

**AVALIAÇÃO DE ESTRATÉGIAS ESPACIAIS PARA OTIMIZAR A  
CONSERVAÇÃO DE REDES DE HABITAT**

Milena Fiuza Diniz

Goiânia  
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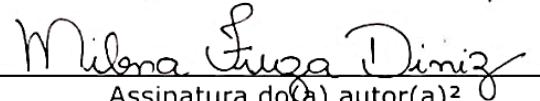
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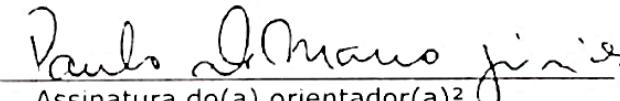
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**INSTITUTO DE CIÊNCIAS BIOLÓGICAS  
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Milena Fiuza Diniz

Tese apresentada à Universidade Federal de Goiás como parte das exigências do Programa de Pós-graduação em Ecologia e Evolução para obtenção do título de Doutor em Ecologia e Evolução.

Orientador: Prof. Dr. Paulo De Marco Júnior  
Co-orientador: Prof. Dr. Arthur Bispo

Goiânia  
Março 2019

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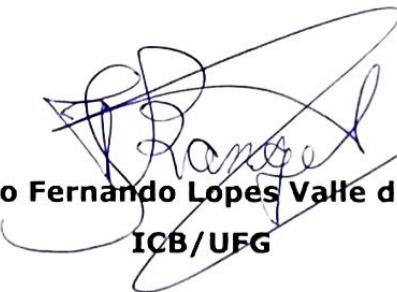
**ATA DA SESSÃO PÚBLICA DE DEFESA DE TESE Nº 83**

Aos vinte e nove dias do mês de março de 2019 (29/03/2019), às oito horas e trinta minutos (8h30minh), na sala 13 do ICB IV, UFG, reuniram-se os componentes da banca examinadora: **Prof. Dr. Paulo De Marco Júnior, ICB/UFG; Prof. Dr. José Alexandre Felizola Diniz Filho, ICB/UFG; Prof. Dr. Thiago Fernando Lopes Valle de Britto Rangel, ICB/UFG; Prof. Dr. Milton Cezar Ribeiro, UNESP/Rio Claro (via videoconferência); Prof. Dr. Daniel De Paiva Silva, IFGoiano/Urutáí;** em sessão pública presidida pelo (a) primeiro(a) examinador(a) citado(a), procederem à avaliação da defesa de tese intitulada: **"Avaliação de estratégias espaciais para otimizar a conservação de redes de habitat"**, em nível de doutorado, área de concentração em Ecologia e Evolução, de autoria de **Milena Fiuza Diniz**, discente do Programa de Pós-Graduação em Ecologia e Evolução da Universidade Federal de Goiás. A sessão foi aberta pelo(a) presidente(a), que fez a apresentação formal dos membros da banca. A palavra, a seguir, foi concedida a(o) autor(a) da tese que, em cerca de 50 minutos, procedeu à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu a(o) examinada(o), tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, procedeu-se à avaliação da tese. Tendo-se em vista o que consta na Resolução nº 1127 de dezembro de 2012 do Conselho de Ensino, Pesquisa, Extensão e Cultura (CEPEC), que regulamenta o Programa de Pós-Graduação em Ecologia e Evolução, a tese foi Aprovada, considerando-se integralmente cumprido este requisito para fins de obtenção do título de Doutor(a) em Ecologia e Evolução pela Universidade Federal de Goiás. A conclusão do curso dar-se-á quando da entrega da versão definitiva da tese na secretaria do programa, com as devidas correções sugeridas pela banca examinadora, no prazo de trinta dias a contar da

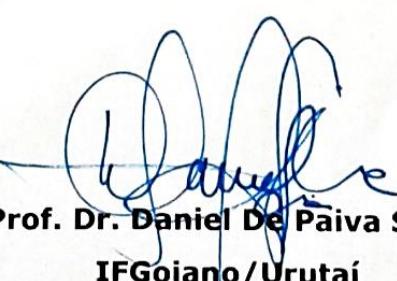
data da defesa. Cumpridas as formalidades de pauta, às 12 h e 50 min., encerrou-se a sessão de defesa e, para constar, eu, Suely Ana Ribeiro, secretária executiva da Universidade Federal de Goiás - UFG, lavrei a presente ata que, após lida e aprovada, será assinada pelos membros da banca examinadora em três vias de igual teor.

