation (Fig. 2.3). With no road mortality and no road avoidance, the whole landscape is occupied (top panel), while with complete road avoidance (middle panel), or complete road mortality (bottom panel), the landscape is only partially occupied.

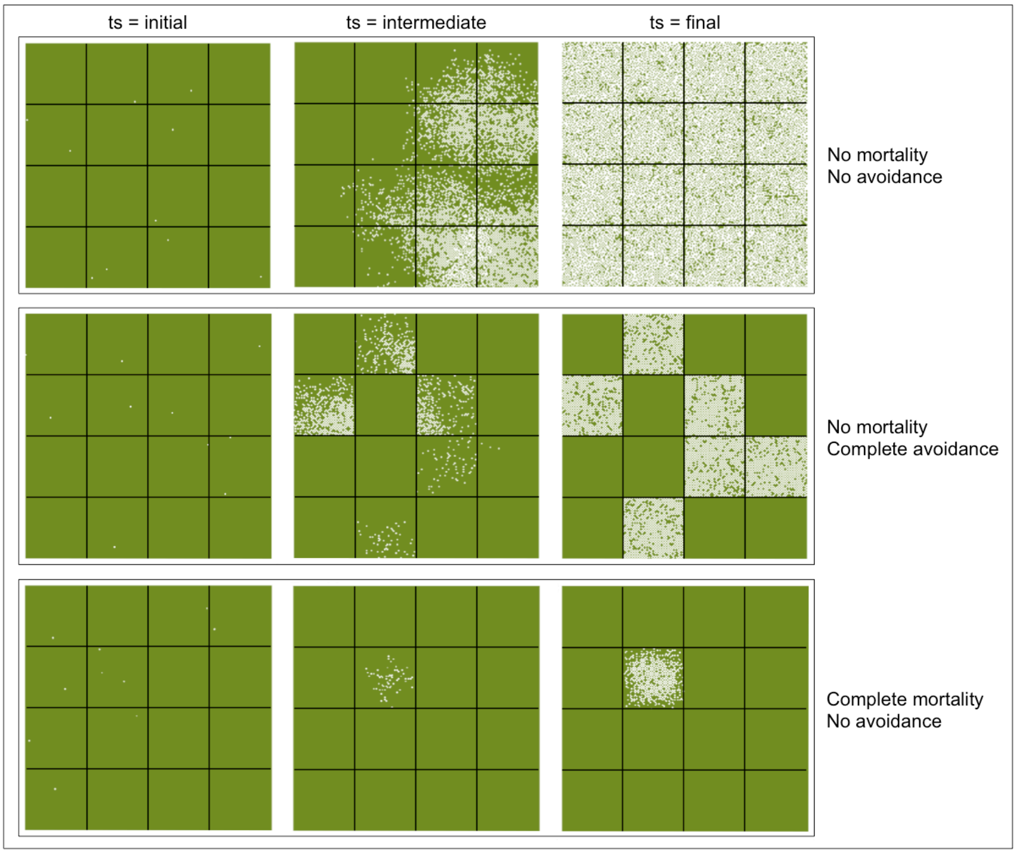
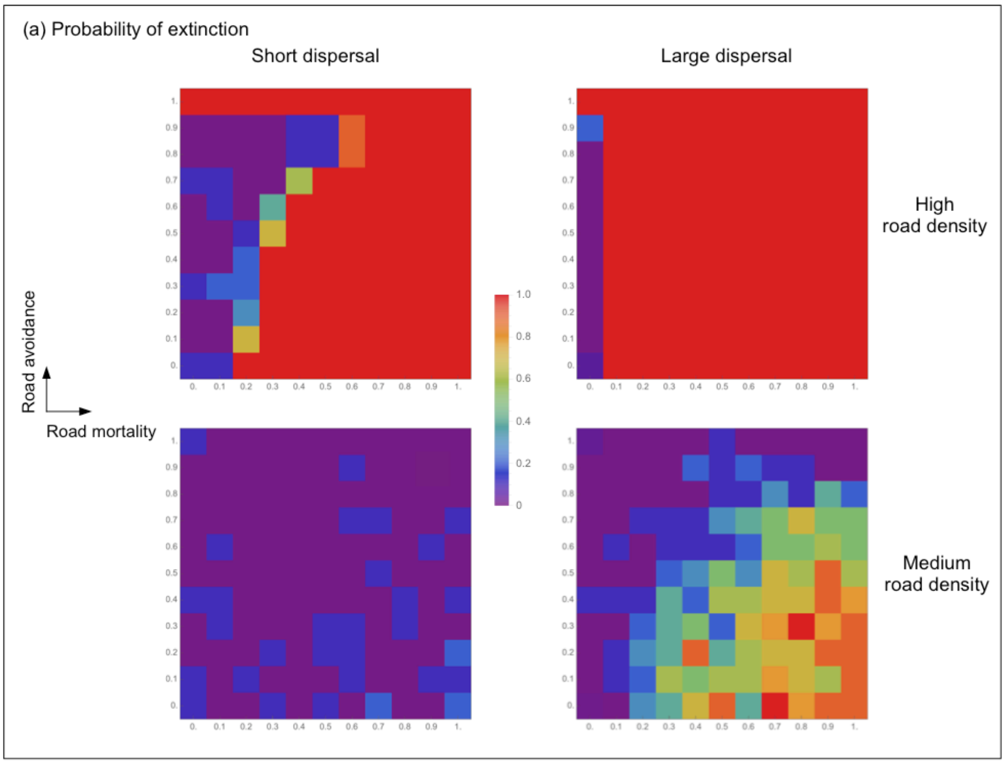


Fig. 2.3. Representation of the colonization of the landscape by a population under different combinations of values of road mortality and of road avoidance, in different time steps (ts) of a model run. “No mortality, no avoidance” (top panel) corresponds to road mortality and road avoidance probabilities of zero. “No mortality, Complete avoidance” (middle panel) corresponds to a road avoidance probability of one, and a road mortality probability of zero. “Complete mortality, No avoidance” (bottom panel) corresponds to a road mortality probability of one, and a road avoidance probability of zero. 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. The individuals are represented by the white dots, roads are in black and the green background corresponds to the non-road cells in the landscape (i.e., “good” habitat).

The influence of dispersal varied with road mortality. The probability of extinction was higher and the population size was smaller for the large dispersal distance when there was road mortality. In contrast, when there was no road mortality, the probability of extinction was higher and population size was smaller for the short dispersal distance (Fig. 2.2, Fig. 2.4). For both dispersal distances, the probability of extinction increased and the population size decreased with increasing road mortality. However, for the same value of road mortality, probability of extinction decreased and population size increased with increasing road avoidance. Here, the main difference between the large and the short dispersal distance was that the probability of extinction increased and the population size decreased much faster with increasing road mortality for the large dispersal distance (Fig. 2.4).



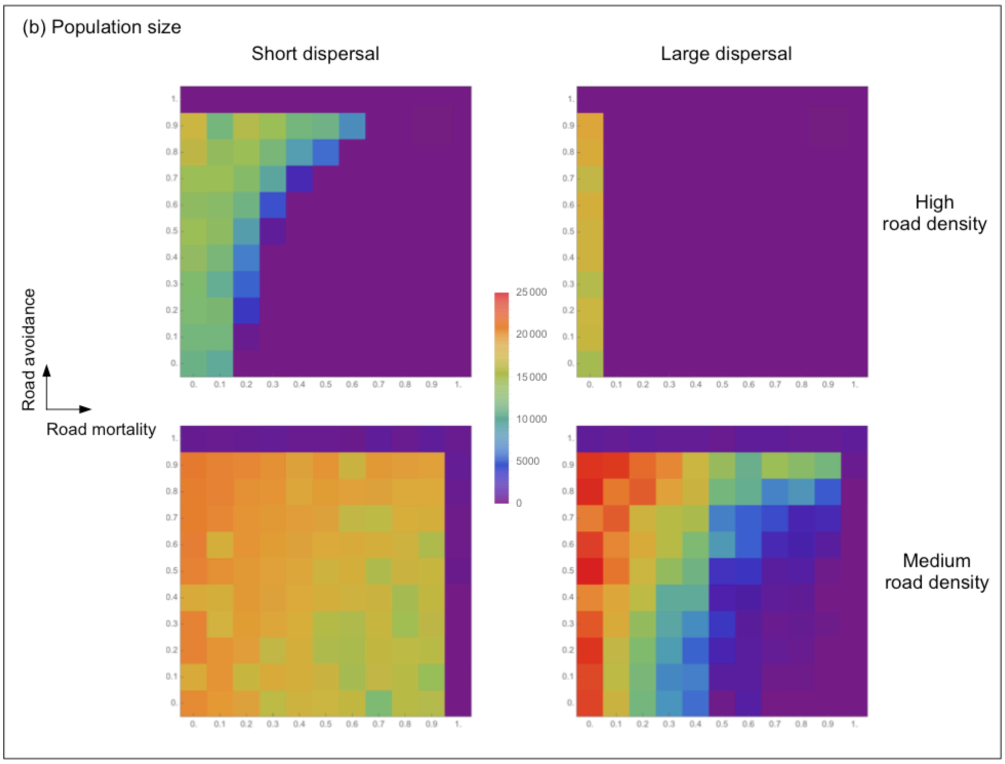


Fig. 2.4. Probability of population extinction (a) and population size (b) as a function of road mortality and road avoidance, for different dispersal distances ("Short dispersal" = 5 cells; "Large dispersal" = 50 cells) in landscapes with different proportions of road cells ("High road density" = 0.35; "Medium road density" = 0.07).

2.5. DISCUSSION

Importance of road mortality *versus* avoidance for population persistence and size

Both road mortality and road avoidance caused population isolation. However, 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 previous studies (Jaeger and Fahrig 2004, Rytwinski and Fahrig 2013).

In our simulations, populations persisted even when road avoidance was very high, provided that the road mortality was low to moderate. In such cases individuals could still cross the roads, and the whole landscape could be occupied. Only complete road avoidance led populations to extinction, when road density was the highest. In those cases where individuals were isolated within the small patches of good habitat that were bounded by roads, the resulting small populations had an increase in the extinction risk due to demographic stochasticity (Lande 1993).

When road avoidance was complete it affected population sizes negatively regardless of the road density, with population sizes being much smaller when compared to the cases with no road avoidance (and no road mortality). As discussed above, this influences population persistence, especially if other factors of disturbance come into play. We could address this by varying the habitat quality of the non-road cells in the landscape (recall that we considered all non-road cells to have maximum habitat quality), since habitat quality can influence how roads affect populations (e.g., Grilo et al. 2014). Additionally, while we accounted for avoidance of the road surface, since individuals only evaluated their immediate neighboring cells in each step of dispersal, in real situations some species avoid roads from a distance (e.g., Jaeger et al. 2005), which exacerbates the effects of habitat loss and fragmentation.

Influence of dispersal on population persistence and size

The role of dispersal varied depending on the values of road mortality. Even in disturbed habitats, as was the case in our simulations since the landscape was always fragmented by roads, populations with a larger dispersal distance had a lower probability of extinction and maintained larger sizes, provided there was no road mortality. However, a large dispersal distance was detrimental for population size and persistence as road mortality increased. Including intermediate 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 spatially explicit, process-based model to analyze the effects of roads on populations. By establishing an explicit link between the environment and population dynamics, process-based models can allow a better understanding of the relationship between environmental change and biodiversity loss (Pereira and Borda-de-Água 2013). We highlight three results of our study: first, that population isolation occurred in extreme cases (i.e., total road mortality or total road avoidance); secondly, that even though population persistence may not be impaired when avoidance of the matrix is complete - except when suitable habitat patches become too small, population size is considerably decreased, which is important to consider in long-term conservation management; and thirdly, that a large dispersal distance may not always be detrimental for population size and persistence in disturbed habitats if mortality in the matrix is low, suggesting the need for further investigation. Finally, our model can potentiate other studies, either theoretical or empirical. For example, our model can be applied to species-specific situations, by using the specific traits of the species or population of interest. Also, the modeled landscape can be adapted to represent real landscapes with real road configurations, and in this sense it can also be used to evaluate the impact of different mitigation options for population persistence, in environmental impact assessments, and for conservation planning.

2.6. ACKNOWLEDGMENTS

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2.7. REFERENCES

Ascensão F, Mata C, Malo JE, Ruiz-Capillas P, Silva C, Silva AP, Santos-Reis M, Fernandes C (2016) Disentangle the Causes of the Road Barrier Effect in Small Mammals through Genetic Patterns. PLoS ONE 11(3): e0151500. doi:10.1371/journal.pone.0151500

Casagrandi R, Gatto M (1999) A mesoscale approach to extinction risk in fragmented habitats. Nature 400: 560-562.

Borda-de-Água L, Navarro L, Gavinhos C, Pereira HM (2011) Spatio-temporal impacts of roads on the persistence of populations: analytic and numerical approaches. Landscape Ecology 26: 253-265.

Borda-de-Água L, Grilo C, Pereira HM (2014) Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. Ecological Modelling 276: 29-37.

Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biological Conservation 74: 177-182.

Gibbs JP (1998) Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13: 263-268.

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(9): e43811.

Grilo C, Reto D, Filipe J, Ascensão F, Revilla E (2014) Understanding the mechanisms behind road effects: linking occurrence with road mortality in owls. Animal Conservation 17: 555-564.

Hanski I. (1998) Metapopulation dynamics. Nature 396: 41-49.

Jaeger JAG, Fahrig L (2004) Effects of road fencing on population persistence. Conservation Biology 18: 1651-1657.

Jaeger JAG, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, Tluk von Toschanowitz K (2005) Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185: 329-348.

Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142: 911-927.

Pereira HM, Daily GC (2006) Modeling biodiversity dynamics in countryside landscapes. Ecology 87: 1877-1885.

Pereira HM, Borda-de-Água L (2013) Modelling biodiversity dynamics in countryside and native habitats. Encyclopedia of Biodiversity (Elsevier, New York), pp 321-328. 2nd Ed.

Pereira HM, Navarro LM, Martins IS (2012) Global Biodiversity Change: The Bad, the Good, and the Unknown. Annual Review of Environment and Resources 37: 25-50.

Pulliam HR (1988) Sources, sinks, and population regulation. American Naturalist 132: 652-661.

Rytwinski T, Fahrig L (2012) Do species life history traits explain population responses to roads? A meta-analysis. Biological Conservation 147: 87-98.

Rytwinski T., Fahrig L. (2013) Why are some animal populations unaffected or positively affected by roads? Oecologia 173: 1143-1156.

Rytwinski T., Fahrig L. (2015) The Impacts of Roads and Traffic on Terrestrial Animal Populations, in Handbook of Road Ecology (eds R. van der Ree, D. J. Smith and C. Grilo), John Wiley & Sons, Ltd, Chichester, UK.

Skellam JG (1951) Random dispersal in theoretical populations. Bulletin of Mathematical Biology 53:135-165.

Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO Jr, Lovejoy TE (2007) Dispersal of Amazonian birds in continuous and fragmented forest. Ecology Letters 10: 219-229.

van der Ree R, Smith DJ, Grilo C (2015) The Ecological Effects of Linear Infrastructure and Traffic, in Handbook of Road Ecology (eds R. van der Ree, D. J. Smith and C. Grilo), John Wiley & Sons, Ltd, Chichester, UK.

Chapter 3. Vulnerability to land-use change

The work presented in this chapter is provisonally accepted for publication pending minor corrrections in Global Ecology and Biogeography as: Ceia Hasse A. [1,2,3,*], Borda-de-Água L. [3,4], Grilo C. [5], Pereira H.M. [1,2,3,4], Global exposure of carnivores to roads.

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3.1. ABSTRACT

Aim Land-use change is one of the main threats to biodiversity globally. Roads cause direct mortality and limitation of individual movements, which may isolate populations and affect their viability in the long-term. Here we provide the first comprehensive global assessment of the exposure of mammalian carnivores to roads using an integrated modelling framework.

Location Global

Methods We estimated critical road densities and critical patch sizes for each species based on a spatially explicit model and life history traits. We calculated the distribution of landscape fragment sizes for each carnivore species by intersecting global road density with each species range. The proportion of a species geographic range with fragments below the critical patch size is used as an index of the vulnerability to roads.

Results We found that the carnivores expected to be most exposed by roads belong to families Felidae, Ursidae, Mustelidae, Canidae and Procyonidae. Approximately one-third of the species most affected has not been identified by IUCN as threatened by roads. Our model projects time to extinction that may be as low as one century for some species, such as the endangered Iberian Lynx. Species are expected to be more exposed in areas with medium to high road density but, surprisingly, also in areas where road density is relatively low. In what regards the number of species endangered by roads locally, hotspots occur in North America and Asia.

Main conclusions Our results suggest the need for the reassessment of the status and threats of those species that had not been previously recognized as strongly affected by roads. Our framework can be applied at different spatial scales, to assess the effects of road network development and inform prioritization schemes for road building, and to identify areas for conservation, and species requiring particular mitigation and restoration measures.

Keywords: Biodiversity conservation, Global assessment, Carnivores, Population viability, Road impact, Mortality, Dispersal.

3.2. INTRODUCTION

Land-use change is one of the major drivers of biodiversity loss (Pereira et al. 2012). The status of biodiversity is projected to continue to decline despite society's increasing efforts to decelerate this trend (Tittensor et al. 2014). The road infrastructure is a cause of mortality for many species and also a major barrier to movement. Roads can subdivide and reduce population sizes, thus affecting their viability (van der Ree et al. 2015). The current and the projected road network expansion pose threats that should be evaluated across scales in order to minimize their negative effects (Laurance et al. 2014) and to ensure the long-term viability of populations. The effect of roads on animal populations has been addressed by various studies at the local and regional scales, focusing on components such as behavioural and physiological responses to roads (Grilo et al. 2012, Navarro-Castilla et al. 2014), the effect of road noise and pollution (Hopkins et al. 2013, McClure et al. 2013), and projections of population declines and loss of genetic diversity (for a review see Balkenhol & Waits 2009; Jackson & Fahrig 2011). However, studies assessing the impact of roads on population persistence remain uncommon and upscale, at best, to national levels, focusing on a limited number of species (Beaudry et al. 2008, Borda-de-Água et al. 2014). Assessments on larger scales up to global, and across species, have never been conducted (but see Torres et al. 2016).

Here, we present a new spatially explicit modelling framework to assess the exposure of biodiversity to a major threat - the road infrastructure, and to map hotspots of road impact on biodiversity globally. We apply this framework to a particularly vulnerable group: terrestrial carnivore species. We carry out an assessment of which terrestrial carnivore species are more affected by roads at the global level, as well as where within their range they are most at risk. Mammalian carnivores usually have life history traits that make them particularly vulnerable to the effects of human-induced environmental changes, such as relatively high mobility and low reproductive rates (Grilo et al. 2015). Moreover, they are important for maintaining ecosystem function, structure and resilience (Ripple et al. 2014).

We use a simple, spatially explicit reaction-diffusion demographic model describing population dynamics and the dispersal of individuals (Skellam 1951; see also Cantrell and Cosner 2003). Skellam's (1951) model can be used to simulate source-sink dynamics (Pulliam 1988) of populations occupying several habitats within a landscape, where the population growth rate can be positive in favourable habitats (source habitats), or negative in unfavourable habitats (sink habitats) (Pereira and Borda-de-Água 2013). It has been used to assess species vulnerability to land-use change (Pereira et al. 2004, Pereira and Daily 2006) and to develop metrics to analyse the impact of road networks on population persistence (Borda-de-Água et al. 2011).

The analysis performed by Borda-de-Água et al. (2011) considered a population occupying a landscape composed of favourable habitat patches, where the population growth rate is positive, surrounded by roads, which are unfavourable habitat where the population growth rate is negative. The model predicts how road density and patch size determine population viability in landscapes fragmented by roads. In particular, it shows that the minimum patch size required for a population to persist increases with population mean dispersal distance, and decreases with intrinsic population growth rate (Borda-de-Água et al. 2011) (see model description in Methods).

This work is the first where a mechanistic population model is combined with life history data, biogeographic data, and land-use data to produce a global assessment of population viability for a complete taxonomic group. Despite not taking into account other factors that influence how populations are affected by roads, such as the behaviour of animals towards roads, the type of road or traffic intensity, or indirect mortality caused by resource inaccessibility and population subdivision (Jaeger and Fahrig 2004, Jaeger et al. 2005), our work opens the way for similar global mechanistic assessments of other threats. Our framework can be applied at different spatial scales, promoting quantitative-based assessments directing road development (or avoidance) and reducing conflicts with biodiversity conservation.

3.3. METHODS

For each species analysed, we determined its intrinsic vulnerability to roads by computing two metrics: i) the maximum road density above which populations are expected to go locally extinct (D_{max}); and ii) the minimum patch size delimited by roads, below which populations are expected to go locally extinct (A_{min}) (Borda-de-Água et al. 2011). These metrics were computed using species-specific empirical data on life history traits (see details below; a list of the data sources is found in Supporting Information). We then calculated the observed road density (D_{obs}), and the sizes of the patches delimited by roads (A_{obs}), that exist within each species range, to compare with the critical values of road density and of patch size, respectively. We applied this approach to 232 terrestrial carnivore species for which an IUCN range map is available (IUCN 2015), but excluded those species that can disperse through water (Table S1 and Table S2 in Supporting Information).

Critical values of road density (D_{max}) and of patch size (A_{min})

The expressions for maximum road density (D_{max}) and minimum patch size (A_{min}) were derived by Borda-de-Água et al. (2011) considering a population in a landscape composed of patches surrounded by roads. The patches consist of favourable habitat where the population growth rate is positive and equal to the intrinsic population growth rate (r_1), and the roads consist of unfavourable habitats, where the growth rate is negative (r_0). The dispersal distance of individuals is modeled by its dispersal variance (σ^2). The dynamics are given by (Skellam 1951, Borda-de-Água et al. 2011):

$$\frac{dN(x,y,t)}{dt}=\begin{cases}\frac{\sigma^2}{2}\nabla^2N(x,y,t)+r_1N(x,y,t)\left(1-\frac{N(x,y,t)}{K}\right) & \mathit{if}\ (x,y)\notin road\\ \frac{\sigma^2}{2}\nabla^2N(x,y,t)+r_0N(x,y,t) & \mathit{if}\ (x,y)\in road\end{cases},$$

where $N(x, y, t)$ is the population density at location (x, y) at time t, K is the carrying capacity, and ∇^2 is $(d^2/dx^2 + d^2/dy^2)$. The first term on the right hand side of the equation (top and bottom branches) describes the changes in population density in space and time on the basis of the dispersal distance, which is assumed to follow a Gaussian distribution. The second term describes logistic growth outside roads (top branch), and the population decay (since r_0 is assumed to be negative) on roads (bottom branch) (Borda-de-Água et al. 2011). While r_0 mathematically is the population growth rate on roads, here it is a measure of the loss of individuals from the population (i.e., roads behave as sink habitat), representing the instantaneous mortality rate when an animal crosses a road.

Maximum road density and minimum patch size

The expressions for the maximum road density above which populations cannot persist (D_{max}), and for the minimum patch size below which populations cannot persist (A_{min}) were obtained solving the equation above for simplified situations, providing easy rules of thumb to estimate population viability in landscapes fragmented by roads. See Borda-de-Água et al. (2011) and its corresponding Supplemental Information for the details on the derivation of D_{max} and of A_{min}. D_{max} was derived assuming very large dispersal ($\sigma^2 \rightarrow \infty$) and large carrying capacity ($K \rightarrow \infty$, so the term "$1-N(x, y, t)/K$" in the top branch of the equation above is not considered), and ignoring the spatial location of the roads and considering road density only:

$$D_{max} = (r_1 / (r_1 + |r_0|)) / 0.01,$$

where r_1 is the growth rate of the population, and r_0 is mortality on roads. We divided D_{max} by a road width of 0.01km to obtain D_{max} in km/km^2, to compare it with the road density that is observed within each species range (D_{obs} in km/km^2; see below).

The expression for the minimum patch size below which populations go extinct (A_{min}) was derived assuming infinite carrying capacity ($K \rightarrow \infty$), and that individuals always die when crossing a road ($r_0 \rightarrow -\infty$), considering the location of the roads explicitly and assuming their configuration to be that of a square grid (Borda-de-Água et al. 2011):

$$A_{min} = \pi^2(\sigma^2/r_1),$$

with units of km^2, where σ^2 is dispersal variance, and r_1 is the growth rate of the population.

