MATHEUS SILVA CORRÊA

ASSESSMENT OF ROADKILL LIKELIHOOD METHODS: THE USE OF SINGLE OCCURRENCES *VERSUS* HOTSPOTS FOR DIFFERENT TAXA

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Ecossistemas Fragmentados e Agrossistemas, para a obtenção do título de Mestre.

Prof(a). Dra. Clara Grilo

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MATHEUS SILVA CORRÊA

ASSESSMENT OF ROADKILL LIKELIHOOD METHODS: THE USE OF SINGLE OCCURRENCES VERSUS HOTSPOTS FOR DIFFERENT TAXA

AVALIAÇÃO DOS MÉTODOS DE PROBABILIDADE DE ATROPELAMENTOS: O USO DE SIMPLES OCORRÊNCIAS *VERSUS* *HOTSPOTS* PARA DIFERENTES TAXA

Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Ecossistemas Fragmentados e Agrossistemas, para a obtenção do título de Mestre.

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RESUMO

As estradas são responsáveis por uma enorme mortalidade de várias espécies anualmente. A fim de definir medidas para reduzir a mortalidade dos animais, muitos estudos têm analisado quais as variáveis ambientais que podem promover o risco de atropelamento. Existem vários tipos de dados para realizar esse tipo de análise: dados com apenas presença de atropelamentos (maior quantidade e menor qualidade de dados) ou com a incidência de atropelamentos (hotspots) (menor quantidade e maior qualidade de dados). No entanto, não existe consenso sobre qual é a melhor abordagem para gerar resultados mais precisos e robustos. Nosso objetivo foi comparar os diferentes tipos de dados (ocorrência de atropelamentos, de hotspots espacial, e hotspots espacial/ temporal) que geram melhor performance e as variáveis que melhor explicam os atropelamentos. Nós analisamos dados de duas espécies de cada classe de vertebrados terrestres no Brasil: anfíbios (*Leptodactylus latrans* e *Rhinella icterica*), répteis (*Philodryas patagoniensis* e *Helicops infrataeniatus*), aves (*Volatinia jacarina*, e *Nothura maculosa*) e mamíferos (*Didelphis albiventris* e *Myocastor coypus)*. Utilizamos o *software* Siriema para identificar *hotspots* de atropelamentos e o *software* MaxEnt para analisar a relação entre os tipos de dados de atropelamento as variáveis ambientais. Todos os nossos modelos obtiveram uma boa performance (AUC > 0.7). Os nossos resultados sugerem que os modelos MaxEnt têm melhor desempenho com hotspots. Em gelral, as variáveis ambientais que explicaram os atropelamentos foram consistentes com os habitats das espécies e não encontramos diferenças de performance de modelo entre as espécies especialistas e generalistas em termos de habitat. Deste modo, nós recomendamos o uso de hotspots para modelar o risco de atropelamento tanto para habitat espacialista e generalistas.

Palavras-chave: Hotspots. Maxent, Modelos de presença. Mortalidade em rodovias. Siriema. Vertebrados.

ABSTRACT

Roads are responsible for a massive mortality of wildlife annually. In order to define measures to reduce roadkill risk many studies have analyzed the spatial environmental variables that explain roadkill likelihood. There are several approaches to conduct this type of analysis such as modelling the roadkill presence-only (high quantity and low quality of the data) or the incidence of roadkill (hereafter hotspots) (low quantity and high quality of the data). However, there is no consensus on which one is the best to generate the most accurate and robust results. We aimed to compare which type of records (only roadkill, spatial hotspots, or spatio-temporal hotspots) generate better model performance and the variables that better explain the roadkill likelihood. We analyzed roadkill records of two species in each class of terrestrial vertebrates collected in Brazil: amphibians (*Leptodactylus latrans* and *Rhinella icterica*), reptiles (*Philodryas patagoniensis* and *Helicops infrataeniatus*), birds (*Volatinia jacarina* and *Nothura maculosa*), and mammals (*Didelphis albiventris* and *Myocastor coypus*). We used the Siriema software to identity roadkill hotspots, and the MaxEnt software to analyze the relationship between the three types of records with the environmental variables. All models had a high performance (AUC > 0.7). Our findings suggest that MaxEnt models performance were better with hotspots. In general, the environmental variables that explained roadkill were consistent with species habitats and no differences were found between habitat specialist and generalist species Therefore, we recommend the use of hotspots for modeling the roadkill risk for either habitat specialist and generalist species.

Keywords: Hotspots. Maxent, Presence-only models. Road mortality. Siriema. Vertebrates.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

Estamos vivendo em uma era que em que a defaunação está ocorrendo de forma evidente, e há muitos fatores antropogênicos que estão fazendo isso acontecer (YOUNG *et al.,* 2016). Estradas e ferrovias são infraestruturas permanentes que contribuem de forma significativa para alterações na paisagem, acelerando o processo de perda de toda uma comunidade local (LAURANCE *et al.* 2006; VAN-DER-REE *et al.* 2015). Há quase 100 anos, foi publicado o primeiro trabalho a alertar sobre o impacto que os automóveis poderiam causar em populações de animais (STONER 1925). Desde então, vários trabalhos contribuem para o melhor entendimento da construção de estradas mais modernas e que consigam reduzir impactos sobre populações de animais (BAGER; BORGHI; SECCO, 2015; FORMAN *et al.,* 2013; GRILO *et al.,* 2018; VAN-DER-REE; SMITH; GRILO 2015).

Vários estudos já relatam sobre os diversos efeitos que as estradas podem causar nos diferentes níveis de organização biológica, podendo atingir desde indivíduos, até comunidades (BORDA-DE-ÁGUA; GRILO; PEREIRA, 2014; TROMBULAK; FRISSELL, 2000). Já é reconhecido que as espécies muitas vezes precisam atravessar as estradas seja para dispersão, migrações e/ou busca de recursos, acabam sofrendo mudanças em sua área de vida, e consequentemente no fluxo gênico e na sua taxa reprodutiva (GRILO *et al.,* 2012; WHITTINGTON; CLAIR; MERCER, 2004). Além disso, as estradas são responsáveis por altas taxas de mortalidade de animais, causadas pela tentativa dos indivíduos atravessarem as rodovias e que pode levar à redução da abundância e fragmentação das suas populações (BISCHOF; STEYAERT; KINDBERG, 2017; FAHRIG; RYTWINSKI, 2009).

Tendo isso em vista, pesquisas recentes têm focado na realização de uma previsão de quantos animais são atropelados por ano para conhecer o potencial impacto nas suas populações. O grupo de insetos é o que tem uma das menores quantidades de trabalhos realizados, devido à dificuldade da sua coleta e identificação, chegando a cerca somente de 2% (BENNETT, 2017). Um dos primeiros trabalhos com esse grupo taxonômico estimou centenas de milhares em apenas dois kms de rodovia, o que pode representar centenas de bilhões na América do Norte de Lepidópteros, Hymenópteros e Dípteros polinizadores a cada verão (BAXTER-GILBERT *et al.*, 2015). Outros grupos com estimativas de milhões de indivíduos atropelados por ano são: os anfíbios nos Estados Unidos (LALO 1987), répteis na Austrália (EHMANN; COGGER 1985) aves na Europa e no Brasil (GONZÁLEZ-SUÁREZ; FERREIRA; GRILO, 2018; GRILO *et al.*, 2020), e mamíferos no Brasil (GONZÁLEZ-SUÁREZ; FERREIRA; GRILO, 2018).

Sendo assim, é importante definir medidas de mitigação nos segmentos de estrada onde ocorrem elevada incidência de atropelamentos para não pôr em causa a viabilidade das populações a longo prazo e evitar acidentes que ponham em causa vidas humanas (BAGER; FONTOURA 2013). Essas medidas, podem também causar um menor custo principalmente para concessionárias das rodovias, visto que são anualmente gastos milhões de reais com atendimento médico e indenização nos acidentes devido à colisão com animais de grande porte (ABRA *et al.*, 2019). Estudos anteriores mostraram que ao aplicar essas medidas de mitigação, poderá haver reduções da mortalidade dos animais em 40%, e se tais medidas fossem realizadas de maneira adequada, essa diminuição poderia chegar a 83% (RYTWINSKI *et al.*, 2016). As medidas de mitigação incluem medidas para reduzir a velocidade do tráfego, viadutos/pontes modificadas como estruturas para passagem da fauna, mudanças no acostamento de estradas, cercas e túneis. (HUIJSER *et al.*, 2008; RYTWINSKI, *et al.*, 2016; VAN DER GRIFT *et al.*, 2013).

Para a implementação dessas medidas de mitigação, há uma necessidade de realização de estudos para uma melhor compreensão dos locais onde os atropelamentos ocorrem, quais espécies são atropeladas e quais os fatores que estão influenciando os atropelamentos (GOMES *et al.*, 2008; RUSSO *et al.*, 2020). Esses estudos indicam que características da estrada como o tipo de pavimento, o número de vias (CHYN *et al.*, 2021; SANTOS *et al.*, 2018) podem promover o número de atropelamentos. Estudos anteriores observaram que características da paisagem podem promover o número de atropelamentos, como o tipo de vegetação, e a conectividade da vegetação ao entorno, a topografia, a presença de corpos d'água, e presença humana como construções e queimadas (CERQUEIRA *et al.*, 2021; GRILO *et al.*, 2011, 2016; VALERIO; BASILE; BALESTRIERI, 2021; WILLIAMS *et al.*, 2019). Por fim, as características das próprias espécies, como o comportamento de forrageamento, o tamanho da sua área de vida, e o grau de especialização das espécies em termos de habitat e dieta (D'AMICO *et al.*, 2016; GONZÁLEZ-SUÁREZ; FERREIRA; GRILO *et al.* 2020; RYTWINSKI; FAHRIG 2011), além do horário e épocas de maior atividade da espécie, e consequentemente de maior mortalidade (SAEKI; MACDONALD, 2004; MEDINAS *et al.* 2020).

Para saber quais são os fatores que influenciam nos atropelamentos, são realizadas análises que estabelecem a relação entre as ocorrências de atropelamentos e as características das estradas e do seu entorno (SILVA *et al.*, 2019). No entanto existem diferentes formas de realizar essas análises. Uma delas é realizada com dados de presença e ausência de atropelamentos nos locais (GRILO; BISSONETTE; SANTOS-REIS, 2009), outros estudos trabalham somente com a ocorrência de atropelamentos (CERQUEIRA *et al.*, 2021; ROGER; RAMP, 2009; WILLIAMS *et al.*, 2019), e o outra abordagem é com o uso de agregação de atropelamentos (hotspots) (FAVILLI *et al.*, 2018; SECCO *et al.*, 2017; SEO *et al.*, 2013). A principal diferença entre essas abordagens é a qualidade e a quantidade dos dados. Há uma maior disponibilidade de dados sobre atropelamentos apenas com presença de atropelamentos, enquanto o uso de *hotspots* significa menos quantidade de dados, mas maior qualidade devido à alta incidência de atropelamentos em determinados segmentos rodoviários (GOMES *et al.*, 2009; MALO; SUÁREZ; DÍEZ, 2004).