  
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*“You, me, or nobody is gonna hit as hard as life. But it ain't about how hard you hit. It's about how hard you can get hit and keep moving forward. How much you can take and keep moving forward. That's how winning is done!” Rocky Balboa*

*Aos três pilares da minha vida, Jocelaine, Mirla e Renato.*

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## SUMÁRIO

RESUMO .....	12
ABSTRACT .....	13
GRAPHICAL ABSTRACTS: COMIC STRIPS .....	14
INTRODUÇÃO GERAL .....	17
REFERENCES .....	21
<b>Capítulo 1.</b> Landscape connectivity modeling from the perspective of animal dispersal .....	25
RESUMO .....	27
ABSTRACT .....	28
INTRODUCTION .....	29
How do the models work? .....	32
How is connectivity assessed through the models? .....	46
What are the main applications of the models in conservation planning? .....	48
What are the main assumptions and limitations of models when representing animal dispersal? .....	51
Which model best explains real-world movement data? .....	62
Synthesis and Future Directions .....	64
REFERENCES .....	67
<b>Capítulo 2.</b> Evaluating analytical tools for designing multispecies habitat network .....	75
RESUMO .....	77
ABSTRACT .....	78
INTRODUCTION .....	79
METHODS .....	82
RESULTS .....	90
DISCUSSION .....	96
REFERENCES .....	100
Supplementary Material 1 .....	105
Supplementary Material 2 .....	112
<b>Capítulo 3.</b> Can we face different types of storms under the same umbrella? Efficiency and consistency of connectivity umbrellas across different patchy landscape patterns .....	114

RESUMO.....	116
ABSTRACT.....	117
INTRODUCTION .....	118
METHODS .....	123
RESULTS .....	128
DISCUSSION.....	132
REFERENCES .....	139
Supplementary Material.....	144
<b>Capítulo 4.</b> Performance of different species-based surrogates to design habitat networks .....	148
RESUMO.....	149
ABSTRACT.....	150
INTRODUCTION .....	151
METHODS .....	153
RESULTS .....	158
DISCUSSION.....	162
REFERENCES .....	165
CONCLUSÕES.....	168

## **RESUMO**

A perda e fragmentação de habitat têm se tornado fatores onipresentes ao longo das paisagens naturais em todo o mundo, e estão entre as principais ameaças à biodiversidade. Em regiões intensamente modificadas pela ação humana, o manejo de áreas isoladas pode ser insuficiente para atingir os objetivos de conservação. Por isso, uma solução mais eficiente pode ser alcançada através do delineamento de redes de habitat, onde as áreas protegidas atuam de forma cooperativa e sinérgica para garantir a persistência regional das espécies. A projeção de redes de habitat requer uma série de etapas metodológicas, todas as quais podem ser desenvolvidas através de diferentes abordagens. O principal objetivo desta tese foi preencher importantes lacunas relacionadas à seleção de espécies substitutas e estratégias metodológicas para otimizar a projeção de redes de habitat. No Capítulo 1, nós revisamos a estrutura e aplicações dos principais modelos de conectividades, destacando seus pressupostos e limitações ao representar a dispersão animal. Nós observamos que os modelos possuem fundamentos e arcabouços próprios e ao escolhermos uma abordagem em particular, estamos assumindo diferenças importantes sobre a ecologia de dispersão das espécies. No Capítulo 2, nós avaliamos a congruência espacial entre redes de habitat derivadas a partir da combinação de diferentes modelos de conectividade e algoritmos de priorização. Nós mostramos que a escolha da estratégia metodológica para projeção de redes de habitats pode ser decisiva para a representação das espécies-alvo. Por isso, sugerimos que as ferramentas analíticas sejam selecionadas de acordo com os objetivos de conservação, ao invés de arbitrariamente, assumindo equivalência entre os diferentes métodos. No Capítulo 3, nós investigamos se o potencial de espécies como guarda-chuvas para conservação da conectividade poderia ser influenciado pela composição e configuração das paisagens. Nós mostramos que a capacidade das espécies para representarem áreas importantes para conectividade de outras é uma propriedade determinada tanto pelas características das espécies quanto pelo padrão espacial de habitat das paisagens. No Capítulo 4, nós construímos redes de qualidade de habitat e conectividade usando diferentes estratégias substitutas baseadas em uma e múltiplas espécies e avaliamos a eficiência dessas estruturas em representar os requerimentos espaciais das espécies-alvo. Nós encontramos que prioridades de conservação identificadas a partir das demandas de uma única espécie guarda-chuva podem ter uma eficiência muito variável em abranger as necessidades das espécies-alvo. Também mostramos que a seleção de algumas espécies com base na diversidade de características ecológicas do conjunto total de espécies pode ser a melhor estratégia para fornecer soluções de conservação eficientes. Nós esperamos que os resultados dessa tese possam ser usados para orientar a seleção futura de espécies substitutas, bem como as decisões relacionadas às estratégias metodológicas mais apropriadas para projetar redes de habitat capazes de garantir a conservação de múltiplas espécies.