Population parameters: growth rates and dispersal

To compute the maximum road density (D_{max}) and the minimum patch size (A_{min}), we first estimated the parameters of the model (r_1, r_0, and σ^2) for each species. The intrinsic population growth rate, r_1, was computed using a simplified version of the Euler equation following the approach by (Pereira and Daily 2006), and assuming: 1) constant mortality rate, μ; 2) zero fecundity before the breeding age, β; 3) fecundity equals the number of female offspring (50% of the litter size), *b*, at regular birth pulses intervals after the breeding age; and 4) birth pulse intervals are spaced by the mean interval between litters, Δ. The implicit equation for r_1 is then:

$$b \times \int_0^\infty \sum_{y=0}^{\infty} \delta\left(x - y\Delta - \beta\right) e^{-(r_1+\mu)x}\, dx = 1 ,$$

where δ(x) is the birth pulse function, which has a value of 1/T for x between 0 and T and 0 elsewhere. This equation can be solved numerically to determine r_1.

We estimated the rate of population growth on roads, r_0, as $-\mu \times 10^3$ (μ is the annual natural mortality rate; see below). We assume 1000 times higher mortality rate (and zero birth rate) on roads than the natural mortality rate. For example, for a species with natural mortality rate of 0.5*yr^{-1}, this corresponds to a mortality rate per crossing of 500*yr^{-1} on roads. We also assessed the robustness of this assumption by comparing the results with $r_0 = -\mu \times 10^2$, and with $r_0 = -\mu \times 10^4$ (Table S3).

Dispersal variance (σ^2) was computed assuming Gaussian dispersal as:

$$\sigma^2 = (\sigma_m/1.18)^2 * \mu,$$

where σ_m is the dispersal median, and μ is the annual mortality rate, which converts the dispersal median from km^2/generation to km^2/year (Pereira and Daily 2006).

These parameters (r_1, r_0, σ^2) were computed for each species using species-specific life history data (see Supporting Information). We computed mortality rate (μ) as the inverse of mean life span, and the dispersal median (σ_m) from home range (HR) data as $\sigma_m = 7*\sqrt{HR}$ (Bowman et al. 2002). Since not all data were available for all species, we established allometric relationships (Table S4) based on the available data, and then used these relationships to estimate the missing life history values. For body mass and litter size, when data were lacking for a given species, we used the mean of the genus, or the mean of the corresponding family (Pereira and Daily 2006). The percentage of missing life history values ranged from 12.9% (for body mass) to 92.7% (for mortality rate).

Observed values of road density (D_{obs}) and of patch size (A_{obs})

After computing the critical values of road density and of patch size, we assessed what is observed within each species range with respect to roads. We did this by intersecting each species range map from the IUCN (IUCN 2015) with the road network from Open Street Map (OSM) (Geofabrik 2015), using QGIS v.2.2.0 (QGIS Development Team 2014). The road categories included from the OSM data were: "motorway", "trunk", "primary", "secondary", "tertiary", "minor", "road", and "unclassified".

We then computed the observed road density (D_{obs}) as the ratio of the road length that exists within the species range to the species range area. We also computed the area of each patch that is delimited by roads (observed patch sizes, A_{obs}), existing within each species range. This differs from the effective mesh size metric proposed by Jaeger (2000), which combines the areas of all patches within the region investigated, as well as its total area, into one metric of landscape fragmentation; in our model each A_{obs} is simply the area of one patch (see below for the use of A_{obs} in ranking species exposure to the road network).

Species exposure to the road network

We ranked the species regarding their exposure to the extant road network by computing for each species: i) the ratio of the maximum road density to the observed road density (D_{max}/D_{obs}); and ii) the proportion of patches delimited by roads observed within the species range with area (A_{obs}) larger than the minimum patch size (A_{min}), P[$A_{obs} > A_{min}$] (Fig. 3.1). Then for each of these quantities, we selected the species within the lower 5th percentile as the species that are expected to be more exposed to roads. In this way, those species that are expected to be most exposed to roads are the ones with a lower D_{max}/D_{obs}, and/or the ones with a smaller P[$A_{obs} > A_{min}$].

For each species in the lower 5th percentile we also mapped where it is expected to be more exposed to roads within its range. We did so using 100x100km grid cells and identifying in which cells D_{obs} is higher than D_{max}, or there is at least one patch with A_{obs} smaller than A_{min} for population persistence. This is a conservative estimate, because it does not imply that a species is more exposed to roads in all the area of a grid cell, but only in parts of that grid cell (where $A_{obs} < A_{min}$).

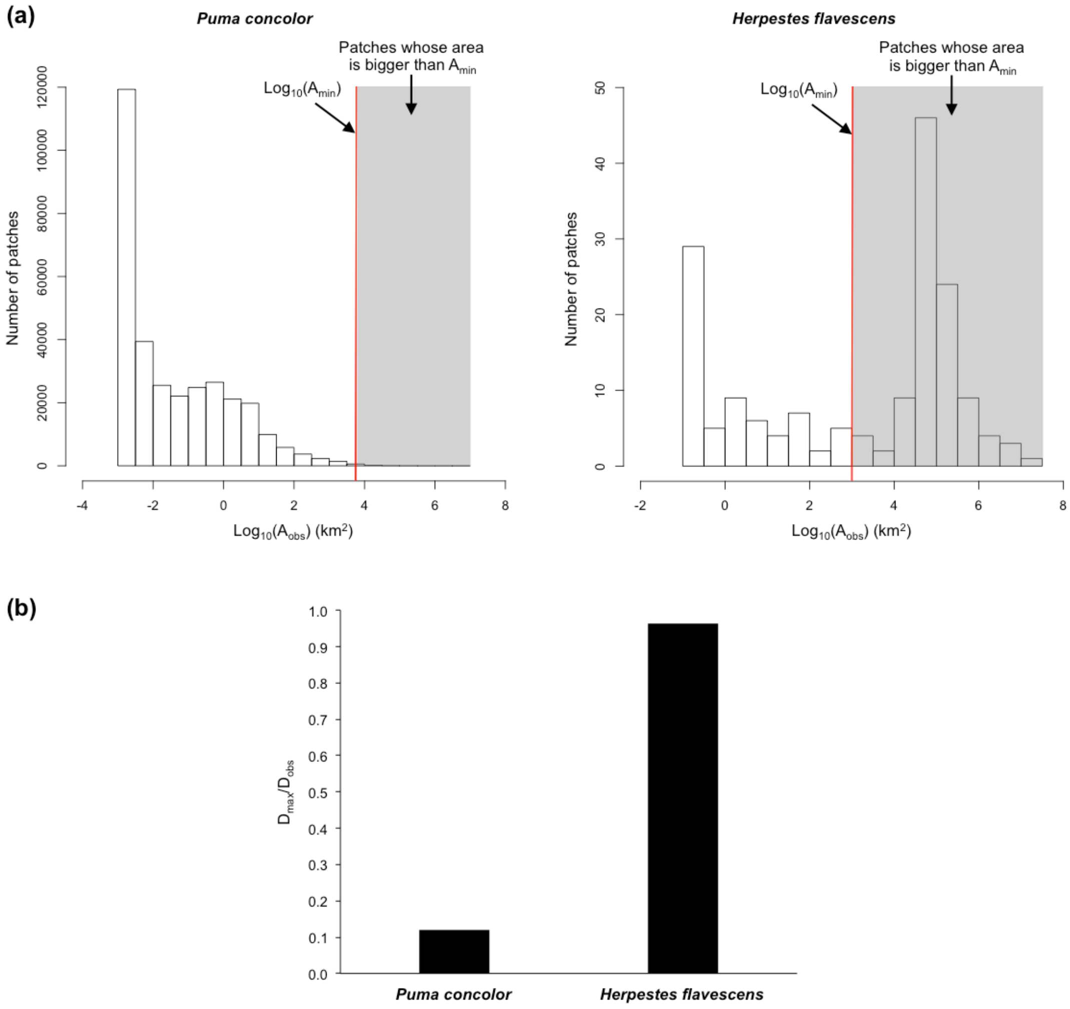

Figure 3.1. Observed and critical values of patch size and of road density for two species. Frequency of observed patch sizes (A_{obs}) and the relation with minimum patch size (A_{min}) (a), and the ratio of theoretical maximum road density to observed road density (D_{max}/D_{obs}) (b). The puma (*Puma concolor* (Linnaeus, 1771)) is among the 5% species with lower P[$A_{obs} > A_{min}$], and the 5% species with smaller D_{max}/D_{obs}. In contrast, the black slender mongoose (*Herpestes flavescens* Bocage, 1889) has high P[$A_{obs} > A_{min}$], and high D_{max}/D_{obs}. Fewer patches larger than A_{min} (areas shaded in grey in (a)), or a small value of D_{max}/D_{obs} (in (b)), reveal a highly vulnerable species.

Time to extinction

Borda-de-Água et al. (2011) also derived an expression for computing the time to extinction of a population in a patch with area smaller than the minimum patch size (A_{min}). Using this expression, we determined the time to extinction (T_{ext}) for the species within the lower 5th percentile of P[$A_{obs} > A_{min}$] for which there is at least one patch with A_{obs} smaller than A_{min} in all the grid cells where those species are present, as follows (Borda-de-Água et al. 2011):

$$T_{ext} = \frac{1}{\left(\frac{\sigma^2 \pi^2}{A_{obs}}\right) - r_1}$$

Time to extinction here is the time that it takes for the species to disappear from 90% of the area where A_{obs} is smaller than A_{min}, and A_{obs} is the area of the largest patch smaller than A_{min} within that area.

3.4. RESULTS

Using the 5th percentile criterion, we identified seventeen species as the most exposed to roads. They belong to the families Felidae (six species, corresponding to 17% of the species analysed in this family), Ursidae (four species, 57%), Mustelidae (four species, 9%), Canidae (two species, 6%), and Procyonidae (one species, 7%) (Table 3.1). The percentage of the range where each species is expected to be affected varies from 38 to 100% (Table 3.1). These are the parts of the range where each species is projected to disappear or have low abundance. The Iberian Lynx (*Lynx pardinus* (Temminck, 1827)), an endangered species endemic to the Iberian Peninsula is estimated to go extinct from 90% of the area where A_{obs} is smaller than A_{min} in 114 years.

Among the species expected to be most exposed to roads, 71% (twelve species) are also classified by the IUCN as threatened by roads (Table 3.1). However, we also identified species for which roads are not listed as a threat by the IUCN (IUCN 2015), some of which are expected to be affected in more than 75% of their range. These include species that have been categorized as Least Concern by the IUCN, and for which we have identified another factor of threat: the Stone Marten (*Martes foina* (Erxleben, 1777)), which despite being widespread is vulnerable to traffic and is frequently road-killed (Grilo et al. 2009); and the Japanese Badger (*Meles anakuma* Temminck, 1844) and the Japanese Marten (*Martes melampus* (Wagner, 1840)), both occuring only in Japan, are estimated to disappear from 90% of the areas where A_{obs} is smaller than A_{min} in nine and seventeen years, respectively.

Table 3.1. Species most exposed to roads. These are the species within the 5% lowest values of D_{max}/D_{obs} or within the 5% lowest values of P[$A_{obs} > A_{min}$]. We indicate the percentage of 100x100km grid cells where each species is present having $D_{obs} > D_{max}$ or at least one patch with A_{obs} smaller than A_{min}, whether the species are identified by the IUCN as being threatened by roads, and the species IUCN Red List status. CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern. Family names are truncated to the first four letters and are: Canidae, Felidae, Mustelidae, Procyonidae and Ursidae.

Common name	Species	Family	Smaller D_{max}/D_{obs}	Smaller P[$A_{obs} > A_{min}$]	Percentage of range affected	Threatened by roads IUCN	Red List status
Iberian lynx	*Lynx pardinus*	Feli.	+	+	100%	+	EN
Japanese Badger	*Meles anakuma*	Must.	+	+	100%		LC
Japanese Marten	*Martes melampus*	Must.	+	+	100%		LC
Bobcat	*Lynx rufus*	Feli.		+	93%	+	LC
Stone Marten	*Martes foina*	Must.	+	+	90%		LC
Sloth Bear	*Melursus ursinus*	Ursi.	+		89%	+	VU
Nilgiri Marten	*Martes gwatkinsii*	Must.	+	+	86%	+	VU
Asiatic Black Bear	*Ursus thibetanus*	Ursi.	+		86%	+	VU
Puma	*Puma concolor*	Feli.	+	+	69%	+	LC
American Black Bear	*Ursus americanus*	Ursi.	+	+	68%	+	LC
Darwin's fox	*Pseudalopex fulvipes*	Cani.		+	67%		CR
Brown Bear	*Ursus arctos*	Ursi.	+		65%	+	LC
Jaguarundi	*Herpailurus yagouaroundi*	Feli.		+	60%	+	LC
Leopard	*Panthera pardus*	Feli.		+	59%	+	NT
Pygmy Racoon	*Procyon pygmaeus*	Procy.		+	50%	+	CR
Coyote	*Canis latrans*	Cani.	+		48%		LC
Jaguar	*Panthera onca*	Feli.	+		38%	+	NT

When using the lower 25th percentile as a criterion to select the species that are expected to be most exposed to roads, we captured 39 out of the 53 species (74%) that are listed by the IUCN as threatened by roads (among the 232 species analysed; Table S2). However, we also identify 50 more species - besides the species already identified at the lower 5th percentile (Table 3.1) - for which roads are not listed as a threat by the IUCN.

Species are clearly affected in regions with medium to high road density, as in Europe (mean road density ± SD: 0.65 ± 0.54 km/km^2), North America (eastern USA: mean ± SD: 0.49 ± 0.24 km/km^2; south-central Canada 0.48 ± 0.31 km/km^2), and Japan (mean ± SD: 0.43 ± 0.32 km/km^2), but also in regions with relatively low road density, such as Africa (mean ± SD: 0.04 ± 0.07 km/km^2) (Fig. 3.2 and Fig. 3.3). In Africa, only one of the 5th percentile selected species occurs, but the Leopard (*Panthera pardus* (Linnaeus, 1758)), having low D_{max} and large A_{min} (Table S2), shows a strong effect of roads throughout its range. The highest number of species affected by roads per 100x100km grid cell is observed in North America (up to six species), followed by Asia (four species), South America (three species) and Europe (two species) (Fig. 3.3). We observe a similar pattern when we use the 25th percentile (Fig. S1).

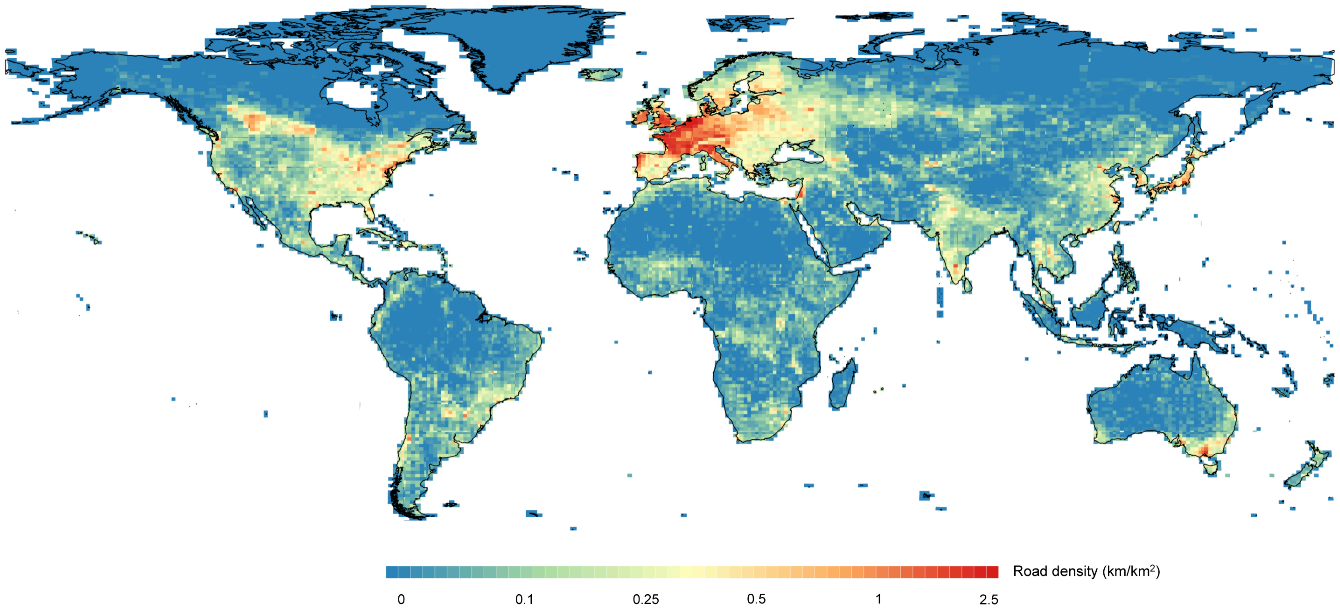

Figure 3.2. Road density (km/km^2) per 100x100km grid cell. We intersected the global road network (Geofabrik 2015) with the world map in 100x100km grid cells and then summed road length in each grid cell. Colours show fifty road density classes obtained using Jenks natural breaks optimization method (QGIS Development Team 2014).

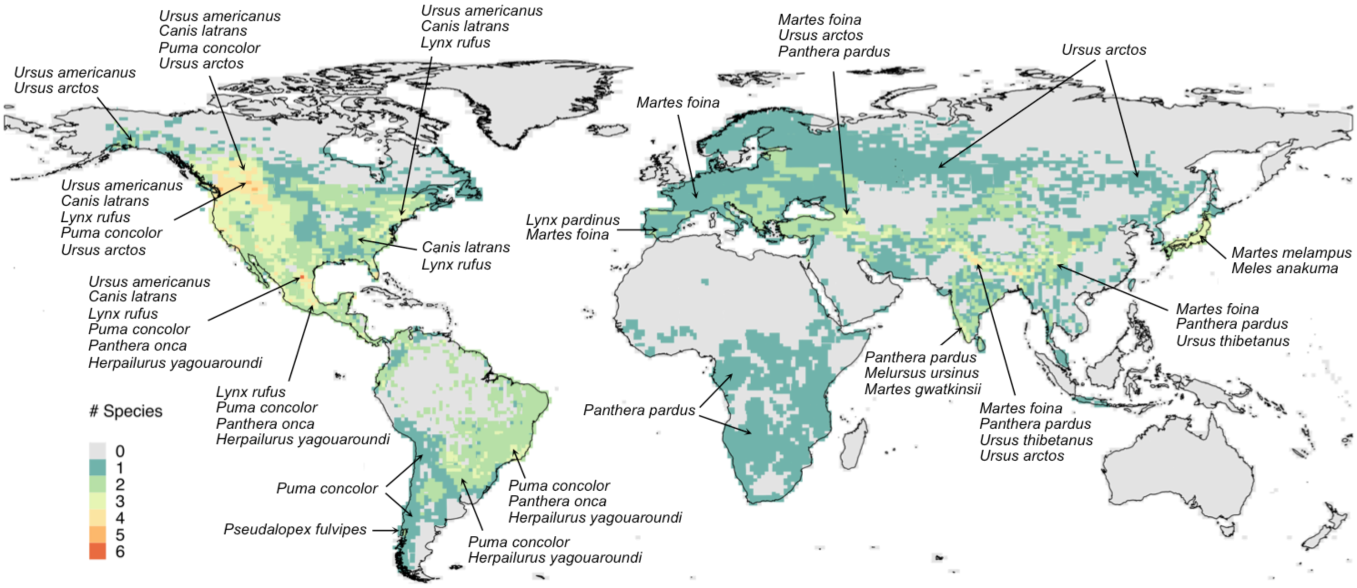

Figure 3.3. Number of species expected to be more exposed to the impact of roads per 100x100km grid cell. The species mapped are within the lower 5th percentile of D_{max}/D_{obs} or of P[$A_{obs} > A_{min}$]. Colours show the total number of species per grid cell for which D_{obs} is higher than D_{max}, or A_{obs} is smaller than A_{min}.

3.5. DISCUSSION

We have assessed the impact of roads on terrestrial carnivore species at the global level, using a species-specific, spatially explicit approach - thereby identifying not only species that are expected to be most exposed to roads at the global level, but also where within its range each species is expected to be more affected.

Our approach has several limitations that need to be considered when interpreting the results of our analysis. The maximum road density (D_{max}) was derived assuming unlimited dispersal ability, and the minimum patch size (A_{min}) assuming that individuals always die when crossing a road (see Methods and Borda-de-Água et al. 2011). Such assumptions are simplifications of real ecological systems: these metrics may underestimate the maximum possible road density and overestimate the minimum possible patch size necessary for population persistence, and it is possible that even if $D_{obs} > D_{max}$, or when $A_{obs} < A_{min}$, populations persist (Borda-de-Água *et al.*, 2011). Moreover, the behaviour of individuals towards roads influences how roads affect species (Jaeger and Fahrig 2004, Jaeger et al. 2005). Many large predator species move along low traffic roads (Forman and Alexander 1998); for example, wolves can select low-use roads as travel routes (e.g., Whittington et al. 2005). Also, road mortality may be compensated for by increased fecundity or survival (e.g., Seiler and Helldin 2006).

For these reasons, it is not appropriate to use D_{max} or A_{min} as strict thresholds for population persistence. Instead, we have ranked the species analysed in relation to one another to detect which species would be more exposed to roads than other species, and we have estimated in which areas within its range a species would be more exposed to roads than in other areas of its range. We did so because, even though populations may persist where $D_{obs} > D_{max}$ or where $A_{obs} < A_{min}$, they are expected to be more exposed to the impact of roads in those areas than in areas where $D_{obs} < D_{max}$, or $A_{obs} > A_{min}$, respectively.

Despite its limitations, our framework provides a way to obtain a first approximation to pinpoint species that may be more exposed to the impact of roads, to identify the areas within a species range where it may be more exposed to roads, and also to highlight regions that may have a higher number of species more exposed to roads.

Time to extinction should also be interpreted with caution given the assumptions made when deriving the expressions for A_{min} and T_{ext} (see Methods and Borda-de-Água et al. 2011), and unknown effects of the behaviour of each species. While our approach allows estimating the time to extinction in the areas within a species range where $A_{obs} < A_{min}$, the assumption that animals always die when crossing a road is a simplification. Moreover, the impact of roads on population persistence, and therefore time to extinction, will also depend on their sensitivity to the effects of roads (including not only road mortality but also habitat loss, resource inaccessibility, and population subdivision), on the type of behavioural response of the animals towards roads, on the type of roads, on traffic intensity (Jaeger et al. 2005), on habitat affinities, and on the variation of population density within species ranges (Grilo et al. 2014).

Because these factors were not explicitly taken into account in our analysis, T_{ext} should be considered as a first approximation.

We have considered all roads together when computing D_{obs}, and we did not take into account that road mortality may vary according to the type of roads (e.g., Jaeger et al. 2005, Grilo et al. 2009), because it would have been impractical in an analysis performed at the global scale and for such a large number of species. Assessments performed at smaller spatial scales, or for a smaller number of species, could consider computing separate D_{obs}, and separate D_{max} for different road types.

Our results suggest the need for the reassessment of the status and threats of those species that had not been previously recognized as exposed to roads. In such cases applying a modelling approach such as ours, that explicitly combines extrinsic factors of threat and intrinsic species traits, allows moving from a descriptive to a mechanistic, biologically sound evaluation of threats (Lee and Jetz 2010, Dirzo et al. 2014).

Our approach brings together process-based models that link species-specific life histories, population dynamics and dispersal, with biogeographic data, and land-use data - in this case, the road infrastructure. However, as discussed above, other factors that we did not account for can influence how roads affect animals. In more localized studies it may be desirable to incorporate those issues in order to obtain a refined understanding of the impacts across species and regions, but for that it is necessary to deepen our knowledge on the impact of roads, and strengthen the link between empirical knowledge and models (e.g., using models to guide data collection, or collecting parameters that are implementable for models).

Our analysis differs from a simple spatial overlap between species ranges and road density. Despite its limitations, it provides a first quantitative approximation to assess whether the road density that is observed within a species range may be beyond a threat threshold. By integrating species traits, this analysis also allowed detecting species that despite having relatively low road density within their range, are nevertheless estimated to be more exposed to roads than other species for which road density is relatively high within their range. Such inferences would not have been possible using a simple spatial overlap analysis between species ranges and road density.