Para alguns autores, o uso de *hotspots* de atropelamentos fornece as características mais confiáveis da estrada e da paisagem que explicam a alta incidência de atropelamentos em certas estradas (CLEVENGER; HARDY; GUNSON 2006). E por essa razão, existem vários trabalhos com as quatro classes de vertebrados terrestres (GOMES *et al.*, 2008; GONÇALVES *et al.*, 2018; SILLERO *et al.* 2019; PEREIRA *et al*., 2021). Entretando, outros autores questionam se realmente o modelo utilizando *hotspots* é o melhor para identificar quais as melhores variáveis que explicam a incidência de atropelamentos EBERHARDT; MITCHELL; FAHRIG 2013).

Como não existe consenso sobre qual é a melhor abordagem para gerar resultados mais precisos e robustos, o presente estudo pretende comparar os dois tipos de dados (somente atropelamentos ou *hotspots*), no que diz respeito à performance e aos tipos de variáveis que melhor explicam os atropelamentos.

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SEGUNDA PARTE

ARTIGO

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ABSTRACT

Roads are responsible for a massive mortality of wildlife annually. In order to define measures to reduce roadkill risk many studies have analyzed the spatial environmental variables that explain roadkill likelihood. There are several approaches to conduct this type of analysis such as modelling the roadkill presence-only (high quantity and low quality of the data) or the incidence of roadkill (hereafter hotspots) (low quantity and high quality of the data). However, there is no consensus on which one is the best to generate the most accurate and robust results. We aimed to compare which type of records (only roadkill, spatial hotspots, or spatio-temporal hotspots) generate better model performance and the variables that better explain the roadkill likelihood. We analyzed roadkill records of two species in each class of terrestrial vertebrates collected in Brazil: amphibians (*Leptodactylus latrans* and *Rhinella icterica*), reptiles (*Philodryas patagoniensis* and *Helicops infrataeniatus*), birds (*Volatinia jacarina* and *Nothura maculosa*), and mammals (*Didelphis albiventris* and *Myocastor coypus*). We used the Siriema software to identity roadkill hotspots, and the MaxEnt software to analyze the relationship between the three types of records with the environmental variables. All models had a high performance (AUC > 0.7). Our findings suggest that MaxEnt models performance were better with hotspots. In general, the environmental variables that explained roadkill were consistent with species habitats and no differences were found between habitat specialist and generalist species Therefore, we recommend the use of hotspots for modeling the roadkill risk for either habitat specialist and generalist species.

Keywords: Hotspots, Maxent, Presence-only models, Road mortality. Siriema, Vertebrates.

ASSESSMENT OF ROADKILL LIKELIHOOD METHODS: THE USE OF SINGLE OCCURRENCES *VERSUS* HOTSPOTS FOR DIFFERENT TAXA

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1 INTRODUCTION

While roads are very important to the economy for many countries, they can have many negative direct and indirect effects for ecological systems (Forman *et al.* 2003; Van-Der-Ree *et al.*, 2015; Pinto *et al.*, 2019). One of the main consequences of roads is the high animal mortality rates caused by wildlife vehicle collisions which can reduce population abundance and increase isolation with implications on species distribution and even communities (Fahrig & Rytwinski 2009, Bischof *et al.* 2017).

There are estimates of millions of roadkill each year in many regions, from insects (Baxter-Gilbert *et al.* 2015; Kantola *et al.* 2019) to large mammals, affecting many threatened species (Langbein, 2011; Loss *et al.*, 2014; Wembridge *et al.*, 2016; González-Suárez *et al*. 2018; Grilo *et al.*, 2020). The growing concerning on how road modernization and expansion can coexist with the biodiversity conservation has led research centers and universities to assess the spatial factors that promote the likelihood of individuals being roadkilled (Gomes *et al.* 2009, Gunson *et al.* 2011, Bager *et al.* 2015, Schwartz *et al.* 2020).

Accurate identification of the factors that cause roadkill is essential to locate more efficiently the measures to reduce the wildlife collisions with vehicles (Ceia-Hasse *et al.* 2017, Russo *et al.* 2020). However, the lack of information on different species and the definition of the best models to carry out research can hinder the environmentally sustainable development of the road network namely, to prevent roadkill (Grilo et al. 2020).

Several authors showed that the risk of collision between individuals and vehicles for many species is not randomly distributed along the roads, and they may be associated with landscape features in the vicinity of roads (Malo *et al.* 2004, Gunson *et al.* 2011). For example, type, connectivity and presence of vegetation, topography, hydrology and human disturbance has been documented as factors that promote the risk of wildlife-vehicle collision (Grilo *et al.* 2011, 2016, Williams *et al.* 2019, Cerqueira *et al.* 2021, Valerio *et al.* 2021). Also, road characteristics such as pavement type, number of lanes (Santos *et al.* 2018, Chyn *et al.* 2021), and the behavior of the species near the road can explain the incidence of roadkill rates among species (e.g. González-Suárez *et al.* 2018). For example, foraging, behavior, the size of the home range, or the degree of habitat specialization can affect the likelihood of species being roadkilled (Rytwinski & Fahrig 2011; D'Amico *et al.* 2016; Gonzáles-Suaréz *et al.* 2018; Grilo *et al.* 2020).

Research on which spatial environmental factors may explain roadkill occurrence has been widely developed to predict where are the most deadliest road segments (Gomes *et al.*, 2008; Malo *et al.*, 2004). There are two types of records to analyze the relationship between roadkill and spatial factors in order to identify the roads segments where mitigation efforts should be applied (Ramp *et al.* 2005): only roadkill occurrence (Roger & Ramp 2009, Williams *et al.* 2019, Cerqueira *et al.* 2021), and aggregation of roadkill (hereafter hotspots)

(Seo *et al.* 2015, Secco *et al.* 2017, Favilli *et al.* 2018). The main difference is in the quality and quantity of the data. There is a higher availability of data on presence-only roadkill while there is a less quantity of data when using roadkill hotspots but represent higher quality due to high incidence of roadkill in the road segment (Malo *et al.* 2004, Gomes *et al.* 2009). The use of models using only roadkill data was also widely applied (Rosa & Bager 2012; Kreling *et al.* 2019; Williams *et al*. 2019). However, the use of roadkill hotspots seems also to provide reliable information to predict the roadkill likelihood (Clevenger *et al.* 2006). Therefore, hotspots have been used for all terrestrial vertebrates such as in amphibians (Coelho *et al.* 2012, Heigl *et al.* 2017, Sillero *et al.* 2019), reptiles (Gonçalves *et al.*, 2018; Patrick *et al.*, 2012), birds (Gomes *et al.*, 2008; Husby, 2016), and mammals (Teixeira *et al.*, 2013; Magioli *et al.*, 2019; Pereira *et al*., 2021). Besides the general use of these two types of records, there is lack of knowledge on which one has better performance to assess the variables that promote roadkill, and whether may vary among species, especially when there are differences in habitat and diet preferences (Chyn *et al*., 2020).

The main goal of this study is to compare the models with roadkill presence-only data, and the occurrence of hotspots (spatial hotspots or spatio-temporal hotspots) regarding the quality of models and the variables that explain the roadkill. We tested two hypotheses: 1) the performance of the model is associated to the quality of the data (hotspots) and 2) presence only roadkill models have a better performance for generalist species while roadkill hotspots provide better model performances for specialist species.

1 METHODS

2.1 SPECIES SELECTED AND ROAD KILL DATA

Road kill records were obtained from the Brazilian data set (Grilo *et al*., 2018) which is a compilation of data from 2002 to 2017. We selected two species of each terrestrial vertebrate class with the highest number of roadkill records on one or more roads to represent a specialist and a generalist habitat species in Brazil, respectively: amphibians: *Leptodactylus latrans* (Lesser foam frog) and *Rinella icterica* (Cururu); reptiles *Philodryas patagoniensis* (Green racer snake) and *Helicops infrataeniatus* (Water Snake); birds *Volatinia jacarina* (Blue-black Grassquit) and *Nothura maculosa* (Spotted tinamou), and mammals *Didelphis albiventris* (White-eared opossum) and *Nothura maculosa* (Spotted tinamou) (Table 1). As the recorded class of amphibia included only habitat generalist species, we did not make that comparison within this taxon.

2.2 ENVIRONMENTAL DATA

For each species, we created grid of cells with the size of the average home range area of the species obtained in the literature that overlap the roads surveyed. The grid cell size used was: 50m² for *L. latrans, R. icterica,* and *V. jacarina* 75m² for *P. patagoniensis* and *H. infrataeniatus*; 200m² for *D. albiventris;* 500m² for *N. maculosa* and 550m² for *M. coypus* (see Table S1 for further details).

We selected environmental variables well documented in the literature that can explain the roadkill risk: land cover (forest, grassland, agriculture, pasture, wetlands), hydrology (water bodies and rivers) and human pressure (urban areas, road type) (Table 2). We used the environmental variables from 2015, which is in line with the roadkill data collection. We calculated the nearest distance from the centroid of each cell to each variable, except for the road type (we used the dominant type to describe the cell). We also calculated the connectivity of all variables (except for urban and road type) using the Effective Mesh

Size estimate (Meff) (see material supplementary for further details) (Moser *et al.* 2007). All analysis were performed with the ArcGIS 10.5 software (ESRI, 2016).

2.3 HOTSPOTS IDENTIFICATION

We estimated the roadkill hotspots of each species using the SIRIEMA software (Coelho *et al*. 2014). Firstly, we used the Ripley K 2D statistics to assess the non-randomness of the spatial distribution of events at the various scales (Ripley, 1981; Levine, 2004) assuming the two-dimensionality of the road (Coelho *et al.* 2008). We introduced the geographic coordinates of roadkill records and the coordinates of the respective roads. We used initial radius of 50m with increases of 100m. We performed 1000 simulations of random distribution events with a 95% confidence interval to identify significant clusters and evaluate if there are significant hotspots in our target scale for each set of data analyzed.

We then performed Hotspots Identification – 2D (Coelho *et al*., 2014), which considered the two-dimensional space to identify where are the significant high incidences of roadkill on each road using the scale evaluated previously on Ripley's analyses. We ran 100 simulations for each species. The confidence interval was 95% and the size of the road segments used for the analyzes followed the diameter of the home range of each species (Table S1).