**PALAVRAS-CHAVE:** espécie guarda-chuva, fragmentação, modelos de conectividade, perda de habitat, prioridades de conservação, redes de habitat

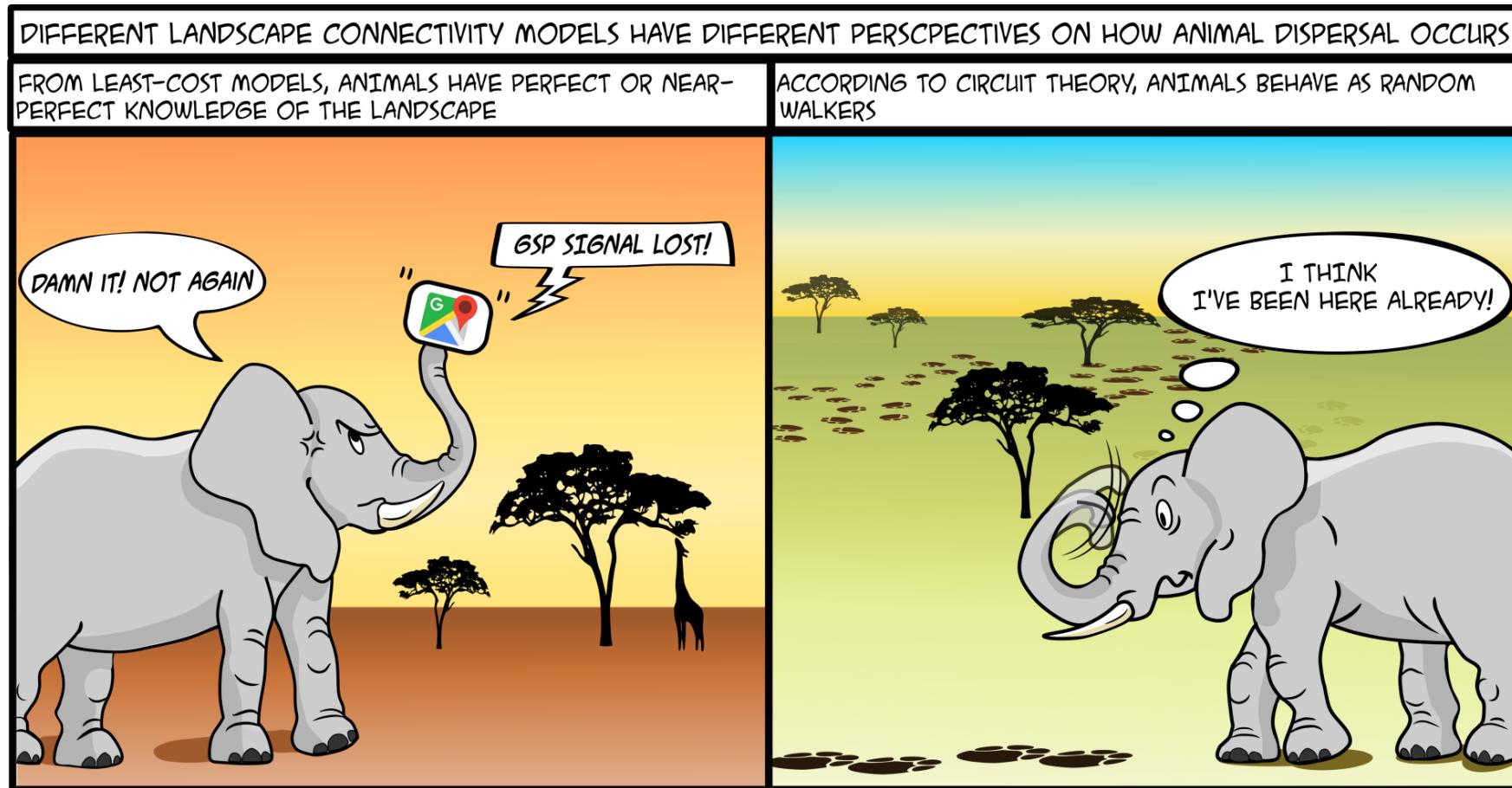
## **ABSTRACT**

Habitat loss and fragmentation have become ubiquitous factors throughout natural landscapes around the world, and are among the major threats to biodiversity. In regions intensely modified by human activity, management of isolated areas may be insufficient to achieve conservation objectives. Therefore, a more efficient solution can be achieved by designing habitat networks, where protected areas and the connections among them act cooperatively and synergistically to ensure the species' regional persistence. Designing a habitat network requires a series of methodological steps, all of which can be developed through different approaches. The main objective of this thesis was to fill important gaps related to the selection of surrogate species and methodological strategies to optimize the projection of habitat networks. In Chapter 1, we reviewed the structure and applications of the major connectivity models, highlighting their assumptions and limitations in representing animal dispersal. We noted that the models have their own foundations and frameworks, and therefore we are assuming important differences on the dispersal ecology of species when choosing a particular approach. In Chapter 2, we evaluated the spatial congruence between habitat networks derived from the combination of different connectivity models and prioritization algorithms. We showed that the choice of methodological strategies for the projection of habitat networks can be decisive for the target species representation. Therefore, we suggested that the analytical tools should be selected according to the conservation objectives, rather than arbitrarily by assuming equivalence between the different methods. In Chapter 3, we investigated whether the potential of species as umbrellas for connectivity conservation can be influenced by the landscape composition and configuration. We showed that the ability of species to represent important areas for connectivity of others is a property determined by the species characteristics, as well as by the spatial pattern of habitat in the landscapes. In Chapter 4, we constructed networks of habitat quality and connectivity using different surrogate strategies based on one and multiple species and evaluated the efficiency of these structures in representing the target species' spatial requirements. We found that determining conservation priorities from the demands of a single umbrella species can have a very variable efficiency in covering the needs of co-occurring species. We also showed that selecting a small set of surrogates based on the species pool diversity may be the best strategy to provide efficient conservation solutions. We hope that the results of this thesis can be used to guide the future selection of surrogate species as well as the decisions related to the most appropriate methodological strategies for designing habitat networks capable of ensuring multispecies conservation.