By pinpointing where species are expected to be affected by roads within their ranges, and which regions have more species vulnerable to roads, this type of spatial analysis can be used for identifying areas for conservation, for prioritizing regions where mitigation measures, such as passages or fences, should be implemented and for informing the development of schemes for road building (Laurance et al. 2014). Moreover, this framework can also be applied at different spatial and temporal scales, e.g. for conservation or management purposes at the local scale, for environmental impact assessments, or for projecting the effects of future large-scale road network developments, which can then feed, for example, World Bank projections or scenarios for global biodiversity change (Pereira et al. 2010).

3.6. ACKNOWLEDGMENTS

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3.7. SUPPORTING INFORMATION IN APPENDIX

Figure S1. Number of species expected to be more exposed to the impact of roads per 100x100km grid cell, within the 25th percentile of D_{max}/D_{obs} or of P[$A_{obs} > A_{min}$].

Table S1. Species analysed and life history data.

Table S2. Parameters for the species analysed.

Table S3. D_{max} and D_{max}/D_{obs} computed using $r_0=-\mu*10^2$, $r_0=-\mu*10^3$, and $r_0=-\mu*10^4$.

Table S4. Allometric relationships.

Supporting references.

3.8. BIOSKETCH

Ana Ceia-Hasse is a PhD student working under the supervision of Henrique M. Pereira. Her work focuses on process based models of biodiversity response to global environmental change. The research team seeks to understand the patterns and processes of global biodiversity change - namely the impact of roads on biodiversity, with the aim of informing environmental policies and ecosystems management.

3.9. REFERENCES

Balkenhol N, Waits LP (2009) Molecular road ecology: exploring the potential of genetics for investigating transportation impacts on wildlife. Molecular Ecology 18: 4151-4164.

Beaudry F, deMaynadier PG, Hunter MLJ (2008) Identifying road mortality threat at multiple spatial scales for semi-aquatic turtles. Biological Conservation 141: 2550-2563.

Borda-de-Água L, Grilo C, Pereira HM (2014) Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. Ecological Modelling 276: 29-37.

Borda-de-Água L, Navarro L, Gavinhos C, Pereira HM (2011) Spatio-temporal impacts of roads on the persistence of populations: analytic and numerical approaches. Landscape Ecology 26: 253-265.

Bowman J, Jaeger JAG, Fahrig L (2002) Dispersal distance of mammals is proportional to home range size. Ecology 83: 2049-2055.

Cantrell RS, Cosner C (2003) Spatial ecology via reaction-diffusion equations. John Wiley & Sons, Chichester, UK.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. Science 345: 401-406.

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annual Review of Ecology and Systematics 29: 207-231.

Geofabrik (2015) OpenStreetMap-Shapefiles. http://www.geofabrik.de.

Grilo C, Bissonette JA, Santos-Reis M (2009) Spatial–temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. Biological Conservation 142: 301-313.

Grilo C, Reto D, Filipe J, Ascensão F, Revilla E (2014) Understanding the mechanisms behind road effects: linking occurrence with road mortality in owls. Animal Conservation 17: 555-564.

Grilo C, Smith DJ, Klar N (2015) Carnivores: struggling for survival in roaded landscapes. In: van Der Ree R, Smith DJ, Grilo C. (Eds.) Handbook of Road Ecology. John Wiley & Sons, Ltd, Chichester, UK. Pp. 300-312.

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.

Hopkins GR, French SS, Brodie EDJ (2013) Increased frequency and severity of developmental deformities in rough-skinned newt (*Taricha granulosa*) embryos exposed to road deicing salts (NaCl & MgCl2). Environmental Pollution 173: 264-269.

IUCN (2015) The IUCN Red List of Threatened Species. Version 2015.4. http://www.iucnredlist.org.

Jackson ND, Fahrig L (2011) Relative effects of road mortality and decreased connectivity on population genetic diversity. Biological Conservation 144: 3143-3148.

Jaeger JAG (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landscape Ecology 15: 115-130.

Jaeger JAG, Fahrig L (2004) Effects of Road Fencing on Population Persistence. Conservation Biology 18: 1651-1657.

Jaeger JAG, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, von Toschanowitz KT (2005) Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185: 329-348.

Laurance, W.F., Clements, G.R., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., Balmford, A., Van Der Ree, R. & Arrea, I.B. (2014) A global strategy for road building. Nature 513: 229-232.

Lee TM, Jetz W (2010) Unravelling the structure of species extinction risk for predictive conservation science. Proceedings of the Royal Society London Series B 278: 1329-1338.

McClure CJW, Ware HE, Carlisle J, Kaltenecker G, Barber JR (2013) An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proceedings of the Royal Society London Series B 280: 20132290.

Navarro-Castilla Á, Mata C, Ruiz-Capillas P, Palme R, Malo JE, Barja I (2014) Are Motorways Potential Stressors of Roadside Wood Mice (Apodemus sylvaticus) Populations? PLoS ONE 9: e91942.

Pereira HM, Borda-de-Água L (2013) Modelling biodiversity dynamics in countryside and native habitats. In: Levin SA (Ed.) Encyclopedia of Biodiversity. Elsevier, New York. Pp. 321-328.

Pereira HM, Daily GC (2006) Modeling biodiversity dynamics in countryside landscapes. Ecology 87: 1877-1885.

Pereira HM, Daily GC, Roughgarden J (2004) A framework for assessing the relative vulnerability of species to land-use change. Ecological Applications 14: 730-742.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for Global Biodiversity in the 21st Century. Science 330: 1496-1501.

Pereira HM, Navarro LM, Martins IS (2012) Global Biodiversity Change: The Bad, the Good, and the Unknown. Annual Review of Environment and Resources 37: 25-50.

Pulliam HR (1988) Sources, sinks, and population regulation. American Naturalist 132: 652-661.

QGIS Development Team (2014) QGIS Geographic Information System. Open Source Geospatial Foundation Project.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith DW, Wallach AD, Wirsing AJ (2014) Status and Ecological Effects of the World's Largest Carnivores. Science 343: 1241484.

Seiler A, Helldin J-O (2016) Mortality in wildlife due to transportation. In: Davenport J, Davenport JL (Eds.) The Ecology of Transportation: Managing Mobility for the Environment. Springer, Netherlands. Pp. 165-189.

Skellam JG (1951) Random dispersal in theoretical populations. Bulletin of Mathematical Biology 53: 135-165.

Tittensor DP, Walpole M, Hill SLL, Boyce DG, Britten GL, Burgess ND, Butchart SHM, Leadley PW, Regan EC, Alkemade R, Baumung R, Bellard C, Bouwman L, Bowles-Newark NJ, Chenery AM, Cheung WWL, Christensen V, Cooper HD, Crowther AR, Dixon MJR, Galli A, Gaveau V, Gregory RD, Gutierrez NL, Hirsch TL, Höft R, Januchowski-Hartley SR, Karmann M, Krug CB, Leverington FJ, Loh J, Lojenga RK, Malsch K, Marques A, Morgan DHW, Mumby PJ, Newbold T, Noonan-Mooney K, Pagad SN, Parks BC, Pereira HM, Robertson T, Rondinini C, Santini L, Scharlemann JPW, Schindler S, Sumaila UR, Teh LSL, van Kolck J, Visconti P, Ye Y (2014) A mid-term analysis of progress toward international biodiversity targets. Science 346: 241-244.

Torres A, Jaeger JAG, Alonso JC (2016) Assessing large-scale wildlife responses to human infrastructure development. Proceedings of the National Academy of Sciences, 113: 8472-8477.

van der Ree R, Smith DJ, Grilo C (2015) The Ecological Effects of Linear Infrastructure and Traffic. In: van Der Ree R, Smith DJ, Grilo C. (Eds.) Handbook of Road Ecology. John Wiley & Sons, Ltd, Chichester, UK. Pp. 1-9.

Whittington J, St. Clair CC, Mercer G (2005) Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications 15: 543-553.

Chapter 4. Range shifts in response to climate change

The work presented in this chapter was published as: Ceia Hasse A. ^{1,2,3,*}, Sinervo B. ^{4} , Vicente L. ^{5}, Pereira H.M. ^{1,2,3,6} (2014) Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. Ecography 37: 679 - 688. doi: 10.1111/j.1600-0587.2013.00600.x [†]

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4.1. ABSTRACT

Uncertainty in projections of global change impacts on biodiversity over the 21st century is high. Improved predictive accuracy is needed, highlighting the importance of using different types of models when predicting species range shifts. However, this is still rarely done. Our approach integrates the outputs of a spatially-explicit physiologically inspired model of extinction and correlative species distribution models to assess climate-change induced range shifts of three European reptile species (*Lacerta lepida*, *Iberolacerta monticola*, and *Hemidactylus turcicus*) in the coming decades. We integrated the two types of models by mapping and quantifying agreement and disagreement between their projections. We analyzed the relationships between climate change and projected range shifts. Agreement between model projections varied greatly between species and depended on whether or not they consider dispersal ability. Under our approach, the reliability of predictions is greatest where the predictions of these different types of models converge, and in this way uncertainty is reduced; sites where this convergence occurs are characterized by both current high temperatures and significant future temperature increase, suggesting they may become hotspots of local extinctions. Moreover, this approach can be readily implemented with other types of models.

[†] Note: there are small corrections in the description of the methods from the published paper that have no implications in the results.

4.2. INTRODUCTION

The projected impacts of global change on biodiversity show species extinctions, loss of natural habitat, and changes in the distribution and abundance of species and biomes over the 21st century (Pereira et al. 2010). Climate change is one of the most important drivers of biodiversity change (Bellard et al. 2012) and is affecting both the distribution and phenology of organisms (Parmesan 2006). Projections of change are essential for conservation planning (Thuiller 2007), but their accuracy needs to be improved to sustain ecosystem services and functions (Millennium Ecosystem Assessment 2005). However, the uncertainty level in projections of biodiversity change is greater than had been previously acknowledged (Pereira et al. 2012). This highlights the importance of using different types of models when predicting species range changes, which allows assessing uncertainty and allows identifying and correcting errors. However, this approach is still rarely undertaken (Leadley et al. 2010).

Global change impacts on biodiversity can be estimated through models that can be broadly classified into phenomenological or process-based models (Pereira et al. 2010). Most phenomenological models are correlative models relying on the establishment of statistical relationships between current species distributions and climate variables to project the future distribution of a species under projected environmental change (Heikkinen et al. 2006). Process-based models determine the mechanistic interactions between the growth or fitness of an organism, and its environment, using theoretical inferences, experiments, or both (Araújo 2009).

Understanding both the strengths and limitations of correlative models, and their conceptual basis, is essential for their correct application (Araújo and Peterson 2012). The relative simplicity of correlative models is one of their main advantages, since they can be used for any species for which there are reliable distribution data and the corresponding environmental variables (Morin and Thuiller 2009). Correlative models can implicitly capture many complex ecological responses (Elith et al. 2010), but may fail to predict range dynamics accurately (Buckley et al. 2010). This is because they are based on correlations between current climates and species distributions, and if climate change leads to new combinations of the states of those environmental variables many future climates will probably lack current analogs (Williams and Jackson 2007). Correlative models have been used extensively for a large number of groups of organisms and in a wide variety of contexts, spanning conservation, ecological and evolutionary questions (Zimmermann et al. 2010, Araújo and Peterson 2012). These include the assessment of the impacts of climate change on the distribution of reptiles in the future (Araújo et al. 2006, Carvalho et al. 2010).

Process-based models require much more natural history and physiological knowledge when compared to correlative models (Thuiller 2007); their parameterization is limited by data availability and their success in predicting range limits depends on identifying the key processes that limit distributions (Elith et al. 2010). On the other hand, they highlight those processes involved in determining range boundaries (Morin and Thuiller 2009) and are expected to be more robust under new environmental conditions, and in new places (Elith et al. 2010).

Defining an unambiguous distinction between correlative and process-based models may however not be straightforward, since most models will be intermediate in what regards the explicit inclusion of processes (Dormann et al. 2012). One such model that defines the interaction between organisms and their environment based on theoretical inferences (Araújo 2009) is the model developed by Sinervo et al. (2010) that predicted extinction rates for reptiles due to climate warming using a simple physiologically inspired model of extinction. Being ectothermic, reptiles are an excellent model system for explicitly incorporating such constraints when modeling range shifts in response to climate change, because their physiology and distribution are more directly influenced by environmental temperature than in endothermic vertebrates (Buckley et al. 2012).

The model proposed by Sinervo et al. (2010) assumes that restriction in activity due to hot weather during lizards' breeding period may lead to population extinction by constraining foraging and therefore the accumulation of the amount of energy that is necessary for reproduction. Under this rationale, they developed the model based on the observation that lizard population extinctions in Mexico were related with an increase in maximum air temperature during the breeding period (Tmax) and with the physiologically active body temperature of the animals (Tb). The duration of restriction in activity (Hr) was also related with the increase in Tmax. They established a relationship to calculate Hr using Tmax and Tb, and determined the maximum value of Hr that populations can sustain without going extinct, for 34 lizard families worldwide (see Methods in this paper and Sinervo et al. 2010). In this model, Sinervo et al. (2010) explicitly postulate a process that leads to extinction, which is restriction in activity time caused by high environmental temperatures. The model does not go all the way to compute energy budgets or fecundity constrained by restriction in activity, but the processes included in the model are explicitly stated, and explicitly modeled. They established a link between Tb, Tmax, and restriction in activity, which was assessed by operative model temperatures. The link between restriction in activity time and reduced fecundity leading to increased extinction risk, is implicit.

This differs from more detailed physiological mechanistic models, that solve coupled energy and mass balance equations to establish an explicit link between the energy and water requirements of an organism, and environmental availability (Mitchell et al. 2008, Kearney and Porter 2009, Kearney et al. 2010). In these models, it is possible to infer range constraints and model potential distributions by reconstructing microclimate conditions (Kearney and Porter 2009). This approach includes microclimate and animal models that incorporate morphology, physiology and behavior to reconstruct microclimates across landscapes, and is implemented in the Niche Mapper system (Porter and Mitchell 2006). It has become a standard of mechanistic models that deal with heat and mass transfer, namely for reptiles (Huang et al. 2013, Mitchell et al. 2013), having also recently been used to provide the environmental input for a dynamic energy budget model (Kearney 2012).

Given the relative advantages and disadvantages of different types of models, none can be considered better than the other per se (Dormann et al. 2012). Moreover, several authors have pointed out that the use of different types of models provides independent lines of evidence that may confer accuracy to projections where they converge (Hijmans and Graham 2006, Kearney and Porter 2009, Morin and Thuiller 2009). This procedure has been used to predict range shifts for both plants (Hijmans and Graham 2006, Morin and Thuiller 2009) and several animal groups (e.g. lizards: Buckley et al. 2010, mammals: Kearney et al. 2010, butterflies: Buckley et al. 2010, 2011), as well as for invasive species (Elith et al. 2010). The most common approach is to apply the models independently to the same raw data and then comparing models' performance in predicting current distributions, and by comparing range shifts projected into the future either qualitatively or quantitatively (Morin and Thuiller 2009, Buckley et al. 2010, Kearney et al. 2010). Other approaches include incorporating species-specific physiological information into correlative models (Buckley et al. 2011), using the outputs of a mechanistic model as input in correlative models (Hijmans and Graham 2006, Elith et al. 2010), or applying ecophysiological bioclimatic modeling techniques (such as the one implemented in CLIMEX; Kitricos and Leriche 2010). A recent approach consists in using the outputs of correlative models as input in mechanistic models. These coupled ecological niche-population models link habitat suitability (the correlative ecological niche model output) to demographic models of population dynamics that incorporate survival, growth, reproduction and dispersal processes. In this way they account for important biological and landscape processes, and their interactions, potentially providing improved estimates of extinction risk and range shifts under climate change (Fordham et al. 2013).

In this paper we present an approach that combines two types of models with the aim of reducing uncertainty in projections of change. Furthermore, we show how this approach can contribute to a better understanding of the constraints underlying species range limits, and inform the further development of both types of models and hybrid models. Our modeling approach consists of using a simple physiologically inspired model of extinction for comparing with the projections of a correlative model, and of assessing species range shifts by comparing projected future distributions with the distribution that is observed, instead of using the distribution predicted for a baseline period. We test this approach with range shifts of European reptile species projected for the coming decades due to climate change. We chose three species: *Lacerta lepida* (ocellated lizard), *Iberolacerta monticola* (Iberian rock lizard), and *Hemidactylus turcicus* (Mediterranean house gecko). The species were chosen because they show different trends in projections of distribution shifts (Araújo et al. 2006, Sinervo et al. 2010). *Iberolacerta monticola* is predicted to contract, *H. turcicus* is predicted to expand, and *L. lepida* is predicted to either contract or expand depending on the combination of correlative modeling technique, climate general circulation model and emissions scenario chosen (Araújo et al. 2006).

4.3. MATERIAL AND METHODS

Species data

For the correlative modeling, we used species observed distribution data in Europe at the spatial resolution of 50 x 50 km, obtained from Gasc et al. (1997). For the physiological model, we used average body temperature (Tb) data, obtained for each species from the available literature: *Lacerta lepida*: 27.8°C (Mateo 2009); *Iberolacerta monticola*: 29.4°C (Martín 2009); *Hemidactylus turcicus*: 31.4°C (Huey et al. 1989).

Climate data

Climate variables were derived from gridded average monthly values of temperature (°C) and precipitation (mm) in Europe (Mitchell et al. 2004) and include: mean annual temperature, mean temperature of the coldest month, mean temperature of the warmest month, mean annual precipitation, and mean precipitation from July to September for the correlative model (Araújo et al. 2006), and mean maximum temperature in the reproduction months of each species for the physiological model (Sinervo et al. 2010). These variables were averaged for 1961–1990 (baseline period) and for 2020–2050 (future period). Climate projections for 2020–2050 were derived from the HadCM3 general circulation model (GCM) with the IPCC-SRES A2 scenario (Nakicenovic and Swart 2000, Mitchell et al. 2004). We chose these GCM and scenario to keep coherence with Araújo et al. (2006) and Sinervo et al. (2010) since these were the studies upon which we based our choice of species. The HadCM3 GCM and the A2 scenario were the only common to both studies.

Correlative modeling

Species distributions were modeled using the techniques implemented in BIOMOD (artificial neural networks, classification tree analysis, generalized additive models, generalized boosting model, generalized linear models, mixture discriminant analysis, multiple adaptive regression splines, and Breiman and Cutler's Random Forest for classification and regression) (Thuiller 2003, Thuiller et al. 2009) run within R (ver. 2.11.1; R Development Core Team). We calibrated the models with a 70% random sample of the observed data and predictive accuracy was evaluated on the remaining 30% of the data using the area under the curve of the receiver operating characteristic curve, Cohen's Kappa statistic, and the true skill statistic (Fielding and Bell 1997). The modeled distributions chosen for integration with the physiological model were the ones with the highest predictive accuracy for the baseline period (1961–1990). We considered two extreme options for dispersal: no dispersal and full dispersal. In the no dispersal option, the species are unable to disperse and establish in new areas, and in the full dispersal option, the species have no constraints to dispersal. We chose these options instead of an intermediate dispersal capacity because we wanted to calculate the full span of future potential ranges.

Physiological modeling

We used the spatially-explicit physiologically inspired model of extinction proposed by Sinervo et al. (2010). Since this model is still relatively novel, we provide an expanded explanation on how it was developed (see also Fig. 4.1). The rationale behind this model is that when environmental temperatures are too high, lizards retreat to cool refuges. However, in this way activity time will be restricted, which will limit foraging, thereby constraining costly metabolic functions such as growth, maintenance, and reproduction, and thus ultimately undermine population growth rates and raise extinction risk. The critical period during which restriction in activity is considered to govern extinction risk is the reproduction period.

Under this approach, the status of a population at a given georeferenced site is modeled as persistent or non-persistent by firstly calculating the hours of restriction in activity (Hr). Hr is computed using the mean daily maximum air temperature during the months of reproduction (Tmax) at that site, and the physiologically active body temperature of the lizards (Tb) (see below). Hr is then compared to a threshold value, which is the maximum number of hours of restriction in activity (Hr_limit). If Hr_limit is exceeded, the population at that site is considered to go extinct.

Step 1: observing an empirical relationship between extinction, Tmax and Tb

Sinervo et al. (2010) compared surveys for 48 *Sceloporus* lizard species at 200 sites in Mexico and observed that 12% of populations had gone extinct between 1975 and 2009. In these comparisons, they excluded the cases in which habitat modification caused extinctions, including only sites characterized by intact habitat as in the historical surveys. The observation that the local extinctions were correlated with the rate of change in Tmax during the breeding season, and with low Tb, originated the development of the model. It suggested that extinctions could have been driven by reduced activity under hot weather leading to insufficient energy accumulation and consequent impaired reproduction.

Step 2: finding a functional relationship between Hr, Tmax and Tb

To assess if extinction could be related to restriction in activity due to hot weather, Sinervo et al. (2010) compared two locations in Mexico from where the lizard species *Sceloporus serrifer* had recently gone extinct, with two other locations where this species was persistent. They deployed thermal models that mimic the thermal properties of a basking lizard to record operative model temperatures (Te) at the two extinct and the two persistent sites. They recorded average Te every hour over a 4-month period from January 2009, and determined the cumulative number of hours each day that Te was above the Tb of *S.*

serrifer. Assuming that during this period animals would be inactive, this corresponds to the hours of restriction in activity (Hr). They also observed that Hr was positively correlated with Tmax, which had significantly increased over the last 36 yr in the same months. Sinervo et al. (2010) determined the relationship between Hr assessed by Te, and Tmax. They related Hr to observed Tmax on a daily basis, and fitted a significant linear regression equation. Then they standardized this equation in terms of Tb, to obtain Hr as a function of Tmax and Tb, given by: $Hr = 6.12 + 0.74 * (Tmax – Tb)$ (Eq. S2 in Sinervo et al. 2010). This formula can be extended to any species of lizard, given data on Tb.

Step 3: calibrating Hr_limit: extending the model to other Sceloporus species

Hr measured at persistent versus extinct sites of *S. serrifer* suggested that the maximum Hr for *S. serrifer*, above which extinction would occur, were 4 h (Sinervo et al. 2010). To extend the model to other *Sceloporus* species, Sinervo et al. (2010) calibrated that value using the local extinction data from the resurveyed sites in Mexico. They computed Hr at each of those sites using the equation presented above, the Tb of each species, and Tmax in 2009. To determine the extinction threshold (Hr_limit), they varied Hr_limit from 1 to 12 h in 0.1 h increments, and computed the overall fit of the model, by calculating the deviations of model predictions from the observed data. Based on this procedure, a value of Hr_limit of 3.85 h provided the best fit between observed and predicted extinctions.

Step 4: generalizing the model to other lizard families

Sinervo et al. (2010) then obtained extinction projections for 34 lizard families with geo-referenced Tb records from 1216 lizard populations. To do so, they estimated an Hr_limit for each family, using a best-fit procedure similar to the one used for the Mexican *Sceloporus* lizards (and thereby scaling Eq. S2 to each family). They computed the Hr each population would sustain in 1975, given Tb and Tmax during the breeding period in 1975 at each of the georeferenced sites, and for each family they used the upper 95% confidence level of Hr as the extinction threshold.

Step 5: validating the model globally

Sinervo et al. (2010) tested the global generality of their model by verifying the concordance between the distributions of current observed local extinctions, and local extinctions predicted by the model, in lizard populations from families in four other continents, besides family Phrynosomatidae in North America. To do this they used data of observed local extinctions from published records, and resurveys of known lizard populations, and compared them with the model predictions, obtained using the family-specific Hr_limit calibrations. In this analysis, disturbed sites were excluded and they focused on sites with intact habitat.

Step 6: projecting extinctions in the future

Besides calculating extinctions for 2009, Sinervo et al. (2010) used the physiological model of extinction as described above to compute extinction probabilities for 2050 and 2080.

Step 7: implementing the physiological model of extinction under our approach

In the present work, we modeled each species' persistence or non-persistence in 2020–2050 at each grid-cell where it is currently present. We used Tmax at each grid-cell and the corresponding species' Tb to compute Hr in each of those grid-cells, using the method developed by Sinervo et al. (2010). For the extinction threshold we used the Hr_limit of the corresponding family as determined by Sinervo et al. (2010). We have also used the physiological model to project species viability or non-viability at the grid-cells where the correlative model had projected colonizations. Being a model of extinction that incorporates only the upper limits of thermal constraints, the model developed by Sinervo et al. (2010) is not appropriate to model species distributions per se. Instead, we have used it to compare ecophysiological limits to persistence with projections of the correlative model. In this way, our modeling approach hybridizes outputs from the two different models.