We evaluated two types of hotspots: 1) spatial hotspots (only taking into account significant spatial aggregations of roadkill); and 2) spatio-temporal hotspots (taking into account the time that collections were carried out and the home range size of the species). Spatial hotspots identified are the result of the combination of sections with high incidence of roadkill that are statistically significant from the rest of the road segments. We considered a spatio-temporal hotspot when there was one or more individuals that are roadkilled in a road segment per year within the length of a species home range diameter (> 1 ind./home range diameter/year). Therefore, for the spatial hotspots, we used the joining of adjacent hotspots as just a single hotspot regardless their size, and for subsequent analysis, we used the centroid of the hotspot.

2.4 EVALUATION OF THE FACTORS THAT EXPLAIN PRESENCE-ONLY ROADKILL AND HOTSPOTS LIKELIHOOD

We ran the MaxEnt software to evaluate the factors that explain the roadkill likelihood. Maxent uses to model niches and species distributions by applying the maximum entropy modeling technique (Phillips *et al.* 2006). From a set of environmental layers and georeferenced events the model expresses a probability of the event in each grid cell (Duque-Lazo *et al.*, 2016; Phillips & Dudík., 2008). For each species we ran three models using different type of records: 1) only single roadkill occurrence 2) using spatial hotspots and 3) spatio-temporal hotspots.

Previously, we performed a correlation test between the variables using the SDM toolbox installed on ArcGIS10.5 (Brown *et al.* 2017). If the correlation is greater than 0.7 then we selected the variable with highest ecological meaning (Boslaugh, 2008).

We ran each model with 500 interactions and 10 replicates, and calculated the AUC values of the three models. An AUC (Area under the curve) value of 0.5 indicates that model performance is no better than random, while values close to 1.0 indicate a very good performance (Young *et al.* 2011). We also obtained the percentage of contribution for each variable in each model, the total sum being 100%. With these results, we can see which variables contributed the most to explain roadkill, spatial hotspots and spatio-temporal hotspots. We also compared the variables that explain road mortality with studies to see if the three main variables correspond to habitat preferences of the species.

2 RESULTS

We analyzed in total 3,553 roadkill records that ranged between 185 and 792 among the eight species (Table 1). Ripley's K-analyses indicated that all species have significant aggregation of roadkill on several spatial scales. We found road-kill clustering from 50m to 175 km varying among species (see Figure S1 for further details).

3.1NUMBER OF ROADKILL *VS* THE NUMBER OF HOTSPOTS

As expected, the number of roadkill locations was greater than the number of hotspots locations for all species. However, there was a variation on the numbers of locations between spatial and spatio-temporal hotspots. For example, the species *L. latrans* which had 269 roadkills, four spatial hotspots and 15 spatio-temporal hotspots, while the species *P. patagoniensis* had 263 roadkill, and 49 in spatial hotspots and only six in spatio-temporal hotspots (Table 3).

3.2 PRESENCE-ONLY ROADKILL *VERSUS* ROADKILL HOTSPOTS LIKELIHOOD

All predictive models performed well with AUC > 0.7. The AUC for presence-only roadkill model had a lower performance than hotspot models except for *L. latrans* that the value was equal for roadkill and spatial hotspot model. We observed that three species (*L. latrans, V. jacarina, N. maculos*a) had the highest AUC value on spatial hotspots models, while the other five (*R.icterica*, *P. patagoniensis*, *H. infrataeniatus. D. albiventris* and *N.maculosa*) had the highest AUC value for spatio-temporal models (Table 4).

We observed higher AUC values for both spatial and spatio-temporal hotspots models than for presence-only roadkill models for habitat generalists and specialists. However, we did not find difference of model performances between habitat specialists and generalists regarding the type of hotspot: the species *H. infrataeniatus* and *M. coypus* (habitat specialists), obtained a higher AUC value, at spatio-temporal hotspot models, whereas the *N. maculosa* (habitat specialist) obtained a higher AUC value at spatial hotspot model. Two generalist species (*L. latrans* and *V. jacarina*) obtained higher AUC in spatial hotspot models while the other three (*R. icterica, P.patagoniensis* and *D. albiventris*) obtained higher AUC at spatio-temporal hotspots (Table 4).

3.3 FACTORS THAT EXPLAIN PRESENCE-ONLY ROADKILL AND HOTSPOTS LIKELIHOOD

We found differences in the variables that contributed most to the models, among the three types of records for the same species. We observed that only *H. infrataeniatus* and *D. albiventris* showed consistency in the variable that contributed the most to explaining the road mortality likelihood and obtained the same effect in the three models: positive relationship with wetlands connectivity and a negative association with pasture. For other three species *L. latrans, R. icterica* and *M. coypus,* we observed the same variables in the three analyzes, but at different levels of significance and with variation in the effect of the variables (Table 4). Regarding only the hotspot models, the species *R.icterica* and *M. coypus* obtained the same three variables, the species *H.infrataeniatus* obtained two (Meff wetlands and distance of wetland) and the species *N. maculosa* (florest) and *D. albiventris* (Meff wetlands) obtained only one variable (Table 4).

3 DISCUSSION

Our findings showed that roadkill hotspots models had better performance than using presence only roadkill, which seems to indicate that the quality of locations is better than the quantity of locations for modelling. Differences of performance between spatial and spatio-temporal hotspots were not clear: we found three species with a higher performance at spatial hotspots models (one amphibian and two species of birds) while five species (one amphibian, two reptiles and two mammals) had a higher performance for spatio-temporal hotspots models. As expected, variables that explained roadkill likelihood were in line with the variables that explain the habitat of the species, except for two species. We also did not find differences between specialist and generalist species among the models regarding the model performance and habitat variables.

In general, we observed some consistency between the three models in relation to the variables that explain the occurrence of roadkill, but with a difference in the contribution to the model. For example, we found species with variables that explain the roadkill likelihood highly associated with their main habitat: the reptile *H. infrataeniatus* had the same type of variable in the three models (wetlands) (Langen et al., 2009; Seo et al., 2013; Medrano-Vizcaíno & Espinosa 2021) as well *M. coypus* which is in line with other studies (Carter & Leonard 2002; Seo et al., 2013; Corriale et al. 2020; Medrano-Vizcaíno & Espinosa 2021). Interestingly, the low connectivity of pastures seems to promotes the likelihood of *R. icterica* roadkill, suggesting that less connectivity they tend to move more, including crossing the road. Although wetlands contributed significantly, we did not see a clear effect in the best model (spatio-temporal hotspots) as found by Coelho *et al.* (2012).

In contrast, other species (mostly generalist species) had differences on the variables among the models, even though the variables that contributed the most corresponded to the preferred habitats of each one. Although, road is not a habitat, we observed for the *V. jacarina* that type 2 of road is relevant to promote the probability of roadkill, which was also observed in another study (Soares & Dias. 2020). In addition to this variable, we found that open areas seem to explain roadkill likelihood in two of our models as also observed in Santos *et al.* (2018). Another species with differences in the variables among models was the reptilian species *P. patagoniensis.* Although, this species occurs in various types of habitat, they are most commonly found in open areas (Hartmann & Marques 2005; Quintela 2011), namely wetlands and pastures which were the main variables explaining the probability of roadkill. One explanation for the difference in the variables is the number of locations (49 spatial hotspots and six spatio temporal hotspots) which may influence the result of the model, indicating that roadkill location analyzed were widespread along the road and concentrated in few places, respectively. Another generalist species *L. latrans* had some inconsistencies regarding the expected variables that explain roadkill and its habitat. Distance to urban had an unexpected negative relationship with *L. latrans* habitat preferences, but it was an important variable in other roadkill studies, but with an obscure effect (Coelho *et al.*, 2012; Sillero *et al.*, 2019). In addition, we expected that hydrology or wetlands would explain roadkill risk for anurans since their behavior, ecology, patterns of activity, movements and locomotor performance are closely related to temperature and water availability for reproduction (Wells & Schwartz 2006 , Glista *et al.*, 2008). However, the distance from water bodies was not found as a variable that could explain higher incidence of road mortality for *L. latrans*. We found in spatial hotspots an unexpected opposite effect even the contribution was low 13%. Therefore, despite the high value of AUC, the small sample size may explain this result.

One species that had variables explaining roadkill differently from the habitat is *D. albiventris.* Although the species is found at human-disturbed landscapes, our three models showed pasture as the variable that most influenced roadkill (Cáceres *et al* . 2016). Other studies have shown that the pasture can serve as a passageway for small animals that are in adjacent forest areas but have not shown any relationship to roadkill by Didelphis (Medrano-Vizcaíno & Espinosa 2021).

We raised the hypothesis that generalists would be in various environments and with that, the aggregation of roadkill would be unlikely. However, we were unable to find differences in the model performances between specialists and habitat generalists. Therefore, we recommend the use of hotspots for modeling instead of just the presence-only roadkill for either habitat specialist and generalist species. Regarding the type of hotspot analysis we found differences among species. In this case, we recommend to analyze both types of records to find which one generate better results in terms of variables and model performance.

TABLES

Table 1: Selected species for analysis with information on Class, scientific name, common name, road identification, number of roadkill (Nº Rkill), Road length, Survey period and source compiled at Grilo et al. 2018. (*specialist habitat species)

Class	Scientific name	Common name	Road	N° Rkill	Road length	Survey period	Original Source
Amphibia	*Leptodactylus latrans*	Lesser foam frog	RS 389	268	4.41Km	07/2002 to 10/2003	Coelho *et al.*, 2012
	Rhinella icterica	Cururu	CS 012 + RS 486	433	18 Km / 66.6 Km	09/2012 to 11/2015 - 07/2009 to 06/ 2010	NERF_ UFRGS/ TEIXEIRA; KINDEL 2012
Reptilia	*Philodryas patagoniensis*	Green racer snake	BR 101 + BR 471	263	276 Km / 160.5 km	09/2012 to 10/2015 - 01/2002 to 04/2007	Gonçalves *et al.*, 2018/ Bager pers.comm
	**Helicops infrataeniatus*	Water Snake	BR 101 + BR 471	792	276 Km / 160.5 km	09/2012 to 10/2015 - 01/2002 to 04/2007	Gonçalves *et al.*, 2018/ Bager pers.comm
Birds	*Volatinia jacarina*	Blue-black Grassquit	DF 001 + BR 010	655	50.2 Km / 11 Km	04/2010 to 03/2015 - 08/2010 to 03/2015	IBRAM 2017
	**Nothura maculosa*	Spotted tinamou	BR 101	185	276 Km	09/2012 to 10/2015	Gonçalves *et al.*, 2018
Mammalia	*Didelphis albiventris*	White-eared opossum	BR 101 + BR 101 (Osório)	699	276 Km / 95 km	09/2012 to 10/2015 - 04/2005 to 01/2008	Gonçalves *et al.*, 2018/ Coelho *et al.*, 2008 /Teixeira *et al.*, 2013
	**Myocastor coypus*	Coypu	BR 471	248	160.5 Km	01/2002 to 04/2007	Bager pers.comm