**KEYWORDS:** umbrella species, fragmentation, connectivity models, habitat loss, conservation priorities, habitat networks

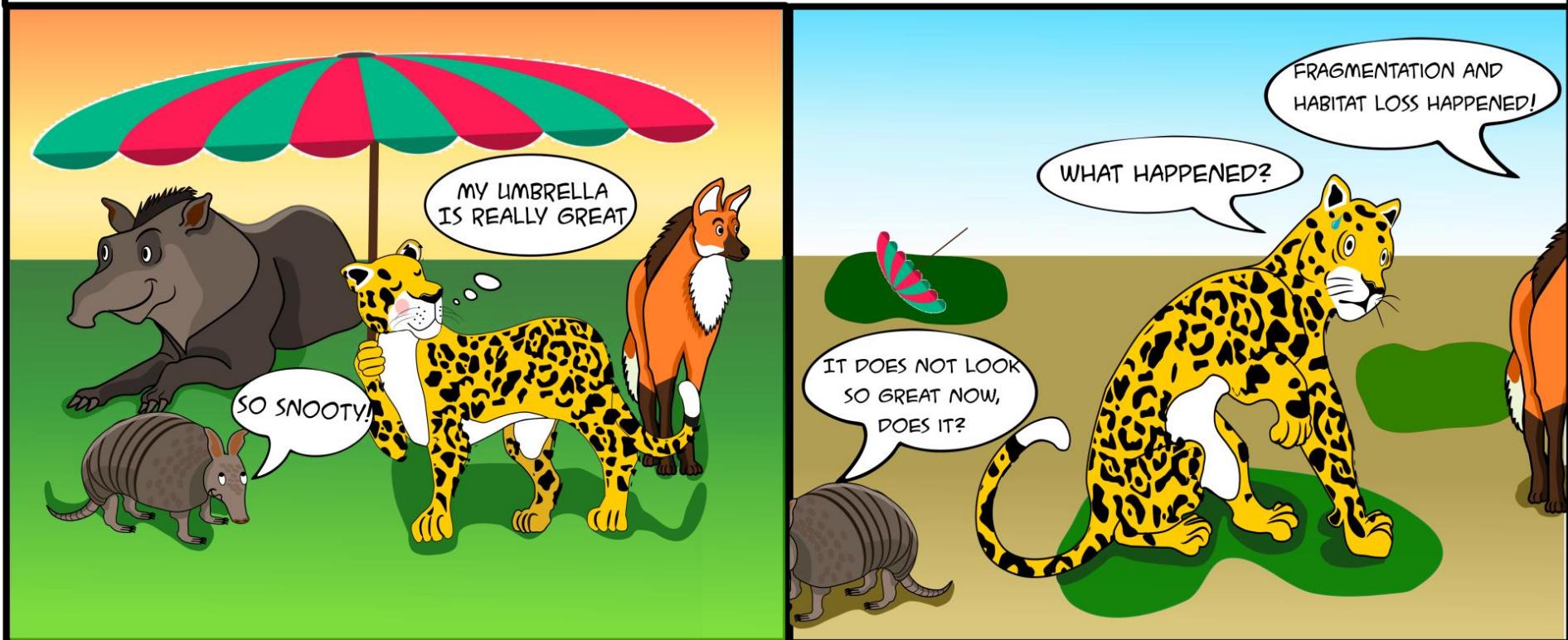
## GRAPHICAL ABSTRACTS: COMIC STRIPS

### Chapter 1 and 2

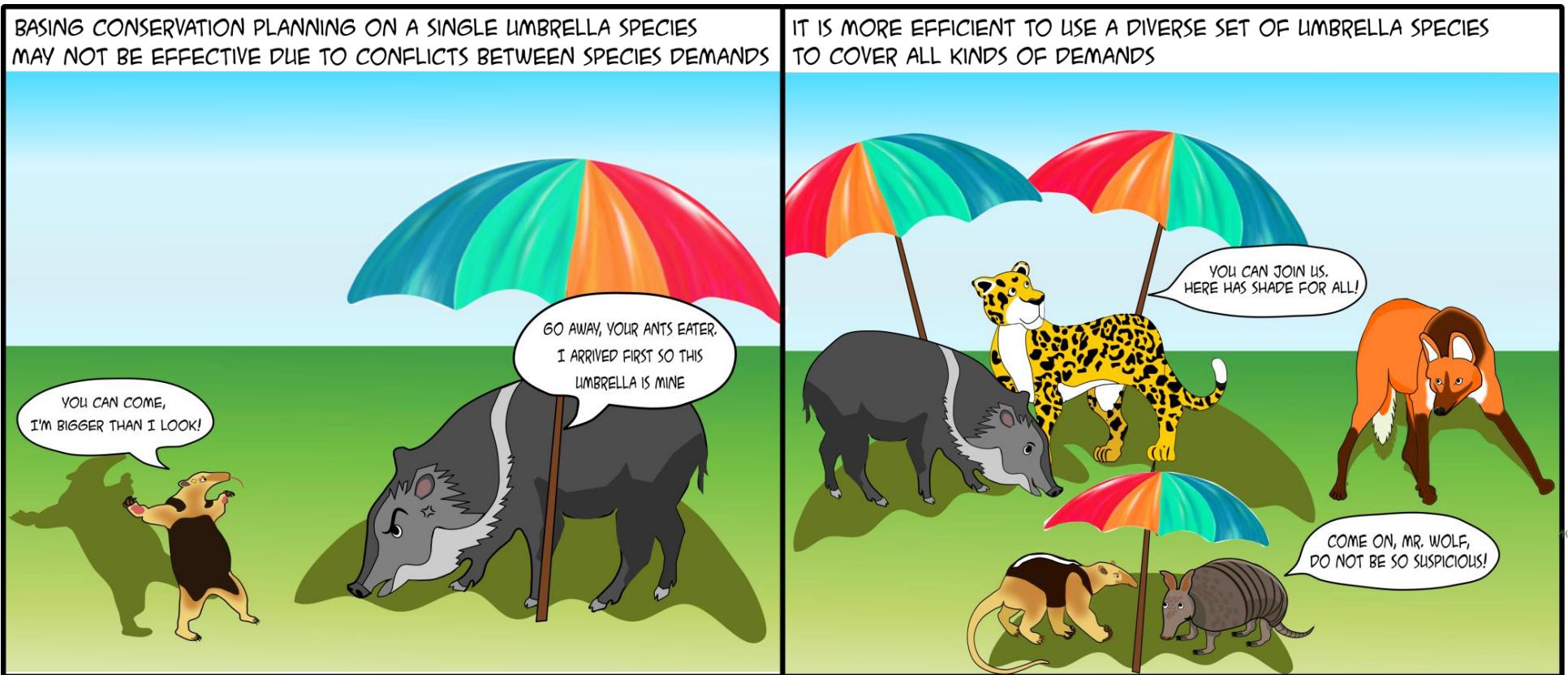


## Chapter 3

THE POTENTIAL OF A SPECIES AS AN UMBRELLA TO THE OTHERS IS NOT A STATIC FEATURE THAT DEPENDS ONLY ON ITS TRAITS, BUT A DYNAMIC PROPERTY THAT ALSO VARIES ACCORDING TO LANDSCAPE PATTERNS



## Chapter 4



## **INTRODUÇÃO GERAL**

A intensa ocupação humana tem levado a uma transformação severa e em larga escala das paisagens naturais (Ellis et al. 2010; Hansen et al. 2013; Gibbs and Salmon 2015). A exploração descontrolada dos ecossistemas tem tornado a perda e a degradação de habitat fatores praticamente onipresentes nas listas das principais ameaças à persistência das espécies (Brooks et al. 2002; IUCN 2018). Diante de um cenário iminente de perda de biodiversidade, o estabelecimento de áreas protegidas tem sido identificado como uma das principais ferramentas de conservação capaz de mitigar as mudanças ambientais causadas pelo homem (Saout et al. 2013). No entanto, o potencial de um conjunto de áreas destinadas a manter a integridade dos sistemas naturais será determinado de acordo com dois objetivos gerais de conservação, o objetivo da persistência e da representatividade (Margules and Pressey 2000). Isso significa que um sistema de áreas protegidas deve representar adequadamente a biodiversidade e garantir a manutenção dos seus componentes no longo prazo (Margules and Pressey 2000). Assim, antes de designar áreas de conservação, os planejadores devem tomar uma série de decisões sobre o que e como proteger, selecionando os componentes da biodiversidade nos quais os esforços de conservação serão concentrados e determinando as estratégias de manejo necessárias para sustentá-los de maneira duradoura (Shafer 1999; Margules and Pressey 2000).