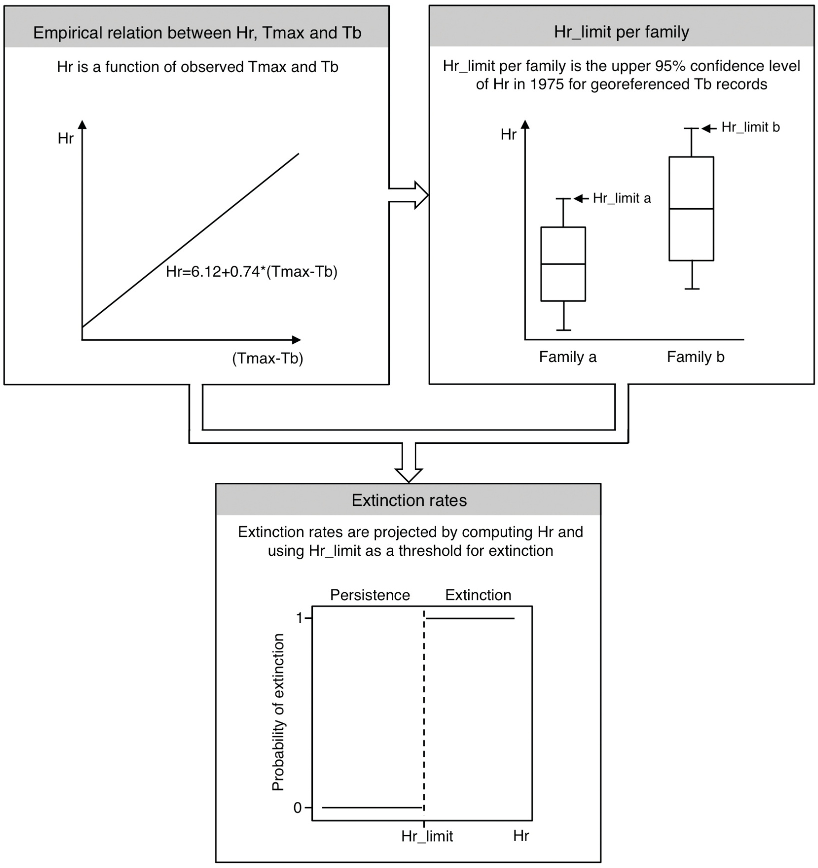

Figure 4.1. Schematic representation of the model proposed by Sinervo et al. (2010). See text for details; for a full description of the model see the original paper and corresponding supplementary materials. Hr: hours of restriction in activity; Tmax: maximum air temperature during the months of reproduction; Tb: physiologically active body temperature; Hr_limit: threshold for extinction (Hr above which populations are assumed to go extinct). For thermoconformers that maintain Tb close to air temperature (Tair), the model is modified by computing Hr as the cumulative number of hours that Tair is above Tb, assuming a sine wave for Tair between Tmin and Tmax (24-h period) (Sinervo et al. 2010). Otherwise the method is the same.

Assessing species distribution shifts

We assessed species range shifts by comparing projected future distributions with observed distributions. This can be considered as a filtered approach, in opposition to a non-filtered one, in which to assess range shifts, future distributions are compared with the distribution predicted for the baseline period. Accordingly, for any grid-cell, in the non-filtered approach an extinction is considered as such when the model predicts absence in the future and presence in the predicted current distribution, regardless of whether the species is present or absent in the observed distribution. In contrast, in the filtered approach, extinctions are only considered as such if the species is present in the observed distribution. The same rationale applies to colonizations: in the filtered approach, colonizations at any given site are only considered as such, if the species is absent from that site in the observed distribution. We developed a classification scheme for the events projected in the future following these approaches (Table 4.1). The filtered approach is important for model integration because it establishes a common baseline – the observed distribution – against which to classify events projected in the future. This approach also has the advantage of avoiding estimating extinctions from areas where the species might not occur, and of estimating colonizations in areas where the species is already present.

Table 4.1. Classification scheme of events projected in the future according to the filtered and non-filtered approaches. Species presence is denoted by '1', and species absence is denoted by '0'. Events with a † indicate that even though the presence/absence status is predicted to change from the observed to the future distribution, the prediction for the current period is inconsistent with the observed status. In those cases, we chose to make the cautious option of classifying the future event with the same status as in the observed distribution.

Observed distribution	Predicted distribution		Classification of future event	
	Current	Future	Non-filtered	Filtered
1	1	1	Persistence	Persistence
		0	Extinction	Extinction
	0	1	Colonization	Persistence
		0	Absence	Persistence †
0	1	1	Persistence	Absence †
		0	Extinction	Absence
	0	1	Colonization	Colonization
		0	Absence	Absence

Integrating models

We considered that the physiological model supported the projections of the correlative model where the projections were the same for both models. In this way, for any grid-cell, the physiological model supports extinctions projected by the correlative model when both models project extinction in that grid-cell. Colonizations are scored as supported when the physiological model projects the species viability in a grid-cell where the correlative model has projected a colonization. Species range shifts were quantified for each species by calculating the percentage of extinctions and colonizations projected relative to the total number of grid-cells with observed presences. Agreement between models was calculated as the percentage of extinctions and colonizations supported by the physiological model relative to the total number of extinctions and colonizations (respectively) projected by the correlative model.

Associations between climate and species range shifts

To analyze the relationships between climate and the events projected by each model in the future, and how climate influences agreement and disagreement between the models, we used generalized linear models (GLMs). Current climate and climate variation between future and current periods (Araújo et al. 2006) were used as predictors, because we wanted to disentangle the effect of these two sets of variables. From the correlative model, we selected the relevant variables using the importance of each variable, given by BIOMOD (Thuiller 2003, Thuiller et al. 2009). For each species, we averaged variable importance across all variables, and the variables with an importance above the mean value were selected (Capinha and Anastácio 2011).

We analyzed how climate differs between sites where different events were projected, using the following comparisons for each species (Table 4.3): extinctions versus persistences projected by the physiological model; extinctions versus persistences projected by the correlative model; extinctions versus persistences projected by both models; colonizations versus absences projected by the correlative model; colonizations projected by the correlative model and not supported by the physiological model versus colonizations supported by the physiological model.

Each comparison was modeled as a binary response variable, and thus GLMs were fitted by specifying a binomial distribution and a logistic link function (Crawley 2007). The probability of an event was modeled as a linear function of the climate variables. We used backwards elimination of non-significant factors to check whether removing one or more explanatory variables would improve the GLM, by examining the differences in the Akaike's information criterion (AIC) values resulting from removing different explanatory variables. Only those variables whose regression coefficient estimates were significant at the 0.05 confidence level (z-test) and whose removal would cause a decrease in Akaike weight (Burnham and Anderson 2002), and thus a worse fit, were maintained. We computed standardized regression coefficients to show the relative importance of significant variables (Gelman and Hill 2006). We fitted all models with the glm and step functions from the stats package within R (ver. 2.11.1; R Development Core Team).

Although the temperature above which extinctions are predicted by the physiological model can be determined simply by reversing the equation for Hr at the threshold temperature, the procedure detailed above enabled us to identify the relative importance of current versus future temperature on the probability of an event being projected by the physiological model, besides assessing the influence of these two predictors on agreement and disagreement between the models.

4.4. RESULTS

Species range shifts and support by the physiological model

Under the no dispersal assumption, *Lacerta lepida* is projected to lose from 8% of its current distribution up to a maximum of 39% (extinctions projected by the correlative model and supported by the physiological model and total extinctions projected by the correlative model, respectively) (Table 4.2). The physiological model also projects 19% extinctions in areas where the correlative model does not project extinctions. The extinctions projected by both models are in the west and southernmost part of the species' current distribution while the correlative model alone also projects extinctions in the south and mostly in the north and northeast parts of the species' current range (Fig. 4.2). When full dispersal is considered, *L. lepida* is projected to colonize between 29 to 33% new areas relative to its current distribution, and mainly to the north of its current range (colonizations projected by the correlative model and supported by the physiological model and total colonizations projected by the correlative model, respectively). The colonizations projected by the correlative model and not supported by the physiological model are located in the Iberian Peninsula and in the Balkan Peninsula.

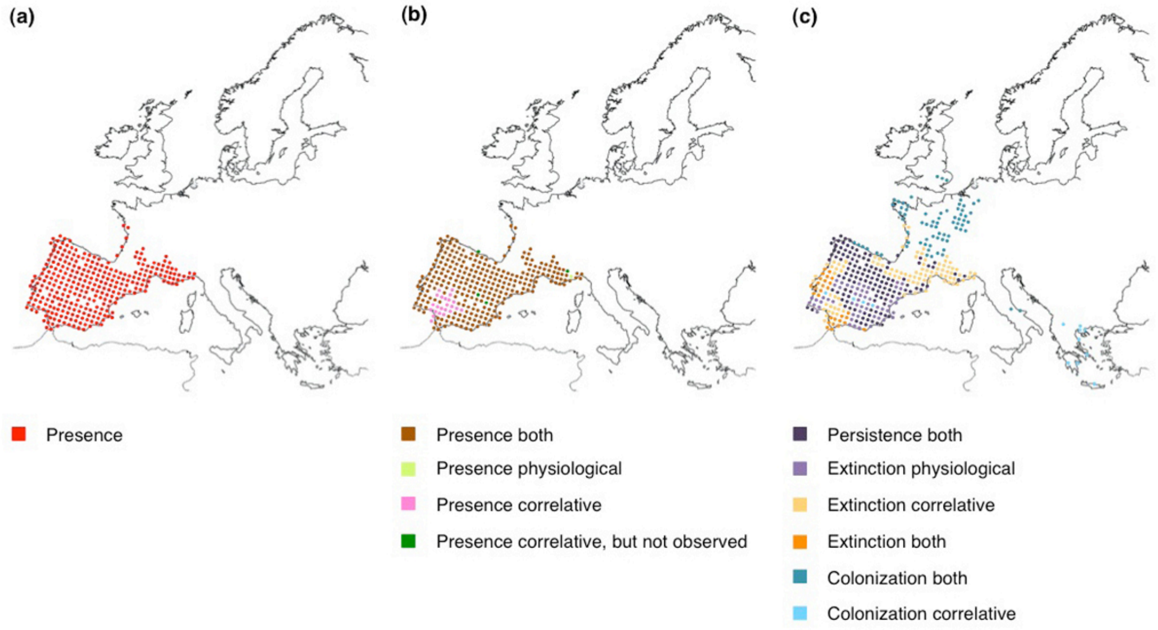

Figure 4.2. Distribution maps for *Lacerta lepida*. (a) Observed distribution, (b) distribution predicted for the baseline period, and (c) distribution projected for the future, for both models superimposed upon each other and upon the observed distribution to illustrate agreement and disagreement between the models.

Iberolacerta monticola is projected to lose all its range according to the correlative model if dispersal is not considered (Table 4.2). However, the physiological model does not support these extinctions. When dispersal ability is considered, the correlative model does not project any colonizations (Fig. 4.3).

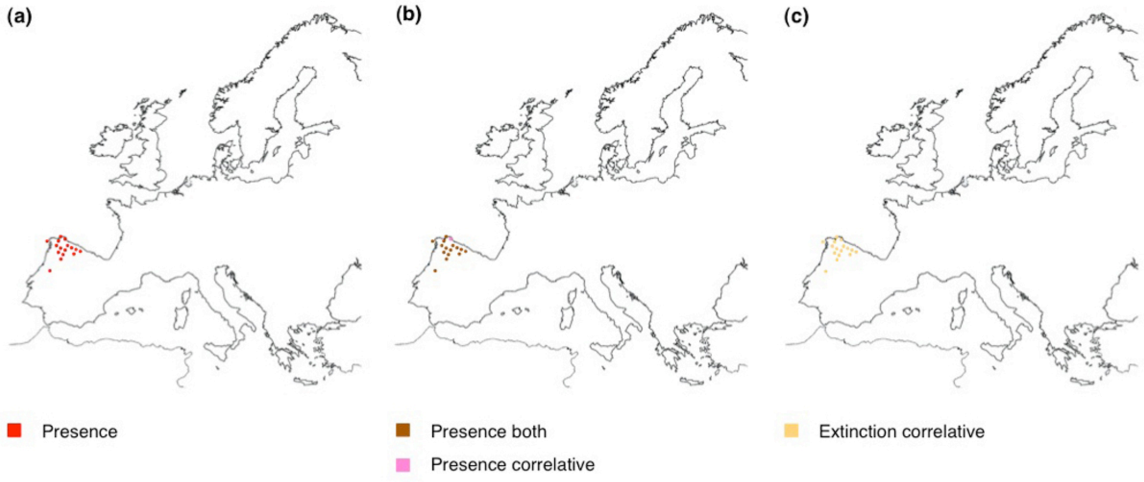

Figure 4.3. Distribution maps for *Iberolacerta monticola*. (a) Observed distribution, (b) distribution predicted for the baseline period, and (c) distribution projected for the future, for both models superimposed upon each other and upon the observed distribution to illustrate agreement and disagreement between the models.

Hemidactylus turcicus is projected to expand its distribution. The correlative model projects 7% extinctions but none are supported by the physiological model, which projects no extinctions (Table 4.2). Regarding colonizations, *H. turcicus* is projected to almost double its current range. This species is projected to colonize new areas into the north along its longitudinal range that correspond to 92% of its current range, and these projections are fully supported by the physiological model (Fig. 4.4).

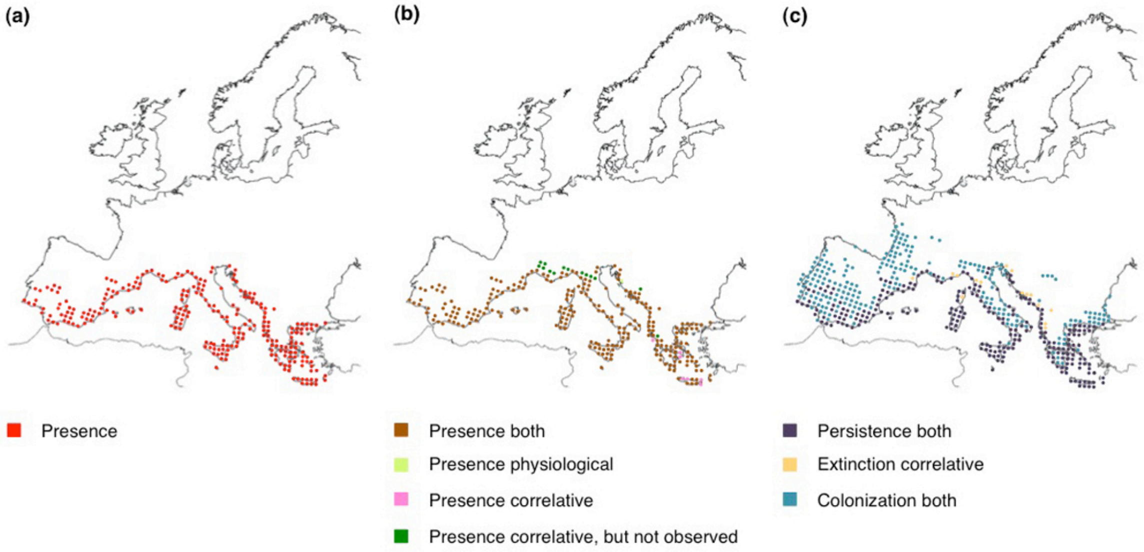

Figure 4.4. Distribution maps for *Hemidactylus turcicus*. (a) Observed distribution, (b) distribution predicted for the baseline period, and (c) distribution projected for the future, for both models superimposed upon each other and upon the observed distribution to illustrate agreement and disagreement between the models.

Agreement between models

Agreement between model projections varies greatly between species and is dependent on whether dispersal ability is considered or not (Table 4.2). The correlative model projects a higher level of extinctions than the physiological model for all species. Agreement between the extinctions projected by the correlative model and the physiological model is low (20% for *Lacerta lepida* and 0% for *Iberolacerta monticola* and *Hemidactylus turcicus*). The correlative model also projects a high level of colonizations for *L. lepida* and *H. turcicus*, which are well supported by the physiological model (87% support for *Lacerta lepida* and 100% for *Hemidactylus turcicus*).

Table 4.2. Percentage of extinctions and colonizations projected for each species for 2020–2050

		Lacerta lepida	*Iberolacerta monticola*	*Hemidactylus turcicus*
Extinctions	Projected by correlative	39	100	7
	Projected by physiological	27	0	0
	Projected by correlative and supported by physiological	8	0	0
Colonizations	Projected by correlative	33	-	92
	Projected by correlative and supported by physiological	29	-	100

Associations between climate and species range shifts

Using the criterion of mean value of variable importance given by BIOMOD, the predictor variables selected from the correlative model were: temperature of the coldest month (T_C) and precipitation between July and September (P_{JS}) for *Lacerta lepida*; and annual temperature (T_A) and annual precipitation (P_A) for *Hemidactylus turcicus*. From the physiological model the climate variable was temperature in the reproduction months (T_R). We excluded *Iberolacerta monticola* from this analysis because the correlative model projected a total loss of the species current range, while projecting no colonizations, and the physiological model did not project any extinctions.

For *Lacerta lepida*, both T_R and ΔT_R are higher at the sites where the physiological model projected extinctions (Table 4.3). The sites where the correlative model projected extinctions have higher T_C and lower P_{JS}, and will become hotter and drier in the future (higher ΔT_C and higher Δ_{PJS}). Sites where both models projected extinctions are characterized by having higher T_C, higher ΔP_{JS}, higher T_R, and higher ΔT_R than the sites where both models projected persistence. The correlative model projected colonizations where T_C is higher but will not increase significantly in the future, and where P_{JS} is higher but will decrease more in the future. Both T_R and ΔT_R are higher where the physiological model did not support the colonizations projected by the correlative model.

For *Hemidactylus turcicus*, the physiological model did not project any extinctions, and supported all the colonizations projected by the correlative model. T_A, ΔT_A and P_A are lower where extinctions were projected than where persistence was projected by the correlative model (Table 4.3). Sites where colonizations were projected differ from sites where absences were projected in that T_A, ΔT_A and ΔP_A are higher where colonizations were projected.

Table 4.3. Climate variables and significant regression coefficients ($p < 0.05$) for each comparison of events projected, from generalized linear modeling.

	Explanatory variables					
	Temperature coldest month		Precipitation July-September		Temperature reproduction months	
Species and events compared	Current	Change	Current	Change	Current	Change
Lacerta lepida						
Extinction vs. persistence physiological					2.44	1.97
Extinction vs. persistence correlative	1.04	0.36	-0.91	0.45		
Extinction vs. persistence both models	8.43	n.s.	n.s.	2.99	4.21	3.87
Colonization vs. absence correlative	1.85	n.s.	0.72	1.51		
Colonization not supported vs. supported					9.43	5.45
	Annual temperature		Annual precipitation			
	Current	Change	Current	Change		
Hemidactylus turcicus						
Extinction vs. persistence correlative	-8.96	-6.07	-2.36	n.s.		
Colonization vs. absence correlative	7.62	2.49	n.s.	0.39		

4.5. DISCUSSION

The physiological model suggests that in the west and southernmost part of *Lacerta lepida*'s current distribution, where extinctions projected by the correlative model are supported, future temperatures during the reproduction period may be too high to allow population persistence. Sites where this convergence occurs are characterized by both current high temperatures, and significant future temperature increase. The same rationale applies to the sites where colonizations projected by the correlative model are not supported by the physiological model. At these sites, even if other climatic factors would allow the presence of *Lacerta lepida*, high temperatures during the reproduction period would prevent the colonization of these new areas.

For *Iberolacerta monticola* and *Hemidactylus turcicus*, the physiological model does not support any of the extinctions projected by the correlative model, and for *H. turcicus* it supports all the colonizations projected by the correlative model. This suggests that even though temperature is projected to increase at these places, high temperatures during the reproduction period in the future would not hinder population persistence in currently occupied (*I. monticola* and *H. turcicus*) or in newly occupied areas (*H. turcicus*). The analysis of the associations between climate and range shifts projected by the correlative model also indicates that high temperature is not the most limiting factor, neither for colonizations nor for extinctions.

Accounting for geographic variation in reproduction dates and body temperatures could refine the predictions of the physiological model (Sinervo et al. 2010, 2011, Clusella-Trullas and Chown 2011) and help explain some of the inconsistencies found in the present study. Habitat characteristics and behavioural thermoregulation in ectotherms can also moderate the effects of climate warming (Kearney et al. 2009) and thus could also be considered (Sinervo et al. 2010, 2011, Clusella-Trullas and Chown 2011), as well as including other climatic data and linking them to demography (Sinervo et al. 2011).

The use of several climate general circulation models (GCM), emissions scenarios, as well as bioclimatic statistical models, is a way of assessing uncertainty in projections of change and has been recommended by several authors (see Beaumont et al. 2007 and references therein). In this study, we chose to use one GCM and one emissions scenario, because our intention was to evaluate and exemplify the use of different models under a common modeling framework. Input from more GCMs and/or scenarios could nevertheless be easily incorporated. Our modeling approach could be further enriched by refining the spatial resolution of the analysis for those areas identified as vulnerable (Carvalho et al. 2010) but also where stronger inconsistencies between the models were found. Other factors shaping species responses to environmental change should be considered, such as biotic interactions (Jankowski et al. 2013), and the synergistic effects between climate change and land use change (Pereira et al. 2010).

Most importantly, the physiological model was developed under the assumption that restriction in activity time due to hot weather in the breeding period would increase extinction risk through energetic deficits that reduce reproductive output. This assumption is supported by independent studies (Huey et al. 2010) showing that lizard annual activity times are positively correlated with annual fecundity (Adolph and Porter 1993). However, in contrast with correlative models, for which there are independent model-data comparisons (Araújo et al. 2005), the hypothesis proposed by Sinervo et al. (2010) has not been proven empirically, and therefore still needs validation with independent datasets.

The extinction model developed by Sinervo et al. (2010) incorporates only thermal constraints, but there are several causes for extinction, which are not necessarily mutually exclusive (Koch and Barnosky 2006). A physiological model can be most useful in indicating where a species may not be able to exist (Elith et al. 2010). By focusing exclusively on the upper bounds of thermal constraints, the extinction model used here can only provide information on the impact of high temperatures on persistence, under future temperature increase as indicated by climate change projections (IPCC 2007). In this context, using the physiological model to assess the colonizations projected by the correlative model allows highlighting potential places where temperatures in the future may be so high they would impair per se the persistence of populations, were individuals able to reach those areas. This could be an asset for conservation planning, such as the design of reserves or habitat restoration efforts. We also assessed species range shifts by comparing the projected future distributions with the observed distribution. This approach avoids estimating extinctions from areas where the species might not occur and colonizations in areas where the species is already present. Therefore, it is more realistic and hence also more useful for conservation planning (Araújo et al. 2011).

Using different types of models in conjunction can inform the selection of variables and processes to be included (Buckley et al. 2010) and is essential to understand the limits to species distributions (Austin et al. 2009). Considering the discussed advantages and disadvantages of the different models and the urgency of producing accurate predictions of biodiversity response to global environmental change, we suggest that the best strategy currently available is the use of different types of models under a common modeling framework. Other authors have highlighted the importance of such an approach (Buckley et al. 2010, Kearney et al. 2010, Dormann et al. 2012), but much work still needs to be done. The main objective of the present work was to suggest an approach to accomplish that, and which can easily be implemented with other models. Since different models rely on different assumptions, their predictions can be considered to be complimentary (Morin and Thuiller 2009). In this way the reliability of predictions is greatest and uncertainty in projections is reduced where the models' predictions converge.

4.6. ACKNOWLEDGEMENTS

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4.7. REFERENCES

Adolph SC, Porter WP (1993) Temperature, activity, and lizard life histories. The American Naturalist 142: 273-295.

Araújo MB (2009) Climate change and spatial conservation planning. In: Moilanen A, Wilson KA, Possingham H (Eds.) Spatial conservation prioritization: quantitative methods and computational tools. Oxford University Press. Pp. 172-184.

Araújo MB, Peterson T (2012) Uses and misuses of bioclimatic envelope modelling. Ecology 93: 1527-1539.

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Global Change Biology 11: 1504-1513.

Araújo MB, Thuiller W, Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. Journal of biogeography 33: 1712-1728.

Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. Ecology Letters 14: 484-492.

Austin MP, Smith TM, Van Niel KP, Wellington AB (2009) Physiological responses and statistical models of the environmental niche: a comparative study of two co-occurring *Eucalyptus* species. Journal of Ecology 97: 496-507.

Beaumont LJ, Pitman AJ, Poulsen M, Hugues L (2007) Where will species go? Incorporating new advances in climate modelling into projections of species distributions. Global Change Biology 13: 1368-1385.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecology Letters 15: 365-377.

Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? Ecology Letters 13: 1041-1054.

Buckley LB, Waaser SA, MacLean HJ, Fox R (2011) Does including physiology improve species distribution model predictions of responses to recent climate change? Ecology 92: 2214-2221.

Buckley LB, Hurlbert AH, Jetz W (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. Global Ecology and Biogeography 21: 873-885.

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Capinha C, Anastácio P (2011) Assessing the environmental requirements of invaders using ensembles of distribution models. *Diversity and Distributions* 17: 13-24.

Carvalho SB, Brito JC, Crespo EJ, Possingham HP (2010) From climate change predictions to actions - conserving vulnerable animal groups in hotspots at a regional scale. Global Change Biology 16: 3257-3270.

Clusella-Trullas S, Chown SL (2011) Comment on "Erosion of lizard diversity by climate change and altered thermal niches". Science 332: 537.

Crawley MJ (2007) The R Book. Wiley, England.

Dormann CF, Schymanski SJ, Cabral J, Chuine I, Graham C, Hartig F, Kearney M, Morin X, Römermann C, Schröder B, Singer A (2012) Correlation and process in species distribution models: bridging a dichotomy. Journal of Biogeography 39: 2119-2131.

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1: 330-342.

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38-49.

Fordham DA, Akçakaya HR, Araújo MB, Keith DA, Brook BW (2013) Tools for integrating range change, extinction risk and climate change information into conservation management. Ecography 36: 001-009.

Gasc JP, Cabela A, Crnobrnja-Isailovic J, Dolmen D, Grossenbacher K, Haffner P, Lescure J, Martens H, Martínez Rica JP, Maurin H, Oliveira ME, Sofianidou TS, Veith M, Zuiderwijk A (1997) Atlas of amphibians and reptiles in Europe. Societas Europaea Herpetologica. Muséum National d'Histoire Naturelle & Service du Patrimoine Naturel, Paris.

Gelman A, Hill J (2006) Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, New York.

Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30: 751-777.

Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology 12: 2272-2281.

Huang S-P, Chiou C-R, Lin T-E, Tu MC, Lin C-C, Porter WP (2013) Future advantages in energetics, activity time, and habitats predicted in a high-altitude pit viper with climate warming. Functional Ecology 27: 446-458.

Huey RB, Niewiarowski PH, Kaufmann J, Herron JC (1989) Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? Physiological Zoology 62: 488-504.

Huey RB, Losos JB, Moritz C (2010) Are lizards toast? Science 328: 832-833.

IPCC 2007. Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Switzerland.

Jankowski JE, Londoño GA, Robinson SK, Chappell MA (2013) Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. Ecography 36: 1-12.

Kearney M (2012) Metabolic theory, life history and the distribution of a terrestrial ectotherm. Functional Ecology 26: 167-179.

Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12: 334-350.

Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. Proceedings of the National Academy of Sciences USA 106: 3835-3840.

Kearney M, Wintle BA, Porter WP (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters 3: 203-213.

Kitricos DJ, Leriche A (2010) The effects of climate data precision on fitting and projecting species niche models. Ecography 33: 115-127.

Koch PL, Barnosky AD (2006) Late quaternary extinctions: state of the debate. Annual Review of Ecology, Evolution, and Systematics 37: 215-250.

Leadley PW, Pereira HM, Alkemade R, Fernandez-Manjarrés J, Proença V, Scharlemann JPW, Walpole M (2010) Biodiversity Scenarios: Projections of 21st century change in biodiversity and associated ecosystem services. Secretariat of the Convention on Biological Diversity, Montreal. 132 p.

Martín J (2009) Lagartija serrana - *Iberolacerta monticola*. In: Salvador A, Marco A (Eds.) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid.

Mateo JA (2009) Lagarto ocelado - *Timon lepidus*. In: Salvador A, Marco A (Eds.) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid.

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC. 86 p.

Mitchell TD, Carter TR, Jones PD, Hulme M, New M (2004) A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901-2000) and 16 scenarios (2001-2100). Tyndall Centre Working Paper 55.

Mitchell NJ, Kearney MR, Nelson NJ, Porter WP (2008) Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? Proceedings of the Royal Society B: Biological Sciences 275: 2185-2193.

Mitchell N, Hipsey MR, Arnall S, McGrath G, Tareque HB, Kuchling G, Vogwil R, Sivapalan M, Porter WP, Kearney MR (2013) Linking eco-energetics and eco-hydrology to select sites for the assisted colonization of Australia's rarest reptile. Biology 2: 1-25.

Morin X, Thuiller W (2009) Comparing niche-and process based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90: 1301-1313.

Nakicenovic N, Swart R (2000) Emissions scenarios: a special report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37: 637-669.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for Global Biodiversity in the 21st Century. Science 330: 1496-1501.

Pereira HM, Navarro LM, Martins IS (2012) Global Biodiversity Change: The Bad, the Good, and the Unknown. Annual Review of Environment and Resources 37: 25-50.

Porter WP, Mitchell JW (2006) Method and system for calculating the spatial-temporal effects of climate and other environmental conditions on animals. US Patent 7155377.

Sinervo B, Mendez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, Gadsden H, Avila L, Morando M, De La Riva I, Sepulveda P, Rocha C, Ibargüengoytía N, Puntriano C, Massot M, Lepetz V, Oksanen T, Chapple D, Bauer A, Branch W, Clobert J, Sites J (2010) Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894-899.

Sinervo B, Miles DB, Martinez-Mendez N, Lara-Resendiz R, Mendez-de-la-Cruz F (2011) Response to comment on "Erosion of lizard diversity by climate change and altered thermal niches". Science 332: 537.

Thuiller W (2003) BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biology 9: 1353-1362.

Thuiller W (2007) Biodiversity: climate change and the ecologist. Nature 448: 550-552.

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD - a platform for ensemble forecasting of species distributions. Ecography 32: 369-373.

Williams JW, Jackson ST (2007) Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5: 475-482.

Zimmermann NE, Edwards TC, Graham CH, Pearman PB, Svenning, J-C (2010) New trends in species distribution modelling. Ecography 33: 985-989.

Chapter 5. Synthesis

This thesis aimed at presenting modeling frameworks that contribute to better understanding and predicting biodiversity responses to environmental change, and that can be applied in several contexts, including at scales that are relevant for decision-making, using process-based models that integrate various types of information, or in combination with other types of models. The issues addressed were population persistence in fragmented landscapes (chapter 2), vulnerability to land-use change (chapter 3), and range shifts in response to climate change (chapter 4).

5.1. General discussion and contributions of the thesis

5.1.1. Population persistence in fragmented landscapes

When analyzing population persistence in landscapes fragmented by roads using an individual-based model of population dynamics (chapter 2), the probability of extinction increased and the population size decreased with increasing road density. The probability of extinction also increased, and the population size decreased, with increasing road mortality, and in this case also much faster for the large than for the short dispersal distance. Both road mortality and road avoidance caused isolation. Road mortality alone had a stronger negative effect on the probability of persistence than road avoidance alone, in agreement with previous studies (Jaeger and Fahrig 2004).

Results from chapter 2 highlight the relevance of identifying the existence and extent of avoidance of sink habitats, besides the levels of mortality, since avoidance could in some situations rescue populations under low to moderate sink mortality from extinction, as suggested in previous studies (e.g., Rytwinski and Fahrig 2013). However, although in the analysis performed population persistence did not decrease when avoidance of the matrix was high, population size became smaller. This is important to consider in long-term conservation management, since small populations may have an increased extinction risk due to demographic stochasticity (Lande 1993).

Other factors could further influence population persistence besides the ones analysed in chapter 2 of this thesis. For example, habitat quality can affect how roads impact populations (e.g., Grilo et al. 2014), which could be tested by varying the habitat quality of the non-road cells in the landscape. Additionally, while individuals only evaluated their immediate neighboring cells in each step of dispersal, the effects of habitat loss and fragmentation may increase if roads are avoided from a distance (e.g., Jaeger et al. 2005).

A large dispersal distance decreased population size and persistence as road mortality increased. However, this was not observed when there was no road mortality. The role of dispersal is beneficial in metapopulation models (e.g., Hanski 1998) because it allows the colonization of more patches. In contrast, dispersal is disadvantageous in source-sink models (e.g., Skellam 1951, Pulliam 1988), because it can occur into sink habitats (Pereira and Borda-de-Água 2013). Empirical studies suggest dispersal has a negative effect in disturbed habitats (e.g., Gibbs 1998, Van Houtan et al. 2007), and a higher mobility has also been associated with negative effects of roads in mammal and bird species (Rytwinski and Fahrig 2012).

The analysis performed in chapter 2 suggests that a large dispersal distance may not always be detrimental for population size and persistence in disturbed habitats, provided mortality in the matrix is low, indicating that the role of dispersal may be influenced by the level of disturbance. Including intermediate dispersal distances (Casagrandi and Gatto 1999) could help further clarify the role of dispersal in disturbed landscapes.

The model presented in chapter 2 can potentiate other studies, either theoretical or empirical. For example, it could be applied to species-specific situations, by using the specific traits of the species or population of interest. Also, the modeled landscape can be adapted to represent real landscape configurations, and therefore it can also be used to evaluate the impact of different mitigation options for population persistence, in environmental impact assessments, and for conservation planning.

5.1.2. Vulnerability to land-use change

The use of a species-specific, spatially explicit mechanistic approach to assess the impact of roads on terrestrial carnivore species at the global level (chapter 3) allowed the identification of the species that are expected to be most exposed to roads, but also where within its range each species is expected to be exposed, and which regions are expected to have more species exposed to roads. This assessment predicted that species are exposed in regions with medium to high road density, but also in regions with relatively low road density. Hotspots of road impact were predicted for North America and Asia. The percentage of the range where each of the most exposed species was predicted to be affected, and therefore to disappear or have low abundance, ranged from 38 to 100%.

The framework presented in chapter 3 has limitations that need to be considered: the maximum road density (D_{max}) was derived assuming unlimited dispersal ability, and the minimum patch size (A_{min}) assuming that individuals always die when crossing a road, and it is possible that even if $D_{obs} > D_{max}$, or when $A_{obs} < A_{min}$, populations persist (Borda-de-Água *et al.*, 2011). Therefore, it is not appropriate to use D_{max} or A_{min} as strict thresholds for population persistence. Instead, the species were ranked in relation to one another to obtain a first approximation of which species would be more exposed to roads than other species, and in which areas within its range a species would be more exposed to roads than in other areas of its range. This is because even though populations may persist where $D_{obs} > D_{max}$, or where $A_{obs} < A_{min}$, they are expected to be more exposed to roads when $D_{obs} > D_{max}$, or $A_{obs} < A_{min}$.

Explicitly combining extrinsic factors of threat and intrinsic species traits is important to move from a descriptive to a mechanistic, biologically sound evaluation of threats (Lee and Jetz 2010, Dirzo et al. 2014). The modeling approach presented in chapter 3 does so by bringing together process-based models that link species-specific life histories, population dynamics and dispersal, with biogeographic data, and land-use data - in this case, the road infrastructure.

By integrating species traits, this analysis also allowed detecting species that despite having relatively low road density within their range, are estimated to be more exposed to roads than other species for which road density is relatively high within their range. Such inferences would not have been possible using a simple spatial overlap analysis between species ranges and road density.

The framework developed in chapter 3 could be applied at different spatial and also temporal scales, e.g. for conservation or management purposes: to select areas for conservation and for implementing mitigation measures at the local scale, in environmental impact assessments, to inform prioritization schemes for road building (Laurance et al. 2014), or for projecting the effects of future large-scale road network developments, which could then feed, for example, World Bank projections or scenarios for global biodiversity change (Pereira et al. 2010).

5.1.3. Range shifts in response to climate change

Producing more accurate predictions of biodiversity responses to global environmental change is urgent. Several authors have highlighted the importance of using different types of models under a common modeling framework (Buckley et al. 2010, Kearney et al. 2010, Dormann et al. 2012). Different models rely on different assumptions, and therefore their predictions can be considered complimentary (Morin and Thuiller 2009), reducing uncertainty where the model's predictions converge. This thesis proposed such an approach in chapter 4, which can be easily implemented with other models.

Combining different models can help selecting significant variables and processes (Buckley et al. 2010) and to understand what limits species distributions (Austin et al. 2009). Chapter 4 of this thesis integrated a process-based, physiologically inspired model of extinction (Sinervo et al. 2010) with phenomenological species distribution models (Thuiller 2003, Thuiller et al. 2009), to assess climate change induced range shifts for reptile species. This analysis suggested that future temperatures during the breeding period may be too high to allow population persistence, at the sites where the physiological model supported extinctions, and where it did not support colonizations, projected by the correlative model. Conversely, high temperatures in the future should not hinder population persistence where the physiological model did not support extinctions, and where it supported colonizations projected by the correlative model.

In the analysis performed in chapter 4, one climate general circulation model (GCM) and one emissions scenario were used. However, input from more GCMs and/or emissions scenarios could be incorporated in this type of analysis, which is a way of assessing uncertainty in projections of change (see Beaumont et al. 2007 and references therein). The spatial resolution of the analysis performed in chapter 4 could also be refined, especially for the areas that were identified as vulnerable (Carvalho et al. 2010), and where greater discrepancies between the models were found.

A physiological model can be most useful in indicating where a species may not be able to exist (Elith et al. 2010). The model proposed by Sinervo et al. (2010) incorporates only thermal constraints, but its use to assess the projections of the correlative model highlighted areas where future high temperatures could impair population persistence. This type of approach can be an asset for conservation planning, such as the design of reserves or habitat restoration efforts. Also, range shifts were identified by comparing the projected future distributions with the observed distributions, instead of comparing with predicted distributions for the baseline period. In this sense, extinctions were only considered as such if a species was present in the observed distribution, and colonizations at a given site were only considered as such if a species was absent from that site in the observed distribution. This type of analysis is more useful for conservation planning (Araújo et al. 2011), since it avoids estimating extinctions from areas where a species might not occur, and colonizations in areas where the species is already present.

5.2. General issues and ways forward for process-based models

By establishing an explicit link between the environment and population dynamics, process-based models can allow a better understanding of the relationship between environmental change and biodiversity loss (Pereira and Borda-de-Água 2013). Nevertheless, there are several issues to consider and ways in which process-based models can be developed, some of which are specific to process-based models, others that are applicable to biodiversity models in general.

Process-based models usually require more parameters and more knowledge than other types of models (Thuiller 2007, Pereira and Borda-de-Água 2013), and their parameterization is limited by data that are usually not available for large numbers of species (Araújo 2009, Elith et al. 2010). Moreover, a process-based model will uncover only the effects of the processes that are explicitly incorporated in the model (Dormann et al. 2012, Brotons et al. 2016). For example, the extinction model proposed by Sinervo et al. (2010), used in chapter 4 of this thesis, incorporates only the upper bounds of thermal constraints. While such a physiological model can be most useful in indicating where a species may not be able to exist (Elith et al. 2010), Sinervo's et al. (2010) model can only provide information on the impact of future temperature increase as indicated by climate change projections (IPCC 2007).

Improving process-based models will depend on several factors, at different levels of the modeling process. There is a need for improved data, which can be achieved by (Akçakaya et al. 2016): i) identifying common metrics of biodiversity; ii) increasing the availability of data for calibrating and validating models; and iii) facilitating data access, for example through open tools and by improving data sharing.

Improved data and data access will help improve model validation, which is also an important step for increasing the utility of models for conservation planning and decision making (Akçakaya et al. 2016). For example, while some independent model-data comparisons exist for phenomenological models (Araújo et al. 2005), and although independent studies show a positive correlation between lizard annual activity times and fecundity (Adolph and Porter 1993, Huey et al. 2010), the hypothesis that restriction in activity increases extinction risk, proposed by Sinervo et al. (2010) in their model of reptile extinction, still needs validation with independent datasets.

Our ability to understand and predict biodiversity responses to environmental change will also be improved by integrating process-based models with different types of information. Chapter 3 developed an approach to do so, by combining a process-based population model with species traits, biogeography and land-use data to assess the exposure of species to the road network at the global level. To gain a better understanding of the impacts of roads across species and regions, it may desirable to consider other factors that can influence how roads affect populations, and that were not accounted for in the analysis performed in chapter 3. These include the type of road, traffic intensity, the behavior of animals towards roads, population sensitivity to the effects of roads (including road mortality but also habitat loss, resource inaccessibility, and population subdivision) (Jaeger and Fahrig 2004, Jaeger et al. 2005, Grilo et al. 2009), habitat affinities, or the variation of population density within species ranges (Grilo et al. 2014). To achieve this, road-impact knowledge needs to be deepened, and the link between empirical knowledge and models needs to be strengthened, for example by using models to guide data collection, or by collecting parameters that are implementable for models.

The physiological model used in Chapter 4 of this thesis could also be refined, by considering geographic variation in reproduction dates and in body temperatures, habitat characteristics and behavioral thermoregulation, or by including other climatic data linked to demography (Kearney et al. 2009, Sinervo et al. 2010, 2011, Clusella-Trullas and Chown 2011). Other factors that shape species responses to environmental change, such as biotic interactions (Jankowski et al. 2013), and the synergistic effects between climate change and land-use change (Pereira et al. 2010), should be considered.

Individual-based models could be improved for example by linking them with trait-based modeling, and by including microevolution, which is fundamental to capture the response of organisms to changing conditions (Grimm and Berger 2016). Also, basing the description of the behavior and interactions of individuals on first principles, grounded in energetic or evolutionary theory, is also a key feature for advancing ecological modeling (Grimm and Berger 2016).

Integrating process-based models with other types of models will also improve our ability to understand and predict biodiversity responses to environmental change, and is a way of assessing and reducing uncertainty (Morin and Thuiller 2009, Buckley et al. 2010, Kearney et al. 2010, Dormann et al. 2012, Akçakaya et al. 2016, Brotons et al. 2016). Moreover, using different types of models in conjunction can inform the selection of variables and processes to be included (Buckley et al. 2010), thereby contributing to further model development and to refining ecological theory (Brotons et al. 2016).

Finally, reporting uncertainty together with model outputs, as well as model limitations and assumptions, is also crucial for model development and for communicating with decision makers (Akçakaya et al. 2016, Brotons et al. 2016). This will contribute to further develop process-based models (and models of biodiversity in general), so that they effectively contribute to increase our ability - as scientists and society - to more successfully conserve biodiversity.

5.3. References

Adolph SC, Porter WP (1993) Temperature, activity, and lizard life histories. The American Naturalist 142: 273-295.

Akçakaya HR, Pereira HM, Canziani GA, Mbow C, Mori A, Palomo MG, Soberon J, Thuiller W, Yachi S (2016) Improving the rigour and usefulness of scenarios and models through ongoing evaluation and refinement. In: Ferrier S, Ninan KN, Leadley P, Alkemade R, Acosta LA, Akçakaya HR, Brotons L, Cheung WWL, Christensen V, Harhash KA, Kabubo-Mariara J, Lundquist C, Obersteiner M, Pereira H, Peterson G, Pichs-Madruga R, Ravindranath N, Rondinini C, Wintle BA (Eds.) IPBES, 2016: Methodological assessment of scenarios and models of biodiversity and ecosystem services. Secretariat of the Intergovernmental Platform for Biodiversity and Ecosystem Services, Bonn, Germany.

Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. Global Change Biology 11: 1504-1513.

Araújo MB (2009) Climate change and spatial conservation planning. In: Moilanen A, Wilson KA, Possingham H (Eds.) Spatial conservation prioritization: quantitative methods and computational tools. Oxford University Press. Pp. 172-184.

Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. Ecology Letters 14: 484-492.

Austin MP, Smith TM, Van Niel KP, Wellington AB (2009) Physiological responses and statistical models of the environmental niche: a comparative study of two co-occurring *Eucalyptus* species. Journal of Ecology 97: 496-507.

Beaumont LJ, Pitman AJ, Poulsen M, Hugues L (2007) Where will species go? Incorporating new advances in climate modelling into projections of species distributions. Global Change Biology 13: 1368-1385.

Borda-de-Água L, Navarro L, Gavinhos C, Pereira HM (2011) Spatio-temporal impacts of roads on the persistence of populations: analytic and numerical approaches. Landscape Ecology 26: 253-265.

Brotons L, Christensen V, Ravindranath NH, Cao M, Chun JH, Maury O, Peri PL, Proença V, Salihoglu B (2016) Modelling impacts of drivers on biodiversity and ecosystems. In: Ferrier S, Ninan KN, Leadley P, Alkemade R, Acosta LA, Akçakaya HR, Brotons L, Cheung WWL, Christensen V, Harhash KA, Kabubo-Mariara J, Lundquist C, Obersteiner M, Pereira H, Peterson G, Pichs-Madruga R, Ravindranath N, Rondinini C, Wintle BA (Eds.) IPBES, 2016: Methodological assessment of scenarios and models of biodiversity and ecosystem services. Secretariat of the Intergovernmental Platform for Biodiversity and Ecosystem Services, Bonn, Germany.

Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? Ecology Letters 13: 1041-1054.

Carvalho SB, Brito JC, Crespo EJ, Possingham HP (2010) From climate change predictions to actions - conserving vulnerable animal groups in hotspots at a regional scale. Global Change Biology 16: 3257-3270.

Casagrandi R, Gatto M (1999) A mesoscale approach to extinction risk in fragmented habitats. Nature 400: 560-562.

Clusella-Trullas S, Chown SL (2011) Comment on "Erosion of lizard diversity by climate change and altered thermal niches". Science 332: 537.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. Science 345: 401-406.

Dormann CF, Schymanski SJ, Cabral J, Chuine I, Graham C, Hartig F, Kearney M, Morin X, Römermann C, Schröder B, Singer A (2012) Correlation and process in species distribution models: bridging a dichotomy. Journal of Biogeography 39: 2119-2131.

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1: 330-342.

Gibbs JP (1998) Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13: 263-268.

Grilo C, Bissonette JA, Santos-Reis M (2009) Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. Biological Conservation 142: 301-313.

Grilo C, Reto D, Filipe J, Ascensão F, Revilla E (2014) Understanding the mechanisms behind road effects: linking occurrence with road mortality in owls. Animal Conservation 17: 555-564.

Grimm V, Berger U (2016) Structural realism, emergence, and predictions in next-generation ecological modelling: Synthesis from a special issue. Ecological Modelling 326: 177-187.

Hanski I (1998) Metapopulation dynamics. Nature 396: 41-49.

Huey RB, Losos JB, Moritz C (2010) Are lizards toast? Science 328: 832-833.

IPCC 2007. Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Switzerland.

Jaeger JAG, Fahrig L (2004) Effects of road fencing on population persistence. Conservation Biology 18: 1651-1657.

Jaeger JAG, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, Tluk von Toschanowitz K (2005) Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185: 329-348.

Jankowski JE, Londoño GA, Robinson SK, Chappell MA (2013) Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. Ecography 36: 1-12.

Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. Proceedings of the National Academy of Sciences USA 106: 3835-3840.

Kearney M, Wintle BA, Porter WP (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters 3: 203-213.

Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142: 911-927.

Laurance WF, Clements GR, Sloan S, O'Connell CS, Mueller ND, Goosem M, Venter O, Edwards DP, Phalan B, Balmford A, Van Der Ree R, Arrea IB (2014) A global strategy for road building. Nature 513: 229-232.

Lee TM, Jetz W (2010) Unravelling the structure of species extinction risk for predictive conservation science. Proceedings of the Royal Society of London Series B 278: 1329-1338.

Morin X, Thuiller W (2009) Comparing niche-and process based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90: 1301-1313.

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for Global Biodiversity in the 21st Century. Science 330: 1496-1501.

Pereira HM, Borda-de-Água L (2013) Modelling biodiversity dynamics in countryside and native habitats. In: Levin SA (Ed.) Encyclopedia of Biodiversity. Elsevier, New York. Pp. 321-328.

Pulliam HR (1988) Sources, sinks, and population regulation. American Naturalist 132: 652-661.

Rytwinski T, Fahrig L (2012) Do species life history traits explain population responses to roads? A meta-analysis. Biological Conservation 147: 87-98.

Rytwinski T, Fahrig L (2013) Why are some animal populations unaffected or positively affected by roads? Oecologia 173: 1143-1156.

Sinervo B, Mendez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro RN, Gadsden H, Avila L, Morando M, De La Riva I, Sepulveda P, Rocha C, Ibargüengoytía N, Puntriano C, Massot M, Lepetz V, Oksanen T, Chapple D, Bauer A, Branch W, Clobert J, Sites J (2010) Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894-899.