Table 2 – Variables used to represent the landscape, with their respective resolution and reference. (*Projeto MapBiomas – Colletion [2015] of the Annual Series of Coverage and Land Use Maps in Brazil, access in [25/02/2020] through the link: https://mapbiomas.org)

Variables	Description	Classes/units	Date	Resolution	Reference
Land cover					
Forest	Distance to vegetation with tree species	Meters	2015	30m	Mapbiomas*
Grassland	Distance to Cerrado; prairie				
Agriculture	Distance to cultivated areas				
Pasture	Distance to Pastures areas				
Wetlands	Distance to floodplain and everglades non forest				
Hidrology	Distance to Water body, rivers, lakes				
Land cover connectivity					
Meff grassland	Grassland connectivity	Meff	2015	30m	Mapbiomas*
Meff agriculture	Agriculture connectivity				
Meff Forest	Forest connectivity				
Meff pasture	Pasture connectivity				
Meff wetlands	Wet área connectivity				
Meff hidrology	Hidrology connectivity				
Human pressure					
Urban	Distance to urban areas	Meters	2015	30m	Mapbiomas*
Road type	Types of roads separated by pavement and number of lanes	1 - Unpaved 2 - 2/3 paved lane paved 3 - 3 or more paved lanes	2019		Open street map

Table 3 - Representing the total number of roadkills and the number of hotspot locations for spatial and spatio-temporal analysis.

	Roadkill	Spatial hotspots	Spatio-temporal hotspots
Scientific name	N° roadkill	N°	N°
Leptodactylus latrans	269	4	15
Rhinella icterica	433	32	48
Philodryas patagoniensis	263	49	6
Helicops infrataeniatus	793	57	53
Volatinia jacarina	655	37	18
Nothura maculosa	185	21	18
Didelphis albiventris	699	65	50
Myocastor coypus	248	8	14

Table 4 - Results of the MaxEnt models for each species, containing the type of the analyses, the three variables that contributed most to explain the roadkill likelihood, % of contribution, their effects (+ positive; - negative or no effect), and AUC value.

Classe	Species	Type of analyses	Most important variables	% contribution	Effect	AUC
Amphibians	*L. latrans*	Roadkill	Meff pasture	43.1	+	0.864
			Urban	17.1	+	
			Grassland	13	+	
		Spatial	**Urban**	39.6	-	0.864
			Meff pasture	36.2		
			Hydrology	13.3	+	
		Spatio-temporal	**Urban**	68.4	-	0.846
			Forest	8.5		
			Pasture	6.8	-	
	R. icterica	Roadkill	**Meff grassland**	26.9	-	0.869
			Wetlands	19.8	+	
			Hydrology	16.6	+	
		Spatial	**Meff grassland**	22.6	-	0.918
			Wetlands	20.5		
			Forest	14.9	+	
		Spatio-temporal	**Wetlands**	24.4		0.926
			Meff grassland	21.2	-	
			Meff forest	12.2	+	
Reptiles	*P. patagoniensis*	Roadkill	**Urban**	16.7		0.743
			Hydrology	14.9	-	
			Meff wetlands	13.7	-	
		Spatial	Agriculture	19.1	-	0.784
			Urban	14.5	-	
			Forest	14.1	+	
		Spatio-temporal	**Meff wetlands**	24.9		0.854
			Wetlands	21.6	-	
			Meff grassland	20.5		
	H. infrataeniatus	Roadkill	**Meff wetlands**	67	+	0.848
			Roadtype	7.9	3	
			Wetlands	5.8		
		Spatial	**Meff wetlands**	56.6	+	0.934
			Wetlands	15.5	-	

			Meff grassland	6.4		
		Spatio-temporal	**Meff weatlands**	72.7	+	0.981
			Roadtype	12.3	3	
			Wetlands	3.7	-	
Birds	*V. jacarina*	Roadkill	Urban	34.5	-	0.731
			Meff grassland	15.8	-	
			Agriculture	13.6		
		Spatial	Meff grassland	19.6		0.91
			Urban	16.3	-	
			Roadtype	16	2	
		Spatio-temporal	Forest	27.8	-	0.813
			Agriculture	19.7	-	
			Pasture	17.8	-	
	N. maculosa	Roadkill	Meff grassland	23	-	0.801
			Meff agricul	19.7	-	
			Wetlands	15.8	+	
		Spatial	Meff grassland	26.5	-	0.939
			Meff agricul	21.8	+	
			Forest	16.1		
		Spatio-temporal	Forest	20.6	+	0.877
			Wetlands	19.1	+	
			Hydrology	16.4	-	
Mammals	*D. albiventris*	Roadkill	**Pasture**	71.1	-	0.772
			Meff forest	6.6	+	
			Urban	3.9		
		Spatial	**Pasture**	34.7	-	0.835
			Meff agricul	11.2		
			Forest	11.1	-	
		Spatio-temporal	**Pasture**	31.6	-	0.896
			Meff forest	15	+	
			Hydrology	13.4	+	
	M. coypus	Roadkill	**Meff wetlands**	43.2		0.852
			Urban	18.5	-	
			Forest	7.1		
		Spatial	Wetlands	71.8	-	0.871
			Roadtype	6.1		
			Meff wetlands	5.1		
			Meff wetlands	40.4	-	

		Spatio-temporal	Roadtype	16.7	3	0.961
			Wetlands	14.1	-	

In bold the variables that are consistent among models for each species

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6 SUPLEMENTARY MATERIAL

Table S1 - Representing the home range of each species.

Scientific name	Common name	Home range (ha)	Diameter (m)	Reference
L. latrans	Lesser foam frog	0.203	50.96	Henrique & Grant (2019)
R. icterica	Cururu	0.0163	14.43	Caldwell & Shepard (2007)
P.patagoniensis	Green racer snake	0.36	67.80	Hartz *et al.*, (2001)
H. infrataeniatus	Water Snake	0.36	67.80	Hartz *et al.*, (2001)
V. jacarina	Blue-black Grassquit	0.0735	30.63	Aranzamendi (2012)
N. maculosa	Spotted tinamou	19	492.53	Thompson & Carroll (2009)
D. albiventris	White-eared	2.33	172.48	Sanches *et al.* (2012)
M. coypus	Coypu	32.7	550.08	Nolfo-Clements (2009)

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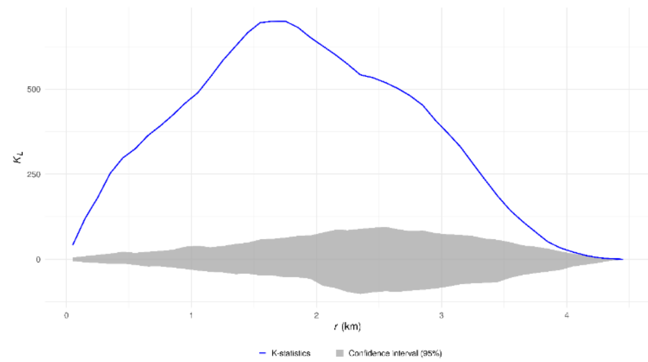
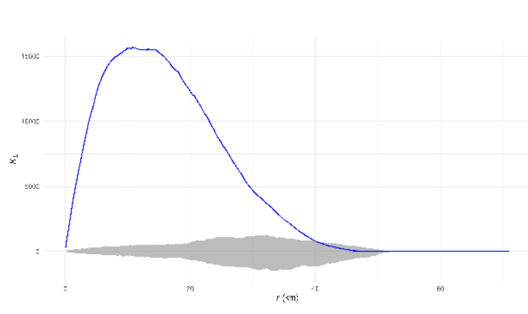
Supplementary Figures

Figure S1: Result of Ripley's K2 test. The L statistic is published as the blue line depending on the radius size; and 95% confidence limits (light gray space). L values above the confidence limits, represent a significant aggregation of hit and roadkill events.

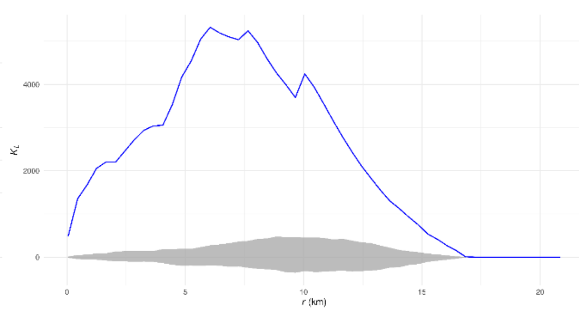
Leptodactylus latrans on the RS389 road.



K2 de Riplay - *Rhinella icterica* in RS 486

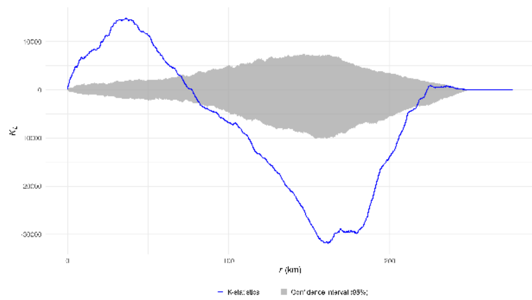


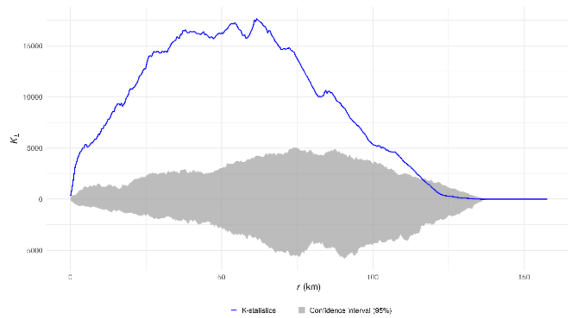
K2 de Riplay - *Rhinella icterica* in CS 012



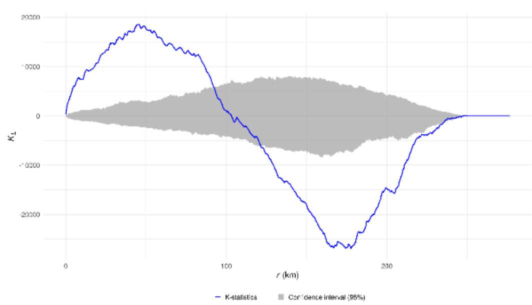
K2 de Riplay – *P. patagoniensis* in BR 101