A fim de assegurar a persistência dos componentes da biodiversidade, é necessário determinar quais as melhores estratégias para delinear ou ampliar os sistemas de áreas protegidas de forma eficiente. Como vivemos em um mundo de habitats cada vez mais fragmentados (Haddad et al. 2014), alcançar o objetivo da persistência tem se tornado uma tarefa desafiadora. Em paisagens severamente fragmentadas dominadas pela ação humana, a vegetação nativa tem sido reduzida a pequenas ilhas de manchas de habitat espalhadas por um vasto oceano de matrizes antropizadas. Portanto, a maioria das áreas protegidas consideradas isoladamente não possui habitat suficiente para abrigar populações viáveis de muitas espécies, mesmo que por algumas gerações (e.g. Brito et al. 2008; Diniz and Brito 2015). Como os objetivos de conservação nesses cenários podem não ser alcançados pelo manejo de unidades de conservação como entidades isoladas, a adoção de redes de habitat onde essas unidades atuam de forma cooperativa e

sinérgica para prover a persistência regional das espécies pode ser uma solução mais eficiente (Hanski 1999; Rudnick et al. 2012; Baguette et al. 2013). Uma rede bem conectada de áreas protegidas pode expandir o habitat disponível para as populações, reduzindo assim o risco de extinção regional devido à estocasticidade demográfica e ambiental, e à erosão genética (Hanski 1999; Rudnick et al. 2012; Baguette et al. 2013). Portanto, a conectividade da paisagem, definida como “o grau com que a paisagem facilita ou impede o movimento de organismos entre manchas de recursos” (Taylor et al. 1993), tem ganhado crescente destaque nos estudos ecológicos e tem sido considerado um elemento essencial no planejamento da conservação (Rudnick et al. 2012). Nas últimas duas décadas, muitos algoritmos foram desenvolvidos com o objetivo de mapear padrões de conectividade através da modelagem de rotas de movimento dos organismos (Rudnick et al. 2012; Kool et al. 2013; Dickson et al. 2018). Portanto, um passo crucial na projeção de redes de habitat é definir a partir de qual perspectiva a conectividade será avaliada. Assim, no **CAPÍTULO 1**, nós fornecemos uma revisão detalhada dos pressupostos sobre a dispersão animal por trás dos principais modelos de conectividade como forma de orientar a escolha da ferramenta mais adequada para a representação do processo dispersivo.

A projeção de redes de habitats para múltiplas espécies ainda requer a definição do método de priorização através do qual os cenários gerados para cada espécie serão processados para produzir uma única estrutura espacial resumindo as demandas de todas as espécies-alvo. Uma das abordagens mais comuns é delinear individualmente redes de habitat para cada espécie e adicioná-las para obter um mapa de consenso das prioridades de conservação (e.g. Cushman and Landguth 2012). Uma solução de conservação alternativa pode ser obtida através do uso do software Zonation (Moilanen et al. 2005), uma ferramenta desenvolvida para a priorização de habitat que permite delinear redes de reserva conectadas considerando os valores de conservação espacial dos pixels da paisagem para várias espécies simultaneamente. Embora os modelos de conectividade e os métodos de priorização pareçam ser usados de forma intercambiável na projeção de redes de habitat, diferentes abordagens podem fornecer diferentes soluções de conservação para um mesmo problema (Avon and Bergès 2016). Portanto, no **CAPÍTULO 2**, nós investigamos a congruência entre as soluções de conservação fornecidas por redes de habitat projetadas a partir de diferentes estratégias

metodológicas. Além disso, nós avaliamos o desempenho dessas estruturas espaciais em representar os requisitos individuais das espécies-alvo.

Idealmente, para alcançar a meta de representatividade, as áreas protegidas deveriam abranger todos os aspectos, ou pelo menos uma amostra representativa, da biodiversidade (Margules and Pressey 2000). No entanto, incorporar toda a biodiversidade de uma região no planejamento da conservação não é uma tarefa factível. Na prática, planejadores e gestores geralmente tomam decisões de conservação com base em substitutos ecológicos. O uso desses atalhos de conservação pressupõe que a representação de aspectos não alvos de um sistema ecológico pode ser alcançada ou que informações sobre esses aspectos podem ser acessadas quando certos componentes da biodiversidade são escolhidos como alvos de conservação (Caro 2010; Hunter et al. 2016). Os substitutos ecológicos são selecionados de acordo com os objetivos de conservação e geralmente são classificados como substitutos indicadores, se usados para o monitoramento ambiental, ou substitutos de manejo, quando sua função principal é informar estratégias de manejo (Hunter et al. 2016). Elementos ou processos da biodiversidade, como espécies, assembleias, ecossistemas, funções ecossistêmicas, ou mesmo fatores abióticos, podem ser usados como substitutos (Hunter et al. 2016). O uso de espécies únicas como substitutos ecológicos é uma estratégia comumente adotada para determinar o projeto de sistemas de áreas protegidas (e.g., Crosby et al. 2015; Albert et al. 2017; Wang et al. 2018). Na abordagem espécie guarda-chuva, por exemplo, os requisitos necessários para a conservação de uma única espécie podem ser usados para determinar o tamanho e a configuração de reservas (Roberge and Angelstam 2004; Caro 2010). Propõe-se que ações de conservação objetivando garantir a persistência das espécies guarda-chuva também beneficiem a conservação de inúmeras espécies co-ocorrentes (Roberge and Angelstam 2004; Caro 2010). Tradicionalmente, as espécies guarda-chuva têm sido usadas para definir limiares para a conservação de habitats primários, como locais de reprodução ou de forrageamento (Roberge and Angelstam 2004; Caro 2010; Breckheimer et al. 2014).