Sinervo B, Miles DB, Martinez-Mendez N, Lara-Resendiz R, Mendez-de-la-Cruz F (2011) Response to comment on "Erosion of lizard diversity by climate change and altered thermal niches". Science 332: 537.

Skellam JG (1951) Random dispersal in theoretical populations. Bulletin of Mathematical Biology 53: 135-165.

Thuiller W (2003) BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biology 9: 1353-1362.

Thuiller W (2007) Biodiversity: climate change and the ecologist. Nature 448: 550-552.

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD - a platform for ensemble forecasting of species distributions. Ecography 32: 369-373.

Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO Jr, Lovejoy TE (2007) Dispersal of Amazonian birds in continuous and fragmented forest. Ecology Letters 10: 219-229.

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"Enquanto houver estrada pr'andar, a gente vai continuar"

"While there is a road to walk, we will not stop"

Jorge Palma

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Appendix

Supporting Information for Chapter 3. Vulnerability to land-use change

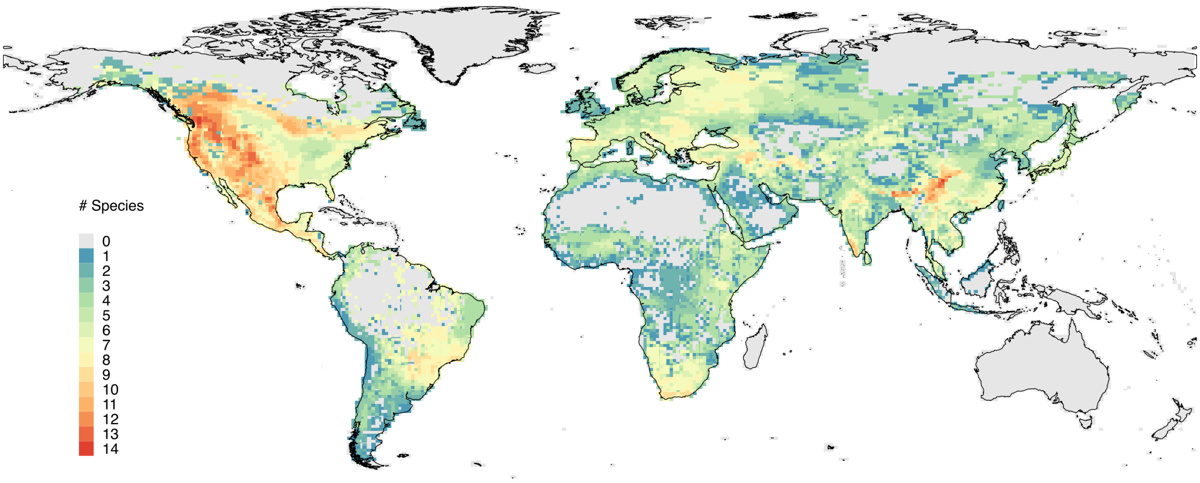

Figure S1. Number of species expected to be more exposed to the impact of roads per 100x100km grid cell. The species mapped are within the 25th percentile of D_{max}/D_{obs} or of P[$A_{obs} > A_{min}$]. Colours show the total number of species per grid cell for which D_{obs} is higher than D_{max}, or A_{obs} is smaller than A_{min}.

Table S1. Species analysed and life history data (see data sources in Supporting references). We indicate for each species: scientific name, common name, family, body mass (g), litter size, litter interval (yr), age at first breeding (yr), mortality rate (yr^{-1}), and population density ($\#/km^2$). To calculate the model parameters (Table S2), missing data were estimated using allometric relationships (Table S4) or mean values from species from the same Genus or Family. Family names are truncated to the first 4 letters and are: Ailuridae, Canidae, Eupleridae, Felidae, Herpestidae, Hyaenidae, Mephitidae, Mustelidae, Nandiniidae, Procyonidae, Ursidae, and Viverridae.

Species name	**Common name**	**Fam.**	**Mass**	**Litter size**	**Litter interv.**	**Breed. Age**	**Morta-lity rate**	**Pop. Density**
Acinonyx jubatus	Cheetah	Feli.	50578	3.28	1.50	3.33		0.01
Ailuropoda melanoleuca	Giant Panda	Ursi.	118000	1.62	1.75			0.18
Ailurus fulgens	Red Panda	Ailu.	5170	1.70	1.00	2.08		
Arctictis binturong	Binturong	Vive.	13000	2.50	0.87			
Arctogalidia trivirgata	Small-toothed Palm Civet	Vive.	2324	2.79	0.50			
Arctonyx collaris	Hog Badger	Must.	8167	3.00				
Atelocynus microtis	Short-eared Dog	Cani.	8363					
Atilax paludinosus	Marsh Mongoose	Herp.	3600	2.00	0.50			
Bassaricyon alleni	Allen's Olingo	Proc.						
Bassaricyon beddardi	Beddard's Olingo	Proc.	1235					
Bassaricyon gabbii	Olingo	Proc.	1250	1.00				6.02
Bassaricyon lasius	Harris's Olingo	Proc.	1200					
Bassaricyon pauli	Chiriqui Olingo	Proc.	1200					
Bassariscus astutus	Ringtail	Proc.	1010	3.00	1.00	1.00		3.58
Bassariscus sumichrasti	Cacomistle	Proc.	906	2.00				17.89
Bdeogale crassicauda	Bushy-tailed Mongoose	Herp.	1722	0.96				
Bdeogale jacksoni	Jackson's Mongoose	Herp.	2500					
Bdeogale nigripes	Black-footed Mongoose	Herp.	2623	1.00				
Bdeogale omnivora	Sokoke Bushy-tailed Mongoose	Herp.						
Canis adustus	Side-striped Jackal	Cani.	10392	4.50				0.74
Canis aureus	Golden Jackal	Cani.	9659	3.74	1.00			0.22
Canis latrans	Coyote	Cani.	11989	5.72	1.00	1.00		0.25
Canis lupus	Gray Wolf	Cani.	31757	4.98	1.00	1.50	0.20	0.01
Canis mesomelas	Black-backed Jackal	Cani.	8247	3.89	0.75			0.74
Canis rufus	Red Wolf	Cani.						
Canis simensis	Ethiopian Wolf	Cani.	14362		1.00			1.20
Caracal aurata	African Golden Cat	Feli.	11277	2.25				
Caracal caracal	Caracal	Feli.	11964	2.30	1.00	1.25		
Catopuma badia	Borneo Bay Cat	Feli.	3430					
Cerdocyon thous	Crab-eating Fox	Cani.	5742	3.09	0.67			3.54
Chrotogale owstoni	Owston's Civet	Vive.	3268					
Chrysocyon brachyurus	Maned Wolf	Cani.	23325	2.00				
Civettictis civetta	African Civet	Vive.	12076	2.31	0.58	1.08		
Conepatus chinga	Molina's Hog-nosed Skunk	Meph.						
Conepatus humboldtii	Humboldt's Hog-nosed Skunk	Meph.	1098	3.49				
Conepatus leuconotus	American Hog-nosed Skunk	Meph.	3294	3.60	0.50			
Conepatus semistriatus	Striped Hog-nosed Skunk	Meph.	1997	3.49				9.52
Crocuta crocuta	Spotted Hyaena	Hyae.	63370	1.91	1.21			0.12
Crossarchus alexandri	Alexander's Cusimanse	Herp.	1503	4.00				
Crossarchus ansorgei	Ansorge's Cusimanse	Herp.	700					
Crossarchus obscurus	Common Cusimanse	Herp.	1395	4.29	0.33			
Crossarchus platycephalus	Cameroon Cusimanse	Herp.						
Cryptoprocta ferox	Fossa	Eupl.	9500	2.98				0.88
Cuon alpinus	Dhole	Cani.	15800	4.30	1.00			0.55
Cynictis penicillata	Yellow Mongoose	Herp.	694	2.15				
Cynogale bennettii	Otter-civet	Vive.	4247	2.30				
Diplogale hosei	Hose's Civet	Vive.	5452					
Dologale dybowskii	Pousargues' Mongoose	Herp.	362	4.00				
Eira barbara	Tayra	Must.	4135	2.14				1.77

Eupleres goudotii	Falanouc	Eupl.	2763	1.00				
Felis chaus	Jungle Cat	Feli.	7158	2.94	0.36			
Felis margarita	Sand Cat	Feli.	2823	4.12	0.54			
Felis nigripes	Black-footed Cat	Feli.	1363	1.78	0.62			
Felis silvestris	Wild Cat	Feli.	4573	3.59	0.41	1.00		0.36
Fossa fossana	Malagasy Civet	Eupl.	1854	1.00	1.00			3.41
Galictis cuja	Lesser Grison	Must.	1000					
Galictis vittata	Greater Grison	Must.						
Galidia elegans	Malagasy Ring-tailed Mongoose	Eupl.	810	1.00				15.85
Galidictis fasciata	Broad-striped Mongoose	Eupl.	550	1.00				
Galidictis grandidieri	Giant-striped Mongoose	Eupl.	1400	1.00				
Genetta abyssinica	Ethiopian Genet	Vive.	1405					
Genetta angolensis	Miombo Genet	Vive.	1860					
Genetta bourloni	Bourlon's Genet	Vive.						
Genetta cristata	Crested Genet	Vive.	1863	2.50				
Genetta genetta	Common Genet	Vive.	1756	2.29	0.50			1.88
Genetta johnstoni	Johnston's Genet	Vive.	2225					
Genetta maculata	Central Afr. Large-spotted Genet	Vive.	1950	2.12				
Genetta pardina	West Afr. Large-spotted Genet	Vive.						
Genetta piscivora	Aquatic Genet	Vive.	1648	0.96				
Genetta poensis	King Genet	Vive.						
Genetta servalina	Servaline Genet	Vive.	1176	1.50				
Genetta thierryi	Hausa Genet	Vive.	1400					
Genetta tigrina	South Afr. Large-spotted Genet	Vive.	2067	2.76	0.83			
Genetta victoriae	Giant Genet	Vive.	2744					
Gulo gulo	Wolverine	Must.	12792	2.84	2.25			0.01
Helarctos malayanus	Sun Bear	Ursi.	57076	1.10				
Helogale hirtula	Somali Dwarf Mongoose	Herp.	485					
Helogale parvula	Common Dwarf Mongoose	Herp.	282	3.49	0.39			
Hemigalus derbyanus	Banded Civet	Vive.	1263	1.73				
Herpailurus yagouaroundi	Jaguarundi	Feli.	6875	2.50	0.50			0.58
Herpestes brachyurus	Short-tailed Mongoose	Herp.	1396	3.49				
Herpestes edwardsi	Indian Grey Mongoose	Herp.	1305	2.00	0.30			
Herpestes flavescens	Black Slender Mongoose	Herp.	750					
Herpestes fuscus	Indian Brown Mongoose	Herp.						
Herpestes ichneumon	Eyptian Mongoose	Herp.	2980	3.00	1.00			
Herpestes javanicus	Small Asian Mongoose	Herp.	750	2.21	0.42			39.59
Herpestes naso	Long-nosed Mongoose	Herp.	3002					
Herpestes ochraceus	Somali Slender Mongoose	Herp.						
Herpestes pulverulentus	Cape Grey Mongoose	Herp.	791	2.25				10.00
Herpestes sanguineus	Slender Mongoose	Herp.	544	2.50	0.50			1.32
Herpestes semitorquatus	Collared Mongoose	Herp.						
Herpestes smithii	Ruddy Mongoose	Herp.	1703	2.50				
Herpestes urva	Crab-eating Mongoose	Herp.	2384	3.00				
Herpestes vitticollis	Stripe-necked Mongoose	Herp.	2380	2.73				
Hyaena hyaena	Striped Hyaena	Hyae.	35071	2.44	0.65			
Ichneumia albicauda	White-tailed Mongoose	Herp.	3628	2.35				3.70
Ictonyx libyca	Libyan Striped Weasel	Must.	225	2.00				
Ictonyx striatus	Zorilla	Must.	811	2.30	1.00	0.83		
Leopardus colocolo	Pampas Cat	Feli.						
Leopardus geoffroyi	Geoffroy's Cat	Feli.						
Leopardus guigna	Guiña	Feli.						
Leopardus jacobita	Andean Cat	Feli.	8134					
Leopardus pardalis	Ocelot	Feli.	11880	1.66	0.99			0.42
Leopardus tigrinus	Oncilla	Feli.						
Leopardus wiedii	Margay	Feli.	3271	1.50				

Leptailurus serval	Serval	Feli.	12000	2.35	0.50	2.33		
Liberiictis kuhni	Liberian Mongoose	Herp.	1825					
Lycaon pictus	African Wild Dog	Cani.	22000	8.10	0.97	2.54		0.01
Lyncodon patagonicus	Patagonian Weasel	Must.	225					
Lynx canadensis	Canada Lynx	Feli.	9683	2.73	1.00			0.05
Lynx lynx	Eurasian Lynx	Feli.	19300	2.30	1.00			0.02
Lynx pardinus	Iberian Lynx	Feli.	11050	2.50				0.32
Lynx rufus	Bobcat	Feli.	6374	2.76	1.00	1.50	0.44	0.10
Macrogalidia musschenbroekii	Brown Palm Civet	Vive.	5149					
Martes americana	American Marten	Must.	874	2.60		1.00		0.67
Martes flavigula	Yellow-throated Marten	Must.	2505	3.53	0.50			
Martes foina	Stone Marten	Must.	1675	3.78	1.00	1.00		
Martes gwatkinsii	Nilgiri Marten	Must.	2038					
Martes martes	European Pine Marten	Must.	1300	3.49		1.00		0.44
Martes melampus	Japanese Marten	Must.	1000					
Martes pennanti	Fisher	Must.	3750	3.02	1.00	2.00		0.17
Martes zibellina	Sable	Must.	1174	3.13			0.88	0.07
Meles anakuma	Japanese Badger	Must.						
Meles leucurus	Asian Badger	Must.						
Meles meles	Eurasian Badger	Must.	11884	3.11	1.00			2.52
Mellivora capensis	Honey Badger	Must.	9000	2.35	0.50			
Melogale everetti	Bornean Ferret Badger	Must.		2.00				
Melogale moschata	Small-toothed Ferret-badger	Must.	939	2.00				
Melogale orientalis	Javan Ferret Badger	Must.						
Melogale personata	Large-toothed Ferret Badger	Must.	1845	2.50				
Melursus ursinus	Sloth Bear	Ursi.	100000	1.54	3.00			0.13
Mephitis macroura	Hooded Skunk	Meph.	1098	4.68			0.17	
Mephitis mephitis	Striped Skunk	Meph.	2400	5.70	1.00			8.15
Mungos gambianus	Gambian Mongoose	Herp.	1645					
Mungos mungo	Banded Mongoose	Herp.	1260	2.68		1.00		16.98
Mungotictis decemlineata	Malagasy Narrow-str. Mongoose	Eupl.	657	0.99				7.33
Mustela africana	Amazon Weasel	Must.	537					
Mustela altaica	Altai Weasel	Must.	180	5.44				
Mustela erminea	Ermine	Must.	285	6.74			1.46	6.25
Mustela eversmanii	Steppe Polecat	Must.	1684	7.82	1.00	1.00		
Mustela felipei	Colombian Weasel	Must.	211					
Mustela frenata	Long-tailed Weasel	Must.	190	6.50				0.76
Mustela itatsi	Japanese Weasel	Must.						
Mustela kathiah	Yellow-bellied Weasel	Must.	264					
Mustela lutreola	European Mink	Must.	566	4.50			0.54	0.07
Mustela lutreolina	Indonesian Mountain Weasel	Must.	466					
Mustela nigripes	Black-footed Ferret	Must.	907	3.36				2.00
Mustela nivalis	Least Weasel	Must.	78	5.07			1.14	12.89
Mustela nudipes	Malay Weasel	Must.	569	4.00				
Mustela putorius	European Polecat	Must.	976	8.48	0.69			0.83
Mustela sibirica	Siberian Weasel	Must.	531	6.48				
Mustela strigidorsa	Stripe-backed Weasel	Must.	1500					
Mustela subpalmata	Egyptian Weasel	Must.						
Mydaus javanensis	Sunda Stink-badger	Meph.	2500					
Mydaus marchei	Palawan Stink-badger	Meph.	2500					
Nandinia binotata	African Palm Civet	Nand.	2167	1.84	0.50			4.99
Nasua narica	White-nosed Coati	Proc.	4578	4.00	1.00			6.07
Nasua nasua	South American Coati	Proc.	3776	3.69	1.00			15.42
Nasuella olivacea	Mountain Coati	Proc.	1340					
Neofelis diardi	Sunda Clouded Leopard	Feli.						
Neofelis nebulosa	Clouded Leopard	Feli.	14945	2.25			0.07	
Neovison vison	American Mink	Must.						
Nyctereutes	Racoon Dog	Cani.	4215	6.36	1.00	2.00		12.02

procyonoides								
Otocolobus manul	Pallas's Cat	Feli.	3050	4.83				
Otocyon megalotis	Bat-eared Fox	Cani.	4098	4.00	0.50			1.18
Paguma larvata	Masked Palm Civet	Vive.	4300	2.16	0.50			
Panthera leo	Lion	Feli.	158624	2.75	2.00	2.87	0.08	0.11
Panthera onca	Jaguar	Feli.	83943	1.96	1.00			0.05
Panthera pardus	Leopard	Feli.	52400	2.14	1.31	3.14	0.08	0.07
Panthera tigris	Tiger	Feli.	161915	2.60	2.25	3.33		0.03
Panthera uncia	Snow Leopard	Feli.	32500	2.12	1.00			0.07
Paracynictis selousi	Selou's Mongoose	Herp.	1670	2.00				
Paradoxurus hermaphroditus	Common Palm Civet	Vive.	3200	3.29	0.50			
Paradoxurus jerdoni	Brown Palm Civet	Vive.	3530	3.00				
Paradoxurus zeylonensis	Golden Palm Civet	Vive.	2821	2.50				
Parahyaena brunnea	Brown Hyaena	Hyae.	42978	2.30	1.46	3.00	0.08	0.01
Pardofelis marmorata	Marbled Cat	Feli.	2827	2.00				
Pardofelis temminckii	Asiatic Golden Cat	Feli.	7726	1.50				
Poecilogale albinucha	African Striped Weasel	Must.	308	2.23	0.67			
Poiana leightoni	Leighton's Linsang	Vive.						
Poiana richardsonii	African Linsang	Vive.	570	2.23				1.00
Potos flavus	Kinkajou	Proc.	2442	1.11	1.00			34.21
Prionailurus bengalensis	Leopard Cat	Feli.	2781	2.50	0.45			
Prionailurus planiceps	Flat-headed Cat	Feli.	3534					
Prionailurus rubiginosus	Rusty-spotted Cat	Feli.	1419	2.23				
Prionailurus viverrinus	Fishing Cat	Feli.	8826	2.00				
Prionodon linsang	Banded Linsang	Vive.	685	2.30	0.50			
Prionodon pardicolor	Spotted Linsang	Vive.	1143	2.00	0.50			
Procyon cancrivorus	Crab-eating Raccoon	Proc.	6932	2.62				5.74
Procyon lotor	Northern Raccoon	Proc.	6374	3.06	1.00		0.33	3.29
Procyon pygmaeus	Pygmy Raccoon	Proc.	2958					
Proteles cristata	Aardwolf	Hyae.	8139	2.64				0.81
Pseudalopex culpaeus	Culpeo	Cani.	8616	4.88	1.00			1.01
Pseudalopex fulvipes	Darwin's Fox	Cani.						
Pseudalopex griseus	South American Grey Fox	Cani.						
Pseudalopex gymnocercus	Pampas Fox	Cani.	4543	3.09	1.00			
Pseudalopex sechurae	Sechura Fox	Cani.	4234					
Pseudalopex vetulus	Hoary Fox	Cani.	4233	3.00	1.00			
Puma concolor	Puma	Feli.	53954	2.76	1.58	1.71	0.06	0.02
Rhynchogale melleri	Meller's Mongoose	Herp.	2240	2.00				
Salanoia concolor	Brown-tailed Mongoose	Eupl.	711					
Speothos venaticus	Bush Dog	Cani.	6325	3.80	0.68			
Spilogale angustifrons	Southern Spotted Skunk	Meph.						
Spilogale gracilis	Western Spotted Skunk	Meph.						
Spilogale putorius	Eastern Spotted Skunk	Meph.	566	5.07	0.67			4.70
Spilogale pygmaea	Pygmy Spotted Skunk	Meph.	365	4.00				
Suricata suricatta	Meerkat	Herp.	730	3.86		1.00		
Taxidea taxus	American Badger	Must.	7842	2.76	1.00		0.68	1.94
Tremarctos ornatus	Spectacled Bear	Ursi.	123177	1.44				
Urocyon cinereoargenteus	Grey Fox	Cani.	3834	3.71	1.00		0.22	2.41
Urocyon littoralis	Island Fox	Cani.	1923	2.17	1.00			7.00
Ursus americanus	American Black Bear	Ursi.	110500	2.39	2.25	4.92		0.72
Ursus arctos	Brown Bear	Ursi.	196288	2.24	2.50	4.00	0.20	0.02
Ursus thibetanus	Asiatic Black Bear	Ursi.	99714	1.50	1.00	3.00		
Viverra civettina	Malabar Civet	Vive.	12061					
Viverra megaspila	Large-spotted Civet	Vive.						
Viverra tangalunga	Malay Civet	Vive.	7350	1.92				

Viverra zibetha	Large Indian Civet	Vive.	9149	2.89	0.50			
Viverricula indica	Small Indian Civet	Vive.	2919	3.74				
Vormela peregusna	European Marbled Polecat	Must.	594	5.07				
Vulpes bengalensis	Bengal Fox	Cani.	2514	3.49	1.00			
Vulpes cana	Blanford's Fox	Cani.	989	2.00				1.25
Vulpes chama	Cape Fox	Cani.	2920	2.50				
Vulpes corsac	Corsac Fox	Cani.	2615	5.62	1.00			
Vulpes ferrilata	Tibetan Fox	Cani.	5544	3.49				
Vulpes lagopus	Arctic Fox	Cani.	3584	7.65	1.00			0.10
Vulpes macrotis	Kit Fox	Cani.	4500	4.50				0.19
Vulpes pallida	Pale Fox	Cani.	2800	4.00				6.11
Vulpes rueppellii	Rüppel's Fox	Cani.	3250	2.12				
Vulpes velox	Swift Fox	Cani.	2088	4.25	1.00			0.41
Vulpes vulpes	Red Fox	Cani.	4820	4.59	1.00		0.56	1.10
Vulpes zerda	Fennec Fox	Cani.	1317	2.36				

Table S2. Parameters for the species analysed. We indicate for each species: scientific name, estimated population growth in favourable habitats (r_1; #/yr), estimated instantaneous mortality rate on roads (r_0; #/yr), dispersal variance (σ^2; km^2/yr), minimum patch size (A_{min}; km^2), maximum road density (D_{max}; km/km^2), proportion of patches with area bigger than the minimum patch size (P[A_{obs}>A_{min}]), ratio of maximum to observed road density (D_{max}/D_{obs}). We indicate r_0 values estimated as (-natural mortality rate x 10^3) (see Methods and Table S1). We indicate the species within the lower 25th percentile of D_{max}/D_{obs} or of P[A_{obs}>A_{min}] (P_{25}), and whether the species are identified by IUCN as threatened by roads.