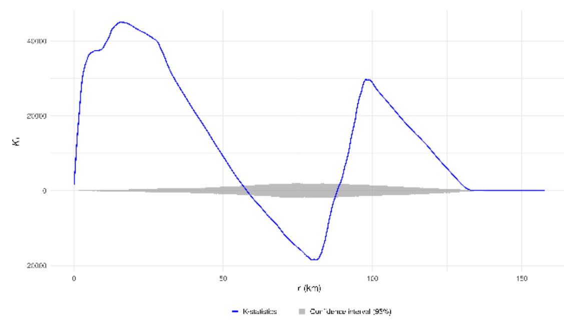
K2 de Riplay – *P. patagoniensis* in BR 471



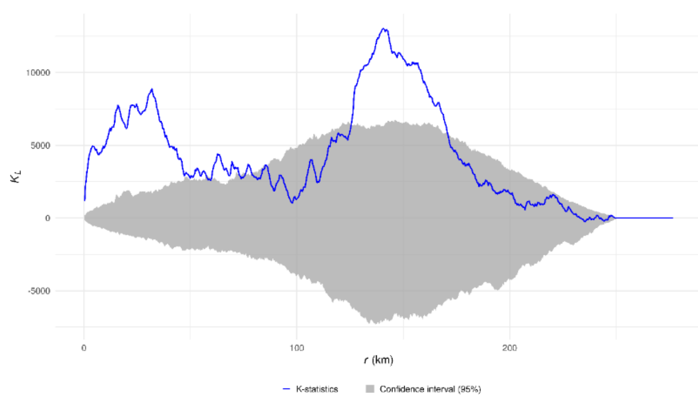


K2 de Riplay - *Helicops infrataeniatus* in BR 101   *Helicops infrataeniatus* in BR 471

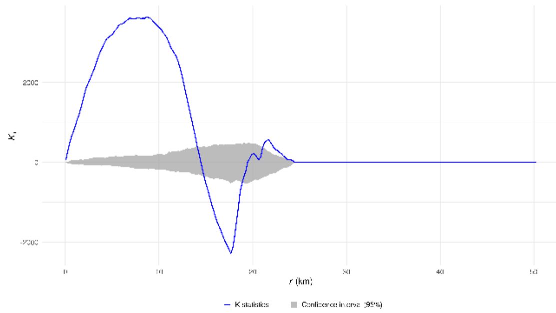


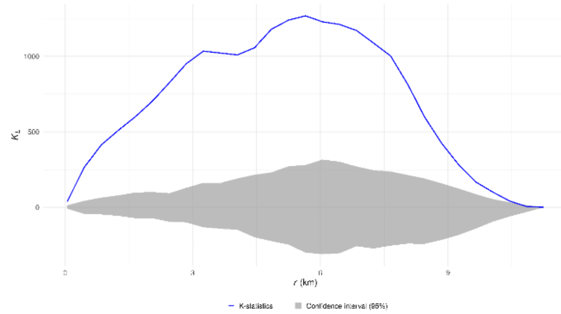


K2 de Riplay – *Nothura maculosa*

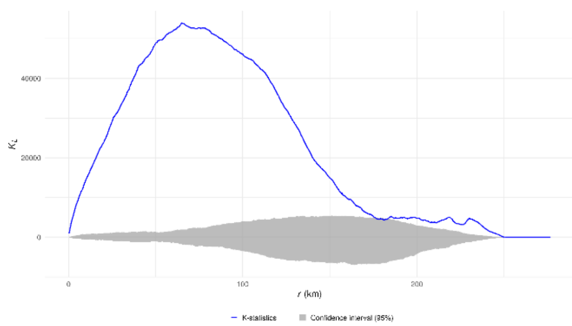


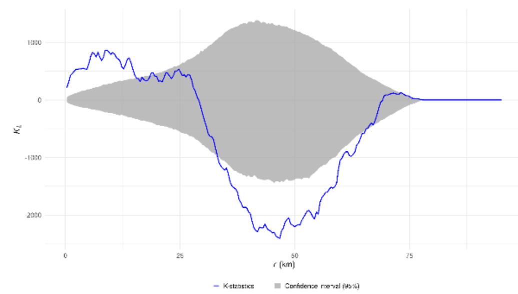
K2 de Riplay – *Volatinia jacarina* in DF 001   K2 de Riplay – *Volatinia jacarina in BR 010*





K2 de Riplay – *D. albiventris* BR 101 K2 de Riplay – *D. albiventris* BR 101 - Osório





K2 de Riplay – *Myocastor coypu*

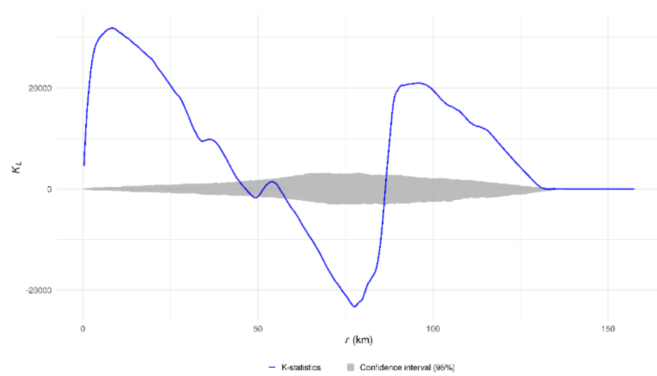
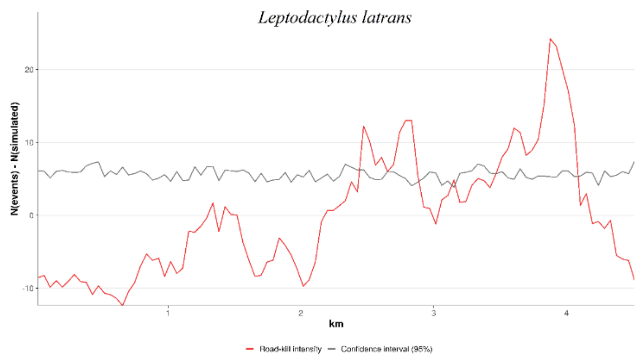
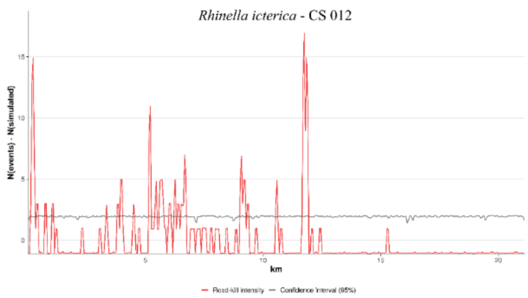


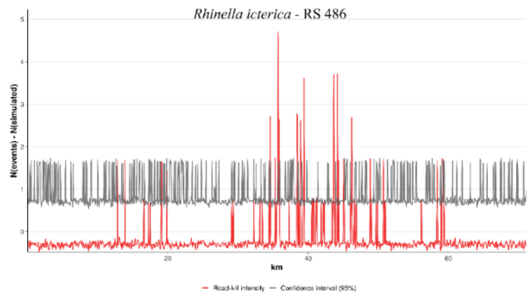
Figure S2: Siriema exit tables indicating the Hotspots, which are in red lines above the confidence interval (gray line) according to the kilometer. For a better quality of the graphics, we used Dornas (2018).



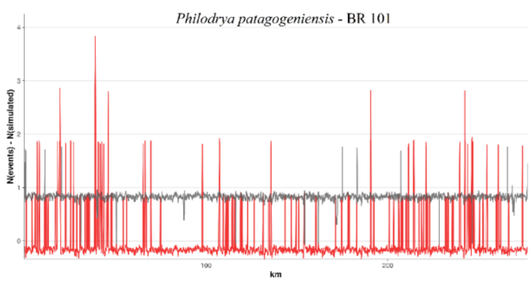
Leptodactylus latrans
N(events) - N(simulated)
km
Road-kill intensity — Confidence interval (95%)



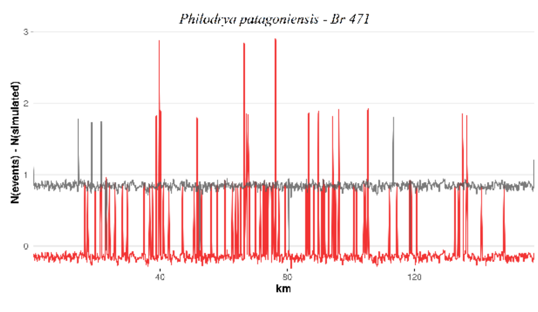
Rhinella icterica - CS 012
N(events) - N(simulated)
km
Road-kill intensity — Confidence interval (95%)



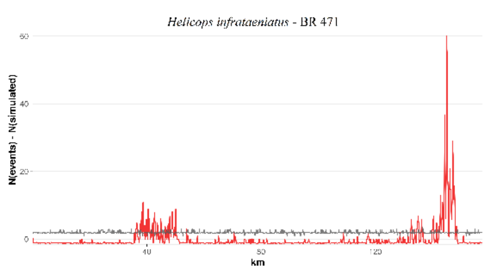
Rhinella icterica - RS 486
N(events) - N(simulated)
km
Road-kill intensity — Confidence interval (95%)



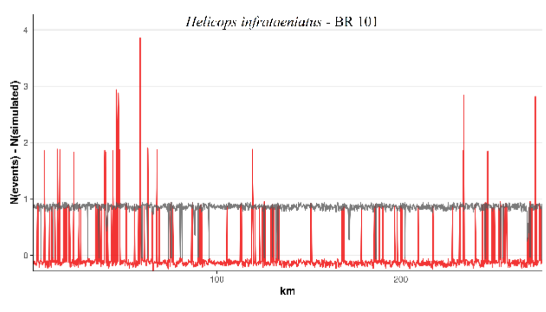
Philodrya patagogeniensis - BR 101
N(events) - N(simulated)
km
Road-kill intensity — Confidence interval (95%)



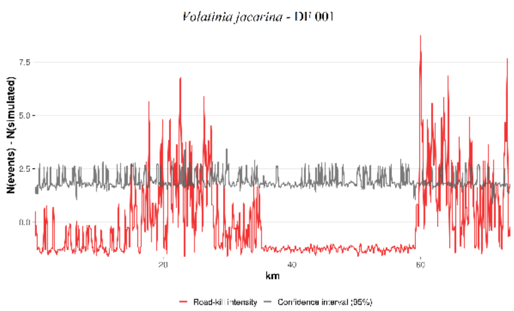
Philodrya patagoniensis - Br 471
N(events) - N(simulated)
km
Road-kill intensity — Confidence interval (95%)