No contexto da conectividade da paisagem, uma espécie guarda-chuva é definida como “uma espécie para a qual a conservação ou restauração de seus habitats de dispersão também facilitará a dispersão de outras espécies-alvo” (Breckheimer et al. 2014). O potencial de uma espécie para ser um bom guarda-chuva de conectividade tem sido

relacionado à sua capacidade de dispersão e o uso do habitat (e.g., Cushman and Landguth 2012). No entanto, não há consenso sobre as principais características que tornam uma espécie um guarda-chuva eficiente. Enquanto alguns estudos mostram que corredores identificados com base em espécies de grande porte e com grande capacidade de dispersão são capazes de fornecer conectividade para um grupo diversificado de espécies (Epps et al. 2011; Cushman and Landguth 2012; Thornton et al. 2016), outros estudos sugerem que essa relação pode não ser tão abrangente (Minor and Lookingbill 2010; Breckheimer et al. 2014). Foi essa inconsistência na predição do potencial guarda-chuva das espécies para a conservação da conectividade da paisagem que motivou o desenvolvimento do **CAPÍTULO 3**. A partir da observação de que apenas as características das espécies aparentemente possuem um baixo poder preditivo para definir o desempenho guarda-chuva de conectividade, nós conjecturamos que a composição e a configuração da paisagem poderiam desempenhar um papel importante na determinação dessa propriedade. Nesse capítulo, nós usamos uma abordagem virtual para resolver essa questão e discutimos como isso pode afetar os planos de conservação que são focados em espécies únicas.

Apesar da praticidade oferecida pelos substitutos ecológicos, alguns estudos sugerem cautela na utilização de espécies únicas ou grupos restritos para monitorar e gerenciar aspectos da biodiversidade (Andelman and Fagan 2000; Roberge and Angelstam 2004; de Moraes et al. 2018). As espécies são limitadas por conjuntos únicos de fatores ambientais e eco-evolutivos e essas diferenças refletem em suas demandas por forrageamento, dispersão e reprodução, bem como suas respostas às mudanças antrópicas (Breckheimer et al. 2014; Osborne et al. 2015). Consequentemente, o manejo baseado em uma única espécie pode não beneficiar ou até mesmo prejudicar a persistência de outras espécies simpátricas (Simberloff 1998; Breckheimer et al. 2014). Portanto, provavelmente não existe uma única espécie cujas exigências espaciais sejam capazes de cobrir as demandas de um grupo diverso de outras espécies, embora algumas delas já tenham mostrado grande valor como substitutos para conservação (e.g., Caro 2003; Thornton et al. 2016). Desenvolver planos de conservação baseados em guarda-chuvas compostos por múltiplas espécies, considerando diretamente características ecológicas distintas, tem sido sugerido como uma abordagem mais eficiente (Lambeck 1997; Nicholson et al. 2006; Beier et al. 2008). No entanto, o problema de manejo conflitante também permeia a construção de redes de habitat para múltiplas espécies

(Breckheimer et al. 2014; Beaudry et al. 2016). Isso ocorre porque nenhum cenário de conservação será tão eficaz quanto aquele projetado para atender exclusivamente às demandas de uma única espécie. Considerando os prós e contras das abordagens de uma e múltiplas espécies, no **CAPÍTULO 4**, nós avaliamos a eficiência das soluções de conservação fornecidas pela aplicação dessas estratégias. Para isso, nós projetamos redes de qualidade de habitat e conectividade para 11 mamíferos em uma ampla região da Mata Atlântica. Diante do potencial conflito entre a diversidade de características biológicas utilizadas para gerar redes para múltiplas espécies e a capacidade das estruturas finais em abranger os requerimentos individuais das espécies-alvo, nós buscamos também responder se as redes restritas a espécies ecologicamente semelhantes apresentam melhor desempenho do que aquelas projetadas para maximizar a diversidade de características representadas.

Em suma, o desenvolvimento desta tese teve como objetivo geral preencher lacunas importantes relacionadas à seleção de estratégias metodológicas para otimizar a projeção de redes de habitat. Os resultados aqui obtidos são importantes para orientar o planejamento de conservação baseado em espécies, uma vez que demonstram as principais implicações, vantagens e desvantagens de se aplicar as ferramentas analíticas e abordagens de conservação mais comumente utilizadas para a seleção de áreas prioritárias.