Species name	r_1	r_0	σ^2	A_{min}	D_{max}	**P[A_{obs}>A_{min}]**	D_{max}/D_{obs}	P_{25}	**Threat roads IUCN**
Acinonyx jubatus	0.21	-184.49	573.09	27322.61	0.11	0.011	2.51		+
Ailuropoda melanoleuca	0.11	-138.96	17.36	1496.91	0.08	0.146	0.12	+	+
Ailurus fulgens	0.03	-395.64	19.91	6532.70	0.01	0.003	0.13	+	+
Arctictis binturong	0.31	-290.63	156.19	4996.13	0.11	0.004	1.08		
Arctogalidia trivirgata	0.81	-516.98	63.59	773.03	0.16	0.015	1.99		
Arctonyx collaris	0.35	-339.53	122.54	3502.59	0.10	0.003	0.81	+	
Atelocynus microtis	0.46	-336.84	124.07	2660.03	0.14	0.010	17.25		
Atilax paludinosus	0.36	-446.55	27.19	747.08	0.08	0.017	1.29		
Bassaricyon alleni	0.11	-411.09	45.46	3937.29	0.03	0.006	1.09		
Bassaricyon beddardi	0.14	-387.11	45.72	3296.69	0.04	0.050	5.08		
Bassaricyon gabbii	0.16	-361.38	46.01	2813.58	0.04	0.004	0.72		
Bassaricyon lasius	0.18	-348.85	45.04	2486.97	0.05	0.004	11.82		
Bassaricyon pauli	0.18	-348.85	45.04	2486.97	0.05	0.020	8.41		
Bassariscus astutus	0.23	-683.08	17.79	758.48	0.03	0.007	0.21	+	+
Bassariscus sumichrasti	0.18	-708.45	38.90	2108.34	0.03	0.004	0.19	+	
Bdeogale crassicauda	0.12	-357.15	54.39	4631.46	0.03	0.009	0.58		
Bdeogale jacksoni	0.09	-350.45	66.07	7094.08	0.03	0.009	0.15	+	
Bdeogale nigripes	0.09	-349.65	67.74	7073.79	0.03	0.016	0.71		
Bdeogale omnivora	0.10	-352.01	62.99	6262.09	0.03	0.017	0.28	+	
Canis adustus	0.48	-313.23	11.13	227.17	0.15	0.079	2.58		
Canis aureus	0.41	-321.00	33.32	796.51	0.13	0.007	1.56		
Canis latrans	1.05	-298.61	198.40	1863.65	0.35	0.001	0.11	+	
Canis lupus	0.74	-200.00	1125.13	15041.05	0.37	0.0003	4.66	+	
Canis mesomelas	0.51	-338.42	142.08	2759.73	0.15	0.006	2.17		
Canis rufus	0.46	-280.85	164.76	3509.20	0.16	0.001	1.44	+	+
Canis simensis	0.48	-281.11	41.55	859.20	0.17	0.487	0.69		+
Caracal aurata	0.24	-304.79	145.02	6032.16	0.08	0.007	1.15		+
Caracal caracal	0.38	-298.82	3090.97	80468.26	0.13	0.0003	1.92	+	
Catopuma badia	0.15	-453.87	77.92	4970.05	0.03	0.500	5.24		
Cerdocyon thous	0.45	-382.00	18.95	411.41	0.12	0.015	1.50		
Chrotogale owstoni	0.28	-461.26	75.98	2697.85	0.06	0.024	0.92		
Chrysocyon brachyurus	0.19	-239.01	179.66	9303.03	0.08	0.001	1.07	+	+
Civettictis civetta	0.64	-297.89	150.29	2329.76	0.21	0.015	3.90		
Conepatus chinga	0.48	-532.29	60.76	1242.34	0.09	0.010	0.79		
Conepatus humboldtii	0.51	-664.41	2.34	45.20	0.08	0.140	0.96		
Conepatus leuconotus	0.63	-460.03	76.29	1200.81	0.14	0.003	2.03	+	+
Conepatus semistriatus	0.48	-543.83	5.17	106.13	0.09	0.029	1.03		
Crocuta crocuta	0.19	-171.09	132.04	6891.83	0.11	0.008	2.00		
Crossarchus alexandri	0.58	-598.05	50.67	868.58	0.10	0.043	1.71		
Crossarchus ansorgei	0.65	-772.30	34.00	513.86	0.08	0.061	1.80		
Crossarchus obscurus	0.93	-613.19	48.73	517.77	0.15	0.016	2.11		
Crossarchus platycephalus	0.61	-644.98	45.03	723.74	0.10	0.037	2.16		
Cryptoprocta ferox	0.34	-322.78	8.52	249.90	0.10	0.053	6.91		
Cuon alpinus	0.45	-272.27	322.33	7018.65	0.17	0.003	1.86		
Cynictis penicillata	0.21	-774.37	51.50	2382.90	0.03	0.006	0.34	+	
Cynogale bennettii	0.26	-422.56	87.11	3282.59	0.06	0.007	0.82		
Diplogale hosei	0.27	-388.67	99.24	3630.84	0.07	0.333	0.87		+
Dologale dybowskii	0.67	-962.98	24.10	357.36	0.07	0.058	1.21		
Eira barbara	0.23	-426.34	171.04	7225.37	0.05	0.003	1.02		

Eupleres goudotii	0.05	-387.87	69.61	13602.07	0.01	0.128	1.13		
Felis chaus	0.63	-354.84	114.40	1783.97	0.18	0.004	1.13		
Felis margarita	0.67	-484.38	70.40	1037.90	0.14	0.015	3.87		
Felis nigripes	0.16	-618.02	48.13	3017.53	0.03	0.010	0.34	+	
Felis silvestris	1.00	-412.21	18.71	184.71	0.24	0.003	2.69	+	+
Fossa fossana	0.18	-205.58	14.72	810.37	0.09	0.250	10.72		
Galictis cuja	0.58	-685.44	40.95	694.49	0.08	0.003	0.69	+	+
Galictis vittata	0.58	-685.44	40.95	694.49	0.08	0.014	2.95		
Galidia elegans	0.18	-397.35	4.40	244.74	0.04	0.300	4.95		
Galidictis fasciata	0.23	-398.37	29.98	1301.14	0.06	0.160	6.40		
Galidictis grandidieri	0.11	-396.12	48.82	4246.55	0.03	1.000	1.21		
Genetta abyssinica	0.20	-611.67	48.92	2407.46	0.03	0.020	0.42	+	
Genetta angolensis	0.21	-556.98	56.61	2710.06	0.04	0.027	0.67		
Genetta bourloni	0.21	-560.32	56.09	2688.37	0.04	0.017	0.48		
Genetta cristata	0.31	-556.62	56.67	1810.87	0.06	0.042	1.48		
Genetta genetta	0.39	-567.75	217.78	5506.10	0.07	0.001	0.66	+	+
Genetta johnstoni	0.21	-524.55	62.17	2943.80	0.04	0.006	0.50		
Genetta maculata	0.23	-548.21	58.03	2501.74	0.04	0.013	0.77		
Genetta pardina	0.21	-560.32	56.09	2688.37	0.04	0.017	0.63		
Genetta piscivora	0.12	-357.99	53.15	4385.71	0.03	0.025	1.02		
Genetta poensis	0.21	-560.32	56.09	2688.37	0.04	0.098	0.61		
Genetta servalina	0.05	-649.29	44.57	9143.03	0.01	0.005	0.12	+	
Genetta thierryi	0.20	-612.47	48.82	2403.58	0.03	0.028	0.60		
Genetta tigrina	0.30	-537.67	0.76	24.58	0.06	0.020	0.27	+	+
Genetta victoriae	0.21	-489.04	69.35	3256.61	0.04	0.017	0.93		
Gulo gulo	0.15	-292.20	3529.79	239641.68	0.05	0.000	1.92	+	+
Helarctos malayanus	0.06	-177.18	338.05	51964.09	0.04	0.004	2.22		
Helogale hirtula	0.54	-873.38	28.06	509.72	0.06	0.032	1.02		
Helogale parvula	0.68	-1047.02	7.74	111.87	0.07	0.065	1.21		
Hemigalus derbyanus	0.12	-633.99	46.26	3800.68	0.02	0.003	0.34	+	
Herpailurus yagouaroundi	0.46	-359.66	662.59	14242.52	0.13	0.0003	2.26	+	+
Herpestes brachyurus	0.50	-613.04	48.75	964.41	0.08	0.006	1.68		
Herpestes edwardsi	0.52	-627.09	47.05	885.39	0.08	0.007	0.46		
Herpestes flavescens	0.34	-754.68	35.25	1022.25	0.05	0.237	0.96		
Herpestes fuscus	0.34	-581.50	52.93	1553.26	0.06	0.003	0.19	+	
Herpestes ichneumon	0.30	-475.71	36.49	1186.79	0.06	0.007	0.94		
Herpestes javanicus	0.39	-754.68	5.84	147.88	0.05	0.029	0.42	+	
Herpestes naso	0.42	-474.53	6.68	156.90	0.09	0.090	1.73		
Herpestes ochraceus	0.34	-581.50	52.93	1553.26	0.06	0.044	0.83		
Herpestes pulverulentus	0.24	-741.24	99.38	4008.20	0.03	0.003	0.32	+	
Herpestes sanguineus	0.35	-840.35	19.52	553.80	0.04	0.030	0.72		
Herpestes semitorquatus	0.34	-581.50	52.93	1553.26	0.06	0.007	2.64		
Herpestes smithii	0.31	-573.68	54.06	1724.59	0.05	0.003	0.27	+	
Herpestes urva	0.39	-512.56	64.45	1613.59	0.08	0.004	0.57		+
Herpestes vitticollis	0.35	-512.86	64.39	1826.35	0.07	0.001	0.21	+	
Hyaena hyaena	0.36	-208.53	331.62	9001.12	0.17	0.003	2.77		
Ichneumia albicauda	0.27	-445.39	7.84	283.52	0.06	0.033	1.06		
Ictonyx libyca	0.09	-1128.64	18.81	2173.63	0.01	0.009	0.16	+	
Ictonyx striatus	0.10	-735.19	36.71	3516.33	0.01	0.006	0.24	+	
Leopardus colocolo	0.13	-345.36	119.33	9047.29	0.04	0.004	0.52		+
Leopardus geoffroyi	0.13	-345.36	119.33	9047.29	0.04	0.003	0.39	+	+
Leopardus guigna	0.13	-345.36	119.33	9047.29	0.04	0.003	0.17	+	
Leopardus jacobita	0.13	-339.99	122.29	9241.11	0.04	0.018	0.64		
Leopardus pardalis	0.15	-299.52	53.55	3439.50	0.05	0.003	0.92	+	+
Leopardus tigrinus	0.13	-345.36	119.33	9047.29	0.04	0.001	0.80	+	+
Leopardus wiedii	0.10	-461.12	138.58	14256.23	0.02	0.001	0.41	+	+
Leptailurus serval	0.33	-298.52	19.33	576.06	0.11	0.016	1.72		
Liberiictis kuhni	0.34	-560.45	56.07	1627.48	0.06	0.016	0.46		
Lycaon pictus	0.55	-243.73	3395.56	60975.36	0.22	0.055	7.10		+

Lyncodon patagonicus	0.66	-1128.94	18.80	282.74	0.06	0.075	0.75		
Lynx canadensis	0.30	-320.73	345.38	11374.77	0.09	0.001	1.43	+	+
Lynx lynx	0.26	-254.65	1221.87	47042.55	0.10	0.0003	1.20	+	+
Lynx pardinus	0.27	-306.87	77.65	2823.50	0.09	0.000000	0.04	+	+
Lynx rufus	0.24	-440.00	483.10	19654.85	0.06	0.0001	0.28	+	+
Macrogalidia musschenbroekii	0.27	-396.18	96.33	3511.33	0.07	0.004	1.49		+
Martes americana	0.31	-717.11	92.36	2914.42	0.04	0.004	0.89		
Martes flavigula	0.62	-504.18	66.13	1049.86	0.12	0.005	1.07		
Martes foina	0.48	-576.81	43.64	891.11	0.08	0.0002	0.05	+	
Martes gwatkinsii	0.44	-540.13	59.39	1323.76	0.08	0.0002	0.08	+	+
Martes martes	0.55	-627.85	47.50	852.99	0.09	0.001	0.18	+	
Martes melampus	0.47	-685.44	40.95	857.78	0.07	0.0001	0.02	+	
Martes pennanti	0.16	-440.50	230.82	14153.14	0.04	0.001	0.37	+	
Martes zibellina	0.21	-880.00	393.60	18599.47	0.02	0.003	0.92		
Meles anakuma	0.36	-299.49	149.05	4116.85	0.12	0.000002	0.03	+	
Meles leucurus	0.36	-299.49	149.05	4116.85	0.12	0.003	1.46		
Meles meles	0.35	-299.49	12.65	360.64	0.12	0.002	0.22	+	
Mellivora capensis	0.43	-328.67	128.92	2925.17	0.13	0.004	2.09		
Melogale everetti	0.19	-613.67	48.67	2464.22	0.03	0.182	0.30	+	+
Melogale moschata	0.18	-700.15	39.62	2132.54	0.03	0.003	0.19	+	
Melogale orientalis	0.24	-613.67	48.67	2039.82	0.04	0.008	0.25	+	
Melogale personata	0.31	-558.43	56.38	1801.17	0.06	0.003	0.47	+	
Melursus ursinus	0.04	-146.88	39.75	9638.57	0.03	0.001	0.03	+	+
Mephitis macroura	1.20	-170.00	11.00	90.81	0.70	0.023	6.72		
Mephitis mephitis	0.64	-511.43	41.75	644.31	0.12	0.002	0.60	+	
Mungos gambianus	0.35	-580.31	53.10	1514.99	0.06	0.018	1.00		
Mungos mungo	0.38	-634.45	37.06	954.86	0.06	0.016	1.08		
Mungotictis decemlineata	0.21	-387.89	33.03	1555.09	0.05	0.667	6.47		
Mustela africana	0.95	-843.92	29.61	307.83	0.11	0.011	12.56		
Mustela altaica	1.02	-1215.89	16.75	162.37	0.08	0.014	1.31		
Mustela erminea	0.76	-1460.00	5.65	73.36	0.05	0.011	0.36	+	
Mustela eversmanii	1.01	-575.75	53.76	523.38	0.18	0.010	1.74		
Mustela felipei	1.07	-1152.91	18.20	167.11	0.09	0.102	0.80		
Mustela frenata	1.21	-1194.57	8.83	72.22	0.10	0.031	0.47		
Mustela itatsi	0.94	-814.83	31.27	330.06	0.11	0.000	0.15	+	
Mustela kathiah	1.05	-1070.51	20.43	192.92	0.10	0.014	0.84		
Mustela lutreola	1.02	-540.00	3.23	31.24	0.19	0.003	0.90	+	+
Mustela lutreolina	0.97	-884.75	27.50	280.33	0.11	0.074	1.61		
Mustela nigripes	0.49	-708.16	20.68	412.88	0.07	0.667	0.35	+	
Mustela nivalis	1.48	-1140.00	2.81	18.76	0.13	0.038	0.79		
Mustela nudipes	0.64	-827.52	30.53	470.77	0.08	0.009	1.43		
Mustela putorius	1.10	-691.14	12.89	115.30	0.16	0.002	0.12	+	+
Mustela sibirica	1.04	-847.17	101.66	965.14	0.12	0.003	1.38		
Mustela strigidorsa	0.81	-598.50	50.61	614.02	0.14	0.025	1.45		
Mustela subpalmata	0.94	-814.83	31.27	330.06	0.11	0.002	0.18	+	
Mydaus javanensis	0.58	-504.49	66.07	1129.86	0.11	0.009	4.78		
Mydaus marchei	0.58	-504.49	66.07	1129.86	0.11	0.017	1.26		+
Nandinia binotata	0.30	-529.18	10.24	340.44	0.06	0.041	0.83		
Nasua narica	0.45	-412.05	11.31	250.74	0.11	0.017	1.07		
Nasua nasua	0.41	-439.51	12.22	296.47	0.09	0.003	2.17	+	
Nasuella olivacea	0.32	-621.52	47.71	1454.70	0.05	0.005	0.44	+	
Neofelis diardi	0.23	-277.39	167.98	7168.17	0.08	0.038	6.92		
Neofelis nebulosa	0.44	-70.00	42.39	953.63	0.62	0.003	6.72	+	
Neovison vison	0.53	-523.06	62.45	1163.92	0.10	0.002	0.65	+	
Nyctereutes procyonoides	0.43	-423.61	17.14	392.42	0.10	0.002	0.64	+	+
Otocolobus manul	0.62	-472.03	73.29	1161.39	0.13	0.016	2.99		
Otocyon megalotis	0.67	-427.62	17.00	249.91	0.16	0.051	2.56		
Paguma larvata	0.40	-420.79	42.65	1061.66	0.09	0.003	0.78		

Panthera leo	0.27	-80.00	155.38	5680.41	0.34	0.033	8.68		
Panthera onca	0.23	-155.73	287.99	12606.44	0.14	0.003	0.08	+	+
Panthera pardus	0.26	-80.00	52.87	1972.35	0.33	0.0002	0.12	+	+
Panthera tigris	0.17	-125.01	285.46	16538.96	0.14	0.008	1.74		
Panthera uncia	0.24	-213.91	171.03	7025.52	0.11	0.003	8.14	+	+
Paracynictis selousi	0.20	-577.42	53.52	2657.70	0.03	0.016	0.89		
Paradoxurus hermaphroditus	0.58	-464.51	67.84	1147.48	0.13	0.006	0.90		
Paradoxurus jerdoni	0.38	-449.49	79.11	2056.13	0.08	0.002	0.30	+	
Paradoxurus zeylonensis	0.30	-484.49	70.37	2289.81	0.06	0.019	0.55		
Parahyaena brunnea	0.27	-80.00	189.47	6895.38	0.34	0.004	5.16		+
Pardofelis marmorata	0.21	-484.19	70.44	3377.83	0.04	0.012	0.67		
Pardofelis temminckii	0.11	-345.88	119.05	10261.09	0.03	0.004	0.38	+	
Poecilogale albinucha	0.03	-1016.20	22.16	6527.33	0.003	0.003	4.21		
Poiana leightoni	0.23	-827.20	30.54	1317.68	0.03	0.197	0.33	+	
Poiana richardsonii	0.23	-827.20	30.54	1317.68	0.03	0.033	0.69		
Potos flavus	0.10	-305.08	3.94	383.15	0.03	0.016	0.77		
Prionailurus bengalensis	0.49	-486.83	32.04	648.83	0.10	0.008	0.80		+
Prionailurus planiceps	0.25	-449.34	79.15	3077.88	0.06	0.231	1.18		
Prionailurus rubiginosus	0.25	-609.75	49.16	1936.50	0.04	0.002	0.19	+	
Prionailurus viverrinus	0.20	-330.82	127.62	6184.92	0.06	0.013	0.63		
Prionodon linsang	0.32	-777.98	33.61	1040.58	0.04	0.006	0.72		
Prionodon pardicolor	0.29	-655.53	43.91	1502.79	0.04	0.010	0.50		
Procyon cancrivorus	0.30	-358.67	112.49	3685.43	0.08	0.003	1.60		
Procyon lotor	0.37	-330.00	53.65	1417.76	0.11	0.002	0.50	+	+
Procyon pygmaeus	0.36	-476.89	72.13	1973.69	0.08	0.0002	0.18	+	+
Proteles cristata	0.30	-339.91	18.06	596.05	0.09	0.018	1.34		
Pseudalopex culpaeus	0.52	-333.50	59.27	1125.25	0.16	0.013	2.05		
Pseudalopex fulvipes	0.45	-389.76	98.81	2188.83	0.11	0.0002	0.56	+	
Pseudalopex griseus	0.45	-389.76	98.81	2188.83	0.11	0.012	1.37		
Pseudalopex gymnocercus	0.33	-413.13	90.23	2688.72	0.08	0.006	0.84		
Pseudalopex sechurae	0.46	-422.97	86.98	1863.92	0.11	0.003	1.01		
Pseudalopex vetulus	0.32	-422.99	86.97	2711.27	0.07	0.006	1.08		
Puma concolor	0.46	-60.00	274.26	5836.85	0.77	0.0001	0.12	+	+
Rhynchogale melleri	0.20	-523.34	62.39	3023.00	0.04	0.012	0.75		
Salanoia concolor	0.07	-627.68	34.29	4540.63	0.01	0.167	24.88		
Speothos venaticus	0.53	-369.84	107.24	1982.09	0.14	0.004	3.36		
Spilogale angustifrons	0.75	-885.07	27.49	359.83	0.09	0.013	0.54		
Spilogale gracilis	0.75	-885.07	27.49	359.83	0.09	0.003	0.70	+	+
Spilogale putorius	0.74	-828.95	8.46	113.32	0.09	0.039	0.34	+	+
Spilogale pygmaea	0.67	-960.25	24.20	359.18	0.07	0.029	0.70		+
Suricata suricatta	0.53	-761.54	315.16	5853.66	0.07	0.003	1.00		
Taxidea taxus	0.04	-680.00	82.32	20653.13	0.01	0.0003	3.12	+	
Tremarctos ornatus	0.11	-136.98	505.05	47224.68	0.08	0.011	1.75		
Urocyon cinereoargenteus	0.63	-220.00	14.17	223.07	0.28	0.013	1.24		
Urocyon littoralis	0.12	-550.78	8.14	657.19	0.02	0.0003	0.27	+	
Ursus americanus	0.08	-142.05	156.22	18803.07	0.06	0.0002	0.11	+	+
Ursus arctos	0.03	-200.00	2187.55	673685.52	0.02	0.0004	0.12	+	+
Ursus thibetanus	0.18	-147.02	3.62	199.73	0.12	0.009	0.12	+	+
Viverra civettina	0.26	-298.01	150.20	5776.45	0.09	0.0003	0.16	+	
Viverra megaspila	0.26	-322.56	132.75	4988.94	0.08	0.004	0.58		
Viverra tangalunga	0.19	-351.71	115.99	5971.98	0.05	0.003	0.70		
Viverra zibetha	0.51	-326.88	107.67	2081.97	0.16	0.003	1.17	+	
Viverricula indica	0.49	-479.02	71.63	1429.62	0.10	0.004	0.64		
Vormela peregusna	0.82	-815.85	31.21	375.06	0.10	0.011	1.22		
Vulpes bengalensis	0.37	-503.52	66.27	1765.26	0.07	0.003	0.41	+	
Vulpes cana	0.19	-688.10	28.33	1510.07	0.03	0.005	0.54		
Vulpes chama	0.30	-478.96	71.64	2335.61	0.06	0.006	0.70		
Vulpes corsac	0.63	-496.94	67.64	1062.20	0.13	0.002	2.43	+	
Vulpes ferrilata	0.42	-386.51	100.11	2329.24	0.11	0.014	3.25		

Vulpes lagopus	0.79	-447.21	221.90	2788.93	0.18	0.008	26.17		
Vulpes macrotis	0.55	-414.44	118.14	2110.39	0.13	0.003	1.50	+	+
Vulpes pallida	0.53	-485.72	70.09	1301.46	0.11	0.047	2.72		+
Vulpes rueppellii	0.23	-462.10	486.72	20814.03	0.05	0.003	2.43		
Vulpes velox	0.47	-535.82	86.55	1810.26	0.09	0.003	0.61	+	+
Vulpes vulpes	0.35	-560.00	68.97	1928.45	0.06	0.003	0.40	+	
Vulpes zerda	0.28	-625.10	47.29	1668.19	0.04	0.028	5.15		+

Table S3. D_{max} and D_{max}/D_{obs} computed using $r_0 = -\mu * 10^2$, $r_0 = -\mu * 10^3$, and $r_0 = -\mu * 10^4$. Species are presented by increasing order of D_{max}/D_{obs}. Species in the 5th and 25th percentiles of D_{max}/D_{obs} are the same regardless of the method selected to estimate r_0.