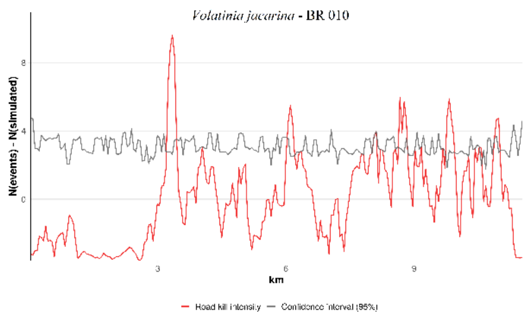


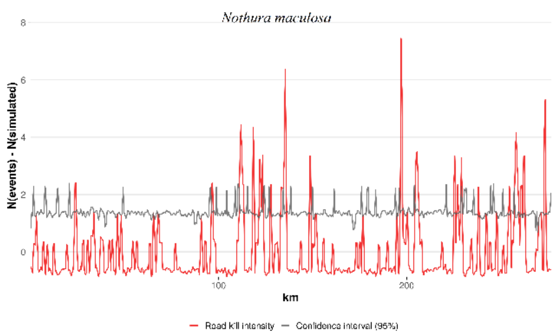
Helicops infrataeniatus - BR 471
N(events) - N(simulated)
km
Road-kill intensity — Confidence interval (95%)

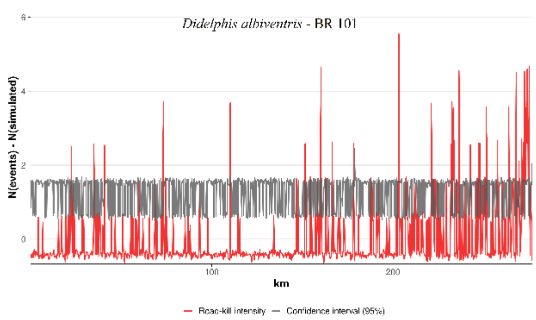


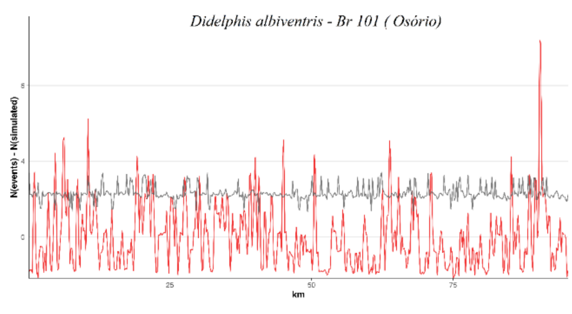
Helicops infrataeniatus - BR 101
N(events) - N(simulated)
km
Road-kill intensity — Confidence interval (95%)

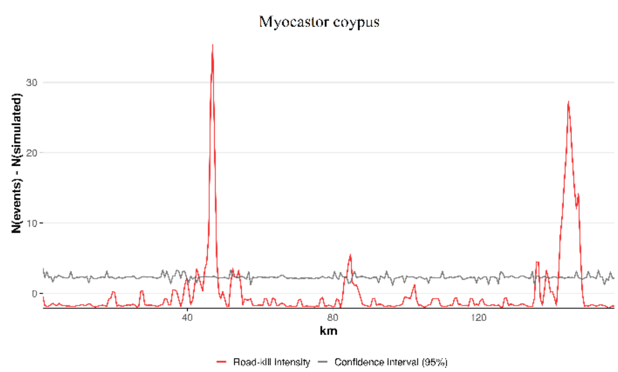










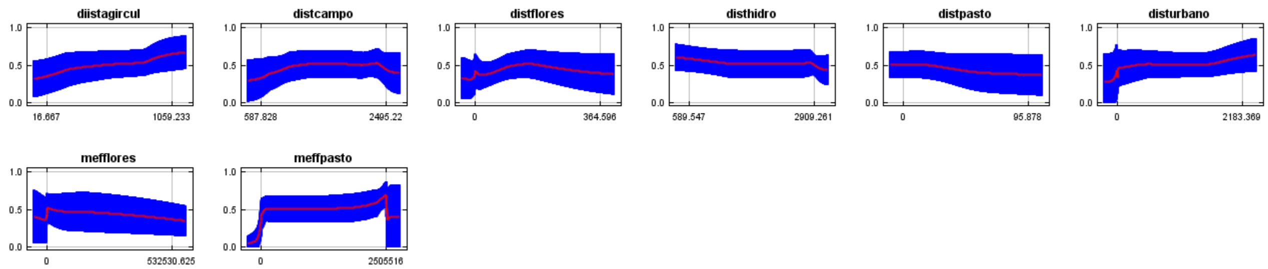


Literature cited

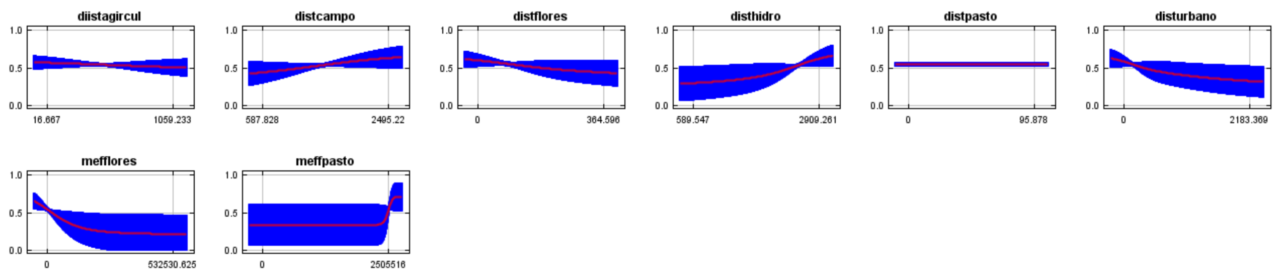
Dornas, Rubem A.P. (2018) Siriema plots. https://rdornas.shinyapps.io/siriema_plots.

Figure S3: These curves show how each environmental variable affects the Maxent prediction. The curves show how the predicted probability of presence changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together.