Species	**D_{max}** ($r_0=-\mu*10^2$)	**D_{max}** ($r_0=-\mu*10^3$)	**D_{max}** ($r_0=-\mu*10^4$)	**D_{max}/D_{obs}** ($r_0=-\mu*10^2$)	**D_{max}/D_{obs}** ($r_0=-\mu*10^3$)	**D_{max}/D_{obs}** ($r_0=-\mu*10^4$)
Martes melampus	0.683	0.069	0.007	0.188	0.019	0.002
Meles anakuma	1.179	0.119	0.012	0.279	0.028	0.003
Melursus ursinus	0.276	0.028	0.003	0.331	0.033	0.003
Lynx pardinus	0.877	0.088	0.009	0.412	0.042	0.004
Martes foina	0.831	0.084	0.008	0.496	0.050	0.005
Martes gwatkinsii	0.813	0.082	0.008	0.776	0.078	0.008
Panthera onca	1.427	0.145	0.014	0.828	0.084	0.008
Ursus americanus	0.574	0.058	0.006	1.059	0.106	0.011
Canis latrans	3.399	0.351	0.035	1.065	0.110	0.011
Ursus thibetanus	1.203	0.122	0.012	1.164	0.118	0.012
Ursus arctos	0.160	0.016	0.002	1.182	0.118	0.012
Puma concolor	7.175	0.767	0.077	1.189	0.119	0.012
Ailuropoda melanoleuca	0.817	0.082	0.008	1.189	0.120	0.012
Mustela putorius	1.571	0.159	0.016	1.190	0.121	0.012
Genetta servalina	0.074	0.007	0.001	1.193	0.121	0.012
Panthera pardus	3.201	0.330	0.033	1.190	0.123	0.012
Ailurus fulgens	0.076	0.008	0.001	1.293	0.129	0.013
Bdeogale jacksoni	0.262	0.026	0.003	1.466	0.147	0.015
Mustela itatsi	1.135	0.115	0.011	1.477	0.149	0.015
Viverra civettina	0.854	0.086	0.009	1.575	0.159	0.016
Ictonyx libyca	0.076	0.008	0.001	1.615	0.162	0.016
Leopardus guigna	0.376	0.038	0.004	1.647	0.165	0.017
Martes martes	0.868	0.087	0.009	1.759	0.177	0.018
Procyon pygmaeus	0.751	0.076	0.008	1.769	0.178	0.018
Mustela subpalmata	1.135	0.115	0.011	1.820	0.184	0.018
Melogale moschata	0.261	0.026	0.003	1.871	0.188	0.019
Herpestes fuscus	0.575	0.058	0.006	1.873	0.188	0.019
Bassariscus sumichrasti	0.256	0.026	0.003	1.901	0.191	0.019
Prionailurus rubiginosus	0.409	0.041	0.004	1.940	0.195	0.019
Herpestes vitticollis	0.674	0.068	0.007	2.086	0.210	0.021
Bassariscus astutus	0.338	0.034	0.003	2.126	0.213	0.021
Meles meles	1.142	0.115	0.012	2.218	0.224	0.022
Ictonyx striatus	0.140	0.014	0.001	2.425	0.243	0.024
Melogale orientalis	0.382	0.038	0.004	2.521	0.253	0.025
Herpestes smithii	0.536	0.054	0.005	2.640	0.265	0.027
Genetta tigrina	0.562	0.056	0.006	2.640	0.265	0.027
Urocyon littoralis	0.221	0.022	0.002	2.678	0.268	0.027
Bdeogale omnivora	0.281	0.028	0.003	2.762	0.277	0.028
Lynx rufus	0.548	0.055	0.006	2.821	0.283	0.028
Paradoxurus jerdoni	0.838	0.084	0.008	2.991	0.301	0.030
Melogale everetti	0.317	0.032	0.003	3.019	0.303	0.030
Herpestes pulverulentus	0.329	0.033	0.003	3.211	0.322	0.032
Poiana leightoni	0.276	0.028	0.003	3.324	0.333	0.033
Hemigalus derbyanus	0.189	0.019	0.002	3.361	0.337	0.034
Cynictis penicillata	0.275	0.028	0.003	3.367	0.338	0.034
Spilogale putorius	0.881	0.089	0.009	3.369	0.340	0.034
Felis nigripes	0.254	0.025	0.003	3.412	0.342	0.034
Mustela nigripes	0.693	0.070	0.007	3.499	0.352	0.035
Mustela erminea	0.518	0.052	0.005	3.552	0.357	0.036
Martes pennanti	0.364	0.037	0.004	3.734	0.375	0.037
Pardofelis temminckii	0.330	0.033	0.003	3.814	0.383	0.038
Leopardus geoffroyi	0.376	0.038	0.004	3.928	0.394	0.039
Vulpes vulpes	0.626	0.063	0.006	3.994	0.402	0.040
Leopardus wiedii	0.208	0.021	0.002	4.121	0.413	0.041
Vulpes bengalensis	0.730	0.074	0.007	4.117	0.414	0.041

Herpestes javanicus	0.514	0.052	0.005	4.143	0.416	0.042
Genetta abyssinica	0.327	0.033	0.003	4.173	0.419	0.042
Nasuella olivacea	0.518	0.052	0.005	4.391	0.441	0.044
Herpestes edwardsi	0.829	0.084	0.008	4.527	0.456	0.046
Liberiictis kuhni	0.603	0.061	0.006	4.568	0.459	0.046
Melogale personata	0.550	0.055	0.006	4.696	0.472	0.047
Mustela frenata	1.000	0.101	0.010	4.700	0.474	0.047
Genetta bourloni	0.366	0.037	0.004	4.814	0.483	0.048
Prionodon pardicolor	0.438	0.044	0.004	4.960	0.498	0.050
Procyon lotor	1.119	0.113	0.011	4.934	0.498	0.050
Genetta johnstoni	0.396	0.040	0.004	5.021	0.504	0.050
Leopardus colocolo	0.376	0.038	0.004	5.155	0.517	0.052
Spilogale angustifrons	0.845	0.085	0.009	5.332	0.537	0.054
Vulpes cana	0.268	0.027	0.003	5.432	0.545	0.054
Paradoxurus zeylonensis	0.622	0.063	0.006	5.485	0.552	0.055
Pseudalopex fulvipes	1.130	0.114	0.011	5.591	0.565	0.057
Herpestes urva	0.763	0.077	0.008	5.655	0.569	0.057
Bdeogale crassicauda	0.323	0.032	0.003	5.824	0.584	0.058
Viverra megaspila	0.808	0.081	0.008	5.804	0.585	0.059
Mephitis mephitis	1.235	0.125	0.013	5.920	0.599	0.060
Genetta thierryi	0.326	0.033	0.003	6.014	0.603	0.060
Genetta poensis	0.366	0.037	0.004	6.081	0.610	0.061
Vulpes velox	0.873	0.088	0.009	6.057	0.611	0.061
Genetta pardina	0.366	0.037	0.004	6.289	0.631	0.063
Prionailurus viverrinus	0.612	0.062	0.006	6.312	0.635	0.064
Nyctereutes procyonoides	1.008	0.102	0.010	6.336	0.639	0.064
Viverricula indica	1.022	0.103	0.010	6.356	0.642	0.064
Leopardus jacobita	0.383	0.038	0.004	6.428	0.645	0.065
Neovison vison	1.002	0.101	0.010	6.425	0.648	0.065
Genetta genetta	0.683	0.069	0.007	6.569	0.661	0.066
Genetta angolensis	0.369	0.037	0.004	6.647	0.667	0.067
Pardofelis marmorata	0.423	0.042	0.004	6.722	0.675	0.068
Canis simensis	1.669	0.169	0.017	6.773	0.688	0.069
Galictis cuja	0.842	0.085	0.008	6.843	0.690	0.069
Poiana richardsonii	0.276	0.028	0.003	6.896	0.691	0.069
Spilogale pygmaea	0.688	0.069	0.007	6.947	0.699	0.070
Viverra tangalunga	0.542	0.054	0.005	6.995	0.703	0.070
Vulpes chama	0.628	0.063	0.006	7.009	0.705	0.071
Spilogale gracilis	0.845	0.085	0.009	6.995	0.705	0.071
Bdeogale nigripes	0.270	0.027	0.003	7.132	0.715	0.072
Bassaricyon gabbii	0.445	0.045	0.004	7.146	0.717	0.072
Herpestes sanguineus	0.412	0.041	0.004	7.163	0.719	0.072
Prionodon linsang	0.408	0.041	0.004	7.186	0.721	0.072
Rhynchogale melleri	0.388	0.039	0.004	7.501	0.753	0.075
Lyncodon patagonicus	0.578	0.058	0.006	7.506	0.755	0.075
Potos flavus	0.331	0.033	0.003	7.670	0.769	0.077
Genetta maculata	0.416	0.042	0.004	7.694	0.772	0.077
Paguma larvata	0.933	0.094	0.009	7.777	0.784	0.078
Conepatus chinga	0.899	0.091	0.009	7.831	0.790	0.079
Mustela nivalis	1.279	0.129	0.013	7.832	0.792	0.079
Leopardus tigrinus	0.376	0.038	0.004	7.935	0.796	0.080
Prionailurus bengalensis	0.991	0.100	0.010	7.912	0.798	0.080
Mustela felipei	0.924	0.093	0.009	7.922	0.799	0.080
Arctonyx collaris	1.007	0.102	0.010	8.022	0.810	0.081
Cynogale bennettii	0.616	0.062	0.006	8.182	0.823	0.082
Herpestes ochraceus	0.575	0.058	0.006	8.231	0.827	0.083
Nandinia binotata	0.558	0.056	0.006	8.246	0.829	0.083
Pseudalopex gymnocercus	0.795	0.080	0.008	8.319	0.838	0.084
Mustela kathiah	0.967	0.098	0.010	8.370	0.844	0.085

Diplogale hosei	0.689	0.069	0.007	8.660	0.871	0.087
Paracynictis selousi	0.343	0.034	0.003	8.829	0.886	0.089
Martes americana	0.434	0.044	0.004	8.892	0.893	0.089
Paradoxurus hermaphroditus	1.241	0.125	0.013	8.892	0.899	0.090
Mustela lutreola	1.855	0.189	0.019	8.897	0.905	0.091
Chrotogale owstoni	0.599	0.060	0.006	9.135	0.918	0.092
Martes zibellina	0.237	0.024	0.002	9.185	0.920	0.092
Leopardus pardalis	0.510	0.051	0.005	9.177	0.922	0.092
Genetta victoriae	0.428	0.043	0.004	9.226	0.926	0.093
Herpestes ichneumon	0.634	0.064	0.006	9.378	0.943	0.094
Conepatus humboldtii	0.763	0.077	0.008	9.538	0.960	0.096
Herpestes flavescens	0.449	0.045	0.005	9.594	0.963	0.096
Mungos gambianus	0.593	0.060	0.006	9.938	0.999	0.100
Suricata suricatta	0.693	0.070	0.007	9.962	1.002	0.100
Pseudalopex sechurae	1.077	0.109	0.011	10.039	1.014	0.101
Genetta piscivora	0.333	0.033	0.003	10.187	1.022	0.102
Eira barbara	0.545	0.055	0.005	10.182	1.023	0.102
Helogale hirtula	0.618	0.062	0.006	10.185	1.024	0.102
Conepatus semistriatus	0.876	0.088	0.009	10.171	1.025	0.103
Ichneumia albicauda	0.609	0.061	0.006	10.520	1.058	0.106
Chrysocyon brachyurus	0.791	0.080	0.008	10.592	1.067	0.107
Martes flavigula	1.218	0.123	0.012	10.574	1.069	0.107
Nasua narica	1.069	0.108	0.011	10.613	1.072	0.107
Pseudalopex vetulus	0.743	0.075	0.007	10.738	1.081	0.108
Mungos mungo	0.600	0.060	0.006	10.775	1.083	0.108
Arctictis binturong	1.051	0.106	0.011	10.746	1.085	0.109
Bassaricyon alleni	0.276	0.028	0.003	10.851	1.088	0.109
Felis chaus	1.752	0.178	0.018	11.080	1.126	0.113
Eupleres goudotii	0.130	0.013	0.001	11.305	1.132	0.113
Caracal aurata	0.773	0.078	0.008	11.398	1.148	0.115
Viverra zibetha	1.537	0.156	0.016	11.558	1.172	0.117
Prionailurus planiceps	0.562	0.056	0.006	11.763	1.182	0.118
Lynx lynx	0.997	0.101	0.010	11.864	1.197	0.120
Galidictis grandidieri	0.286	0.029	0.003	12.064	1.209	0.121
Dologale dybowskii	0.686	0.069	0.007	12.034	1.211	0.121
Helogale parvula	0.648	0.065	0.007	12.067	1.214	0.121
Vormela peregusna	0.997	0.101	0.010	12.093	1.220	0.122
Urocyon cinereoargenteus	2.770	0.284	0.028	12.113	1.242	0.125
Mydaus marchei	1.131	0.114	0.011	12.445	1.257	0.126
Atilax paludinosus	0.798	0.080	0.008	12.830	1.292	0.129
Mustela altaica	0.830	0.084	0.008	13.025	1.312	0.131
Proteles cristata	0.872	0.088	0.009	13.311	1.342	0.134
Pseudalopex griseus	1.130	0.114	0.011	13.602	1.374	0.138
Mustela sibirica	1.212	0.123	0.012	13.607	1.376	0.138
Lynx canadensis	0.926	0.093	0.009	14.139	1.426	0.143
Mustela nudipes	0.767	0.077	0.008	14.190	1.429	0.143
Canis rufus	1.623	0.165	0.016	14.176	1.439	0.144
Mustela strigidorsa	1.341	0.136	0.014	14.291	1.447	0.145
Meles leucurus	1.179	0.119	0.012	14.425	1.458	0.146
Genetta cristata	0.552	0.055	0.006	14.684	1.476	0.148
Macrogalidia musschenbroekii	0.679	0.068	0.007	14.853	1.494	0.150
Vulpes macrotis	1.316	0.133	0.013	14.826	1.500	0.150
Cerdocyon thous	1.176	0.119	0.012	14.866	1.503	0.150
Canis aureus	1.270	0.128	0.013	15.394	1.557	0.156
Procyon cancrivorus	0.833	0.084	0.008	15.871	1.599	0.160
Mustela lutreolina	1.083	0.109	0.011	15.958	1.611	0.161
Herpestes brachyurus	0.807	0.081	0.008	16.661	1.678	0.168
Crossarchus alexandri	0.953	0.096	0.010	16.912	1.706	0.171
Leptailurus serval	1.097	0.111	0.011	16.984	1.715	0.172

Herpestes naso	0.878	0.088	0.009	17.172	1.731	0.173
Mustela eversmanii	1.730	0.176	0.018	17.106	1.738	0.174
Panthera tigris	1.344	0.136	0.014	17.237	1.745	0.175
Tremarctos ornatus	0.765	0.077	0.008	17.365	1.749	0.175
Crossarchus ansorgei	0.838	0.084	0.008	17.872	1.801	0.180
Cuon alpinus	1.637	0.166	0.017	18.321	1.859	0.186
Caracal caracal	1.253	0.127	0.013	18.986	1.920	0.192
Gulo gulo	0.495	0.050	0.005	19.139	1.922	0.192
Arctogalidia trivirgata	1.546	0.157	0.016	19.589	1.987	0.199
Crocuta crocuta	1.093	0.110	0.011	19.768	1.996	0.200
Conepatus leuconotus	1.345	0.136	0.014	20.102	2.035	0.204
Pseudalopex culpaeus	1.535	0.156	0.016	20.200	2.048	0.205
Mellivora capensis	1.306	0.132	0.013	20.657	2.090	0.209
Crossarchus obscurus	1.492	0.151	0.015	20.788	2.107	0.211
Crossarchus platycephalus	0.943	0.095	0.010	21.371	2.155	0.216
Canis mesomelas	1.479	0.150	0.015	21.382	2.167	0.217
Nasua nasua	0.917	0.092	0.009	21.568	2.175	0.218
Helarctos malayanus	0.361	0.036	0.004	22.110	2.218	0.222
Herpailurus yagouaroundi	1.261	0.127	0.013	22.338	2.259	0.226
Vulpes rueppellii	0.497	0.050	0.005	24.175	2.428	0.243
Vulpes corsac	1.249	0.126	0.013	24.071	2.434	0.244
Acinonyx jubatus	1.110	0.112	0.011	24.806	2.506	0.251
Otocyon megalotis	1.546	0.157	0.016	25.247	2.560	0.256
Canis adustus	1.521	0.154	0.015	25.437	2.579	0.258
Herpestes semitorquatus	0.575	0.058	0.006	26.275	2.641	0.264
Felis silvestris	2.368	0.242	0.024	26.349	2.692	0.270
Vulpes pallida	1.082	0.109	0.011	26.915	2.718	0.272
Hyaena hyaena	1.714	0.174	0.017	27.295	2.772	0.278
Galictis vittata	0.842	0.085	0.008	29.305	2.953	0.296
Otocolobus manul	1.302	0.132	0.013	29.522	2.987	0.299
Taxidea taxus	0.058	0.006	0.001	31.137	3.115	0.312
Vulpes ferrilata	1.086	0.110	0.011	32.159	3.248	0.325
Speothos venaticus	1.423	0.144	0.014	33.200	3.363	0.337
Felis margarita	1.363	0.138	0.014	38.195	3.867	0.387
Civettictis civetta	2.093	0.213	0.021	38.248	3.898	0.391
Poecilogale albinucha	0.033	0.003	0.000	42.126	4.214	0.421
Canis lupus	3.560	0.368	0.037	45.130	4.662	0.468
Mydaus javanensis	1.131	0.114	0.011	47.333	4.782	0.479
Galidia elegans	0.445	0.045	0.004	49.290	4.949	0.495
Bassaricyon beddardi	0.352	0.035	0.004	50.675	5.084	0.509
Vulpes zerda	0.446	0.045	0.004	51.324	5.153	0.516
Parahyaena brunnea	3.279	0.338	0.034	50.124	5.165	0.518
Catopuma badia	0.340	0.034	0.003	52.216	5.238	0.524
Galidictis fasciata	0.568	0.057	0.006	63.666	6.399	0.640
Mungotictis decemlineata	0.538	0.054	0.005	64.380	6.469	0.647
Mephitis macroura	6.571	0.698	0.070	63.233	6.721	0.676
Neofelis nebulosa	5.898	0.623	0.063	63.678	6.725	0.676
Cryptoprocta ferox	1.032	0.104	0.010	68.497	6.914	0.692
Neofelis diardi	0.827	0.083	0.008	68.727	6.924	0.693
Lycaon pictus	2.205	0.225	0.023	69.584	7.099	0.711
Panthera uncia	1.111	0.112	0.011	80.585	8.140	0.815
Bassaricyon pauli	0.510	0.051	0.005	83.752	8.414	0.842
Panthera leo	3.264	0.336	0.034	84.270	8.682	0.871
Fossa fossana	0.864	0.087	0.009	106.406	10.724	1.073
Bassaricyon lasius	0.510	0.051	0.005	117.670	11.821	1.183
Mustela africana	1.112	0.112	0.011	124.331	12.559	1.257
Atelocynus microtis	1.348	0.136	0.014	170.407	17.250	1.727
Salanoia concolor	0.119	0.012	0.001	248.522	24.879	2.488
Vulpes lagopus	1.726	0.175	0.018	257.668	26.173	2.621

Table S4. Allometric relationships with body mass (m) in grams for the variables used to compute the model parameters. N: sample size.

Variable	Units	Estimate	R^2	N
Mortality rate (μ)	yr^{-1}	$6.9\ m^{-0.33}$	0.51	17
Breeding age (β)	Yr	$0.18\ m^{0.25}$	0.70	28
Litter interval (Δ)	Yr	$0.15\ m^{0.20}$	0.40	87
Population density	$\#/km^2$	$3.09E3\ m^{-0.81}$	0.39	78
Dispersal median (σ_m)	km/generation	$0.47\ m^{0.43}$	0.45	95

Supporting references

LIFE HISTORY TRAITS SOURCE REFERENCES

Blanco JC (2011) Lobo - *Canis lupus*. In: Salvador A, Cassinello J (Eds.) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid.

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648.

Lynch HJ, Fagan WF (2009) Survivorship curves and their impact on the estimation of maximum population growth rates. Ecology 90: 1116-1124.

Palazón S (2012) Comadreja - *Mustela nivalis*. In: Salvador A, Cassinello J (Eds.) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid.

Palazón S (2010) Visón europeo - *Mustela lutreola*. In: Carrascal LM, Salvador A (Eds.) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid.

Pereira HM, Daily GC (2006) Modeling biodiversity dynamics in countryside landscapes. Ecology 87: 1877-1885.

Appendix

Curriculum vitae

Personal information

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Education

Present	PhD student, Martin-Luther-University Halle-Wittenberg Research topic: "Process-based models of biodiversity response to global change"; supervisor: Prof. Henrique M. Pereira
2002	Graduation in Biology, Faculty of Sciences, University of Lisbon, Portugal. Final grade 16/20 (pre-Bologna Graduation)

Professional and research experience

2016.09-	Research fellow for the Infraestruturas de Portugal Biodiversity Chair, at CIBIO/InBio, Instituto Superior de Agronomia, Lisboa, Portugal
2015.01-06	Student Helper at the Biodiversity and Conservation group of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
2014.07-12	Research fellow for the EU-FP7 project "PATHWAYS - Exploring transitions pathways to sustainable, low carbon societies", at iDiv, Leipzig, Germany
2014.01-06	Research fellow for DIVERSITAS project "GBO4 - Global Biodiversity Outlook 4", at iDiv, Leipzig, Germany
2013	Research fellow for FCT project "MoBiA - Monitoring Biodiversity in Environmental Assessments", PTDC/AAC-AMB/114522/2009, at the Centre for Environmental Biology, Faculty of Sciences, University of Lisbon, Portugal
2012-2015	Member of the Centre for Environmental and Marine Studies, University of Lisbon, Portugal
2007-2015	Member of the Centre for Environmental Biology, University of Lisbon, Portugal
2007-2010	PhD fellowship from Foundation for Science and Technology, Portugal (SFRH/BD/36064/2007)
2005	Research assistant for "Project Grand Singes" in Cameroon, Centre for Research and Conservation, Royal Zoological Society of Antwerp, Belgium
2003-2004	Research assistant for the "Enrichment Programme for primates at the Lisbon Zoo", New University of Lisbon, University of Lisbon, Jane Goodall Institute, and University of Cambridge

Ana Catarina de Ceia Hasse Ferreira Halle (Saale), 10.11.2016

Appendix

List of publications

Publications of the thesis

Ceia Hasse A., Sinervo B., Vicente L., Pereira H.M. (2014) Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. Ecography 37: 679-688.

Ceia Hasse A., Borda-de-Água L., Grilo C., Pereira H.M. (Manuscript) Global exposure of carnivores to roads. Provisonally accepted for publication pending minor corrrections in Global Ecology and Biogeography.

Ceia Hasse A., Navarro L., Borda-de-Água L., Pereira H.M. (Manuscript) Population persistence in fragmented landscapes: disentangling isolation, road mortality, and the effect of dispersal. In preparation.

Conference contributions

Ceia Hasse A., Navarro L., Borda-de-Água L., Pereira H.M. (2016) Population persistence in fragmented landscapes: disentangling isolation, road mortality, and the effect of dispersal. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig Annual Conference, Leipzig, Germany [oral presentation]

Ceia Hasse A., Rytwinski T., Pereira H.M. (2015) Can species traits influence their vulnerability to road impacts? 27th International Congress for Conservation Biology and 4th European Congress for Conservation Biology, Montpellier, France [oral presentation]

Ceia Hasse A., Borda-de-Água L., Grilo C., Pereira H.M. (2014) Global impact of roads on carnivores: which species and where? Fourth Infra Eco Network Europe (IENE) International Conference, Malmö, Sweden [oral presentation]

Ceia Hasse A., Borda-de-Água L., Grilo C., Pereira H.M. (2014) Land use change and biodiversity: modeling the impact of roads on carnivores. 44th Annual Conference of the Ecological Society of Germany, Austria and Switzerland (GfÖ), Hildesheim, Germany [oral presentation]

Ceia Hasse A., Sinervo B., Vicente L., Pereira H.M. (2012) Comparing ecophysiological and species distribution models to project European reptile range shifts. Third European Congress of Conservation Biology, Glasgow, UK [oral presentation]

Appendix

Erklärung über den persöhnlichen Anteil an den Publikationen

Chapter 2

Ceia-Hasse A.*, Navarro L., Borda-de-Água L., Pereira H.M. Population persistence in fragmented landscapes: disentangling isolation, road mortality, and the effect of dispersal. Manuscript.*

Analysis: **Ceia-Hasse A.** (80%), Navarro L. (10%), Pereira H.M. (10%)

Writing: **Ceia-Hasse A.** (90%), Pereira H.M. (10%); corrections by Navarro L. and Borda-de-Água L.

Chapter 3

Ceia-Hasse A.*, Borda-de-Água L., Grilo C., Pereira H.M. Global exposure of carnivores to roads. Provisonally accepted for publication pending minor corrrections in Global Ecology and Biogeography.*

Data collection: **Ceia-Hasse A.** (90%), Grilo C. (10%)

Analysis: **Ceia-Hasse A.** (80%), Pereira H.M. (20%)

Writing: **Ceia-Hasse A.** (90%), Pereira H.M. (10%); corrections by Borda-de-Água L. and Grilo C.

Chapter 4

Ceia-Hasse A.*, Sinervo B., Vicente L., Pereira H.M. (2014) Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. Ecography 37: 679-688.*

Data collection: **Ceia-Hasse A.** (100%)

Analysis: **Ceia-Hasse A.** (90%), Pereira H.M. (10%)

Writing: **Ceia-Hasse A.** (90%), Pereira H.M. (10%); corrections by Sinervo B. and Vicente L.

Halle (Saale), 10.11.2016

Ana Catarina de Ceia Hasse Ferreira

(Applicant and corresponding author)

Appendix

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel "Process-based models of biodiversity response to global change" bisher weder der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den 10.11.2016

Ana Catarina de Ceia Hasse Ferreira