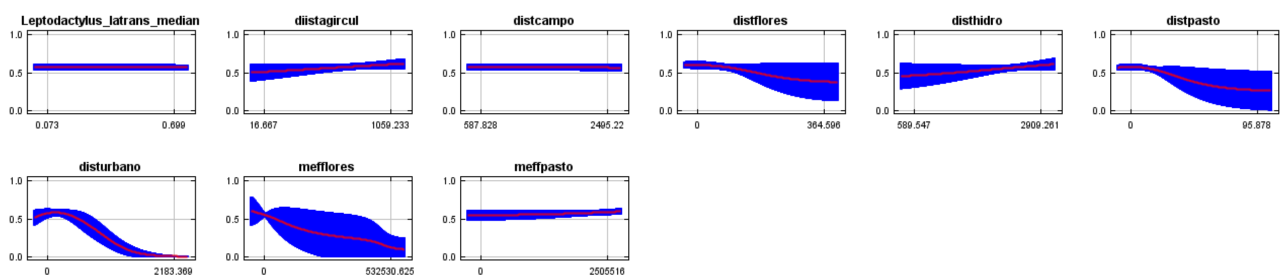
L. latrans - Roadkill



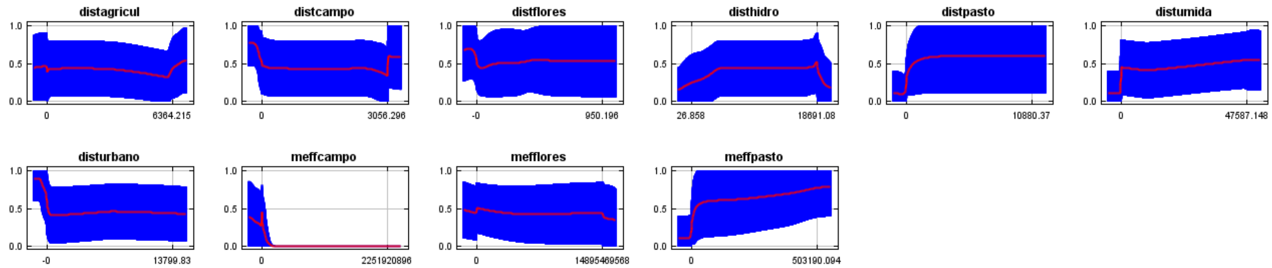
L. latrans - Spatial hotspots



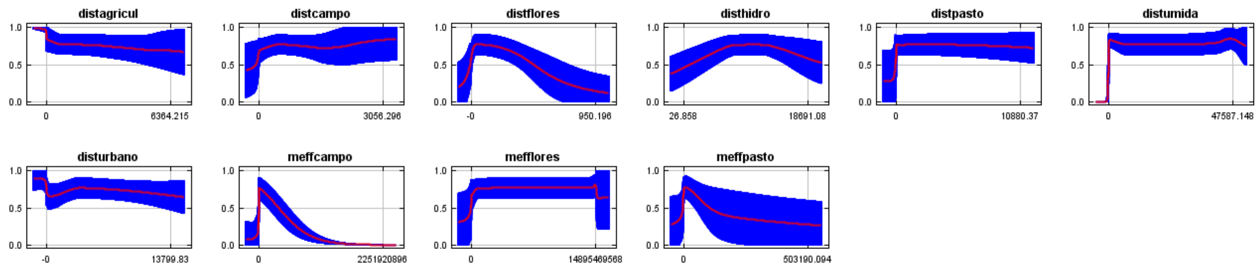
L. latrans – Spatio-temporal hotspots



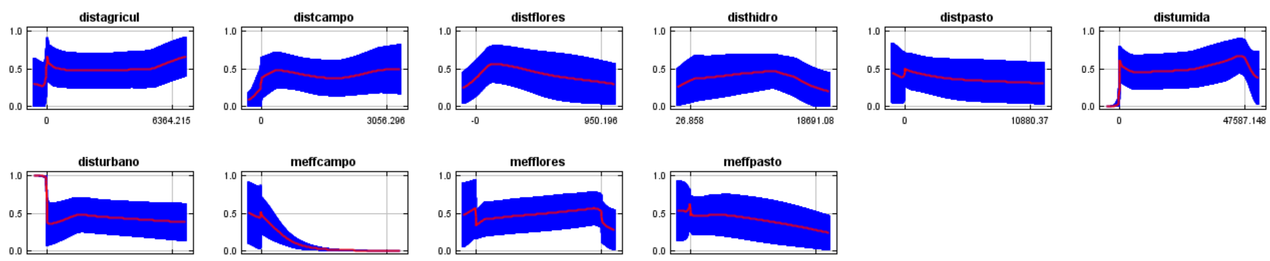
R. icterica - Roadkill



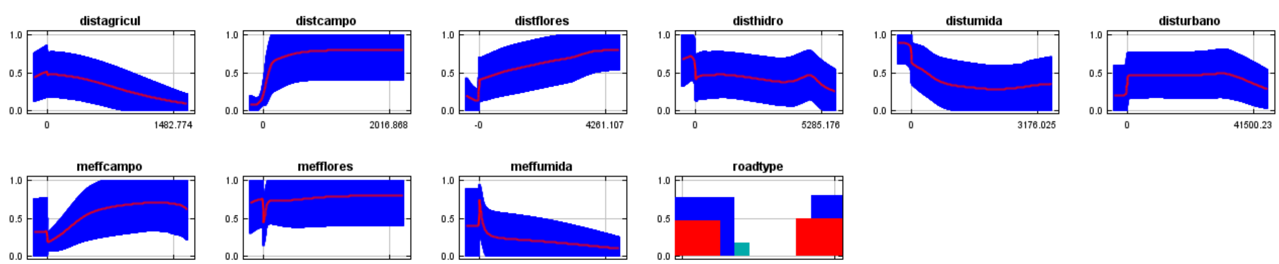
R. icterica - Spatial hotspots



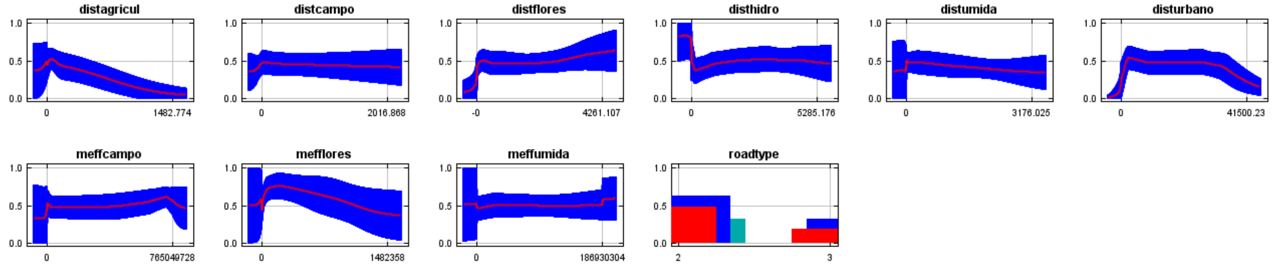
R. icterica – Spatio-temporal hotspots



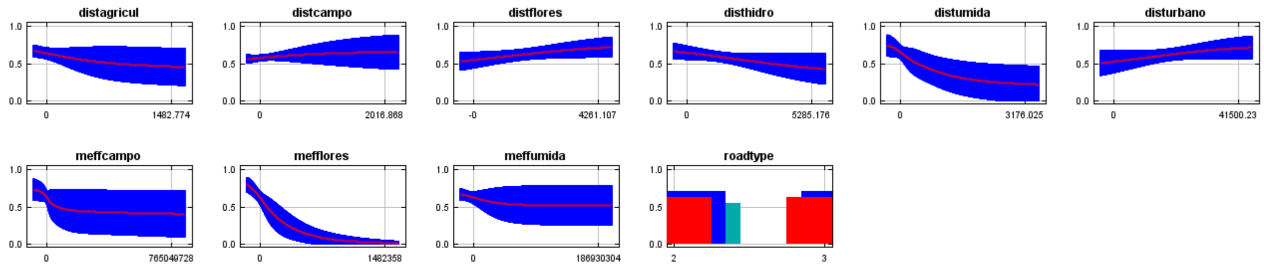
P. patagoniensis - Roadkill



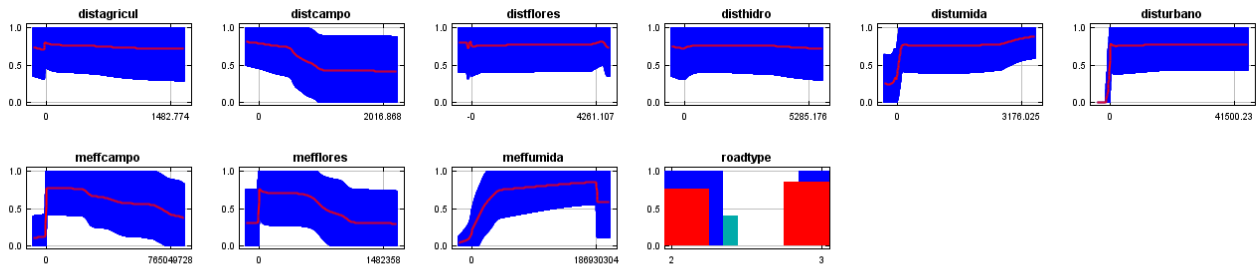
P. patagoniensis – Spatial hotspots



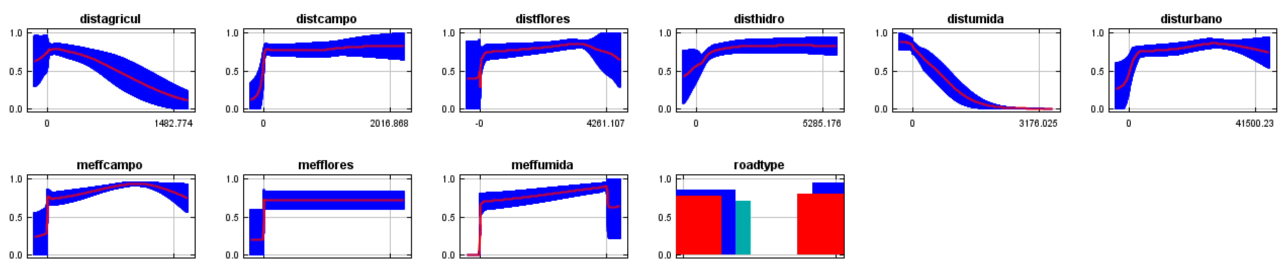
P. patagoniensis – Spatio-temporal hotspots



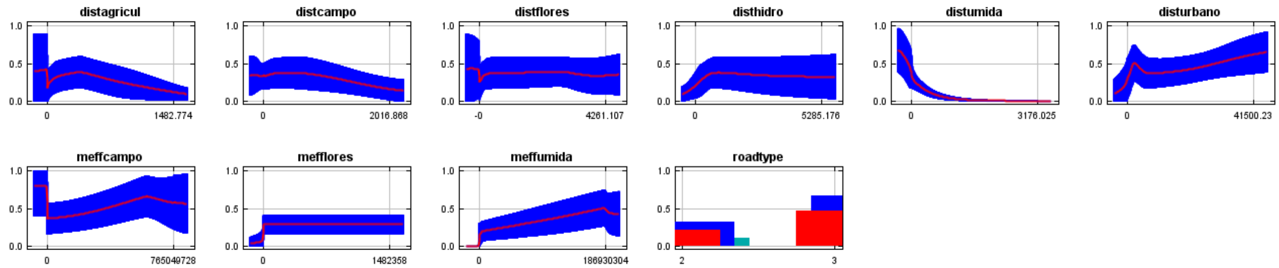
Helicops infrataeniatus - Roadkill



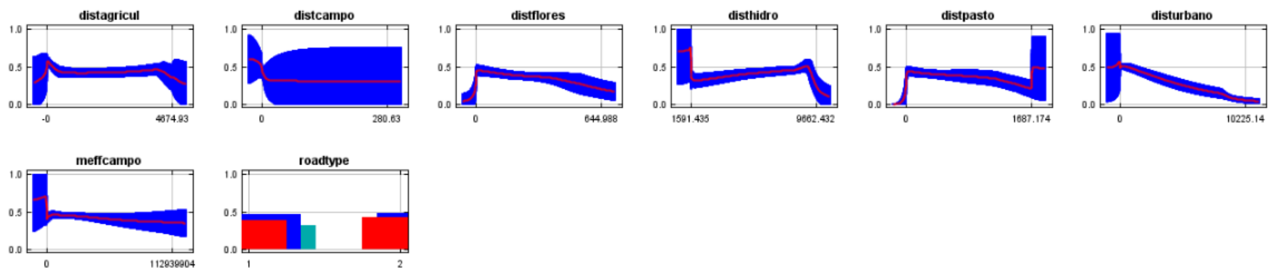
Helicops infrataeniatus – Spatial hotspots



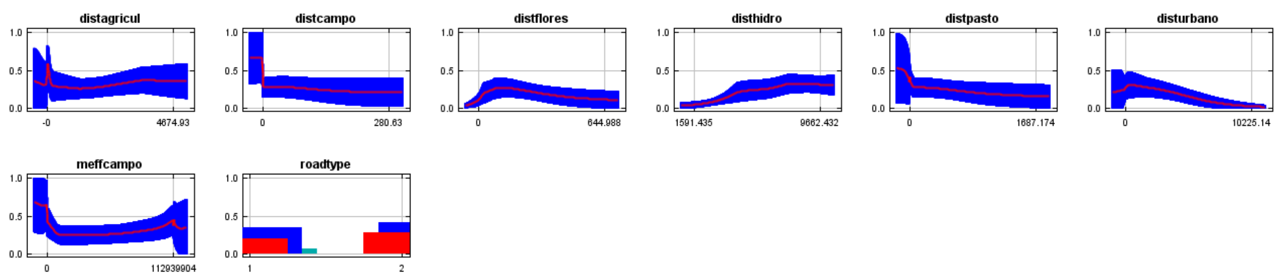
Helicops infrataeniatus – Spatio-temporal hotspots



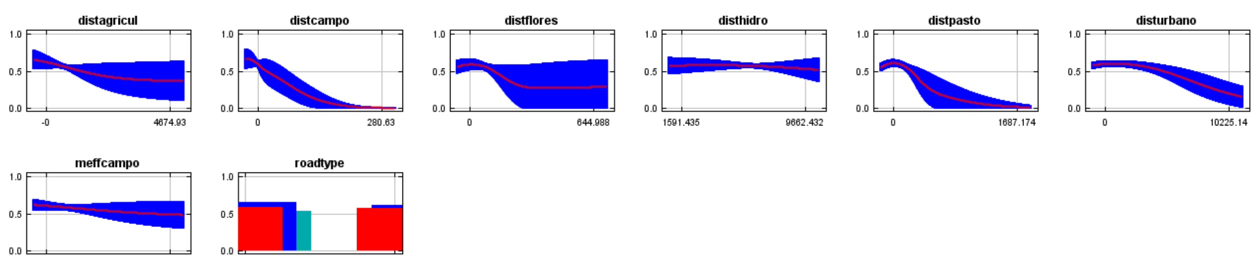
Volatinia jacarina - Roadkill



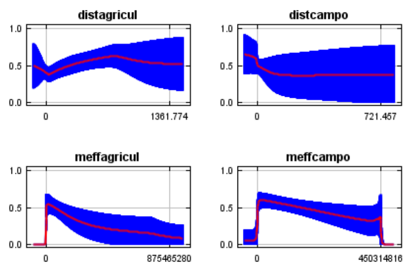
Volatinia jacarina – Spatial hotspots



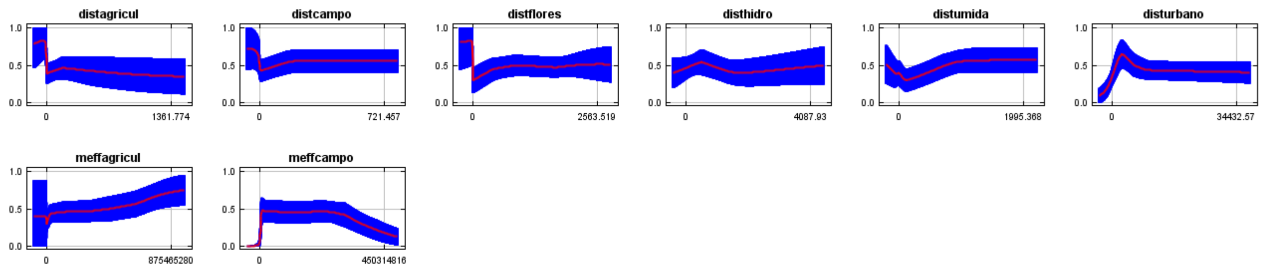
Volatinia jacarina – Spatio-temporal hotspots



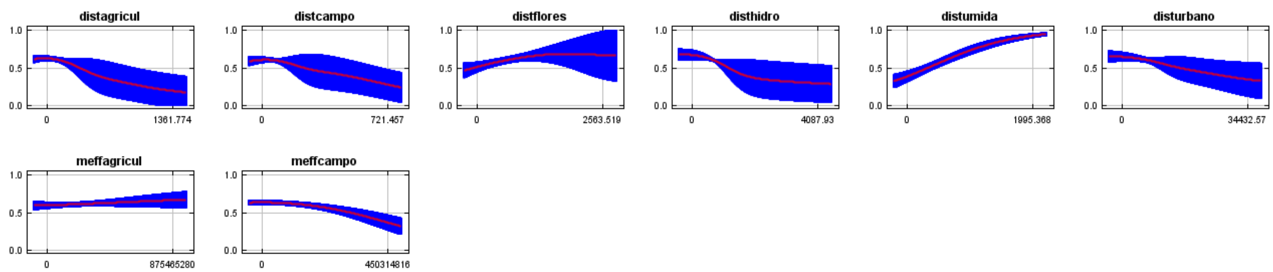
Nothura maculosa - Roadkill



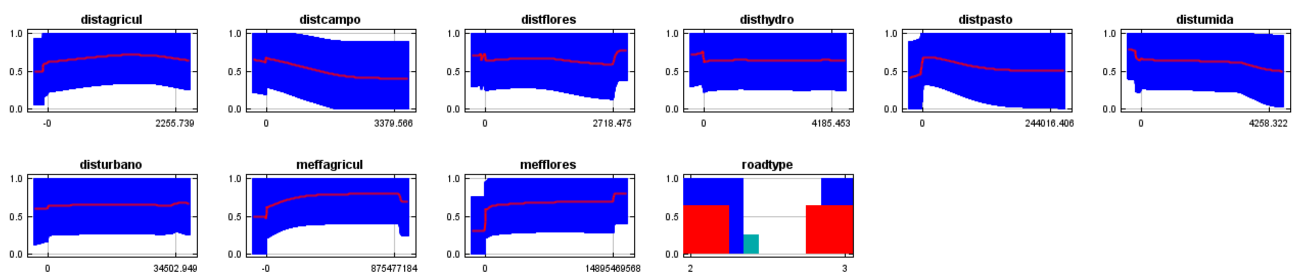
Nothura maculosa - Hotspots



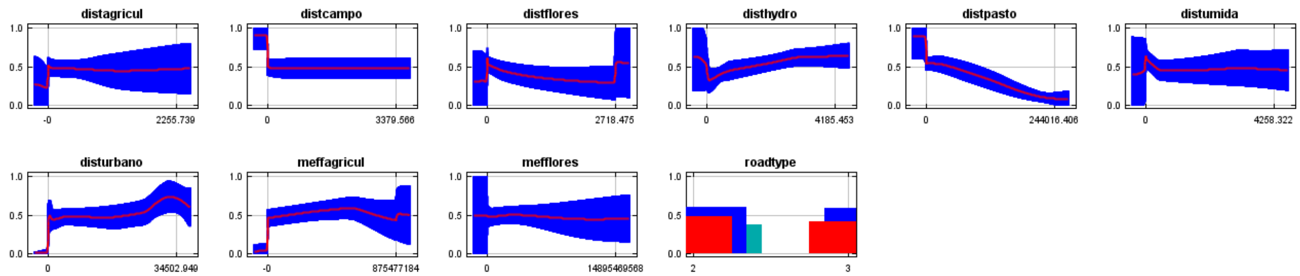
Nothura maculosa – Spatio-temporal hotspots



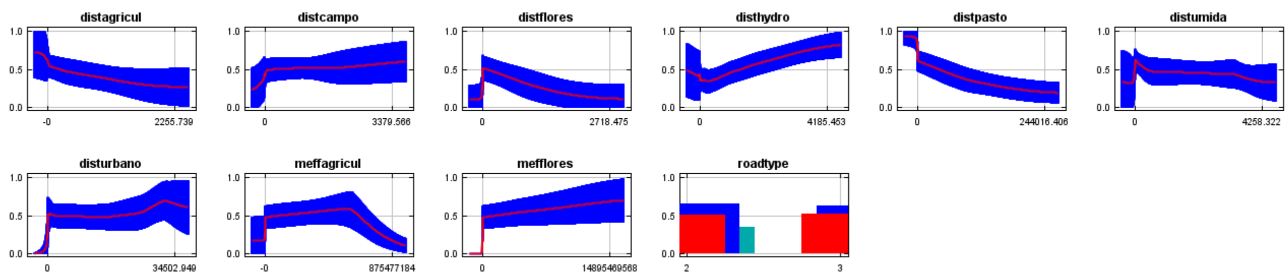
Didelphis albiventris - Roadkill



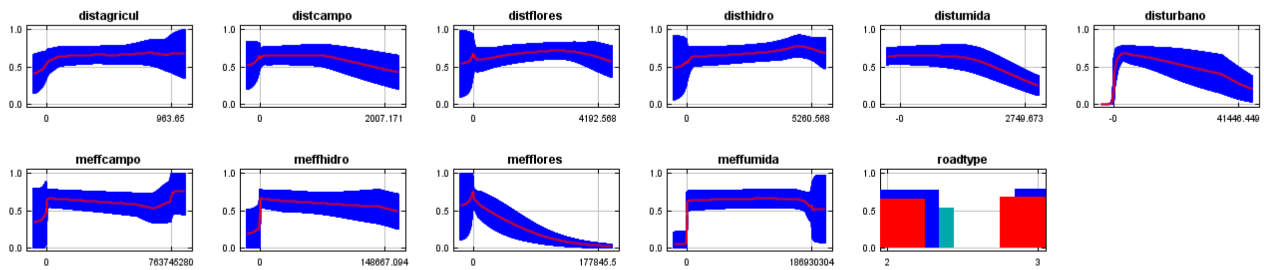
Didelphis albiventris - Spatial hotspots



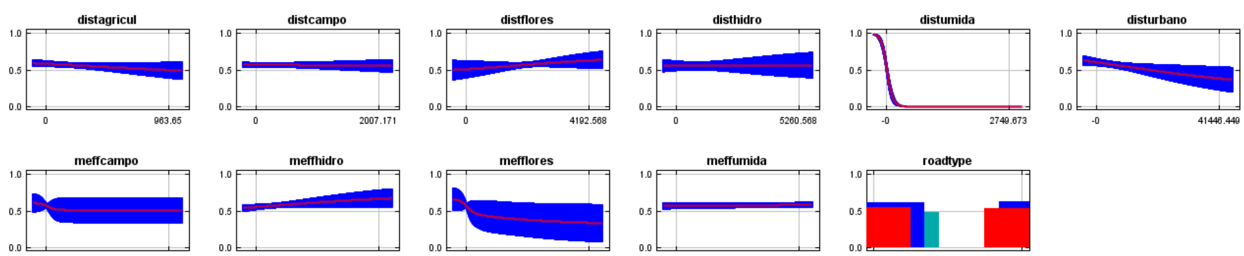
Didelphis albiventris - Spatial / temporal hotspots



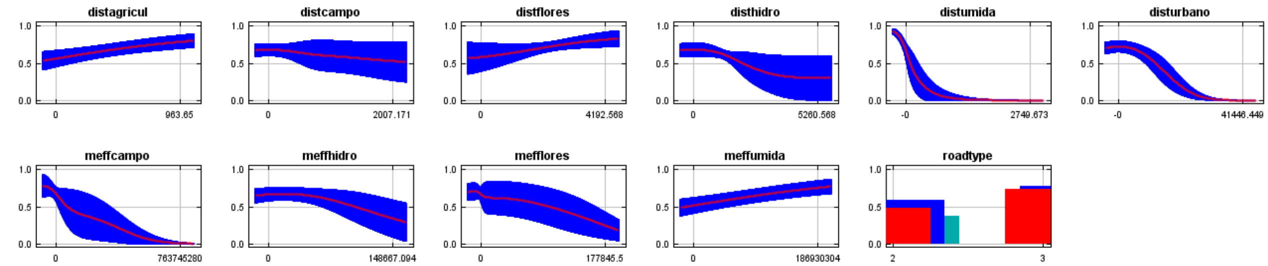
Myocastor coypus - Roadkill



Myocastor coypus - Spatial hotspots



Myocastor coypus – Spatio-temporal hotspots



Supplementary texts

Text S1: The Effective Mesh Size (Meff), which is a metric that is based on the probability that two random points in an area are connected and not separated by barriers, using the formula according to the cross-border connection procedure:

$$\text{meff (cell j)} = \frac{1}{A_{tj}} \sum_{i=1}^{n} A_{ij} \cdot A_{ti\,j},$$

where n is the total number of spots in a cell, *Atj* is the total area of cell *j* (according to the home range of each species), *Aij* is the area of spot *i* within cell *j* and *Atij* is the total area of Patch *i* including the parts that extend beyond the limit of cell *j* (Moser et al. 2007).