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# Capítulo 1

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Landscape connectivity modeling from the perspective of animal dispersal

Diniz MF, Cushman SA, Machado RB, De Marco Jr P. Landscape connectivity modeling from the perspective of animal dispersal. *Landscape Ecology* (in review)

# **Landscape connectivity modeling from the perspective of animal dispersal**

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## **RESUMO**

*Contexto* A dispersão desempenha um papel fundamental em múltiplos processos ecológicos e evolutivos. Como a fragmentação e a perda de habitat são ameaças onipresentes e podem prejudicar a dispersão, a modelagem da conectividade da paisagem tornou-se uma ferramenta valiosa no planejamento de conservação.

*Objetivos* Fornecemos uma visão geral dos modelos mais populares de conectividade baseados no delineamento de rotas de movimento, destacando seus pressupostos e limitações ao representar a dispersão animal, sugerindo uma série de perguntas e análises que podem esclarecer os pontos fortes, fracos, vantagens e desvantagens dos métodos disponíveis.

*Métodos* Revisamos a estrutura dos atuais modelos de conectividade baseados na análise de caminho de custo mínimo, na teoria de circuitos e nos modelos de dispersão baseados em indivíduos. Descrevemos as principais aplicações dos modelos no contexto da conservação e focamos em analisar quais são os pressupostos assumidos sobre a dispersão animal a partir da perspectiva de cada modelo.

*Resultados* A maioria dos modelos de conectividade retrata apenas a fase de transferência da dispersão, que pode ser simulada através de diferentes tipos de passeios aleatórios ou como um processo em que os animais têm um conhecimento quase perfeito da paisagem. Poucos modelos são explicitamente capazes de considerar a capacidade perceptual dos animais. A variação individual na dispersão pode ser incorporada nos modelos de diferentes maneiras. O limiar de dispersão e a mortalidade são definidos apenas em alguns deles. Os poucos estudos validando comparativamente os diferentes modelos ainda não permitem conclusões muito generalizáveis em relação aos seus desempenhos.

*Conclusões* Se quisermos encontrar áreas importantes para a dispersão das espécies, os modelos de conectividade devem ser escolhidos de acordo com as suas habilidades para representar a ecologia de movimento das espécies. Dada a compreensão limitada do desempenho relativo e das diferenças entre os métodos, sugerimos fortemente um esforço abrangente para avaliar o comportamento e comparar as previsões de uma ampla gama de métodos de modelagem de conectividade. Melhorar nossa capacidade de modelar a dispersão é essencial para avançarmos os estudos teóricos e obtermos estratégias de conservação mais eficazes.

**PALAVRAS-CHAVE:** teoria de circuitos, análise fatorial de custo mínimo, modelos baseados em indivíduos, suposições e limitações dos modelos, kernel resistente, superfície de resistência

## ABSTRACT

*Context* Dispersal plays a key role in multiple ecological and evolutionary processes. As fragmentation and habitat loss are ubiquitous threats and can disrupt dispersal, landscape connectivity modeling has become a valuable tool in conservation planning.

*Objectives* We provide an overview of the most popular connectivity models based on the delineation of movement pathways, highlighting their assumptions and limitations when representing animal dispersal, and suggest a series of questions and analyses that could clarify the strengths, weaknesses, advantages and disadvantages of the available methods.

*Methods* We review the structure of the current connectivity models based on least-cost analysis, circuit theory, and the individual-based dispersal models. We describe the main applications of models in conservation context and focus on analyzing what we are assuming about animal dispersal when we choosing a particular model.

*Results* Most connectivity models depict only the dispersal transfer phase, which can be simulated through different types of random walks or as a process in which animals have a near perfect knowledge of the landscape. Very few models are explicitly able to consider animal's perceptual range. Individual variation in dispersal can be incorporated into the models in different ways, and dispersal threshold and mortality are defined only in some of them. The few studies validating comparatively the different models do not yet allow very generalizable conclusions regarding their performance.

*Conclusions* If we want to find important areas for animal dispersal, connectivity models should be chosen according to their abilities to represent species' dispersal, besides the available data and study goals. Given the limited understanding of the relative performance and differences among methods we strongly suggest a comprehensive effort to evaluate the behavior and compare the predictions of a wide range of connectivity modeling methods. Improving our capacity to realistically model dispersal is essential to advance theoretical studies and obtain more effective conservation strategies.

**KEYWORDS:** circuit theory, factorial least-cost path analysis, individual-based models, models' assumptions and limitations, resistant kernel, resistance surface

## INTRODUCTION

Dispersal is a life-history trait essential for survival and reproduction of many organisms. Albeit with great variation, dispersal is often seen as a three-stage process (emigration, transfer, and immigration stages) in which individuals move from their natal locations to the first reproduction site or between successive reproductive sites (Clobert et al. 2012). Although dispersers have to deal with many risks and costs throughout the process (Bonte et al. 2012), dispersal allows the animals to escape from the immediate environment of their parents and may provide many advantages at the individual level, such as 1) avoiding the reduction of fitness due to kin competition, 2) increased population density and/or inbreeding, 3) besides allowing the spatial and temporal exploitation of variable resources (Bowler and Benton 2005; Clobert et al 2012). Beyond individual consequences, dispersal is one of the key processes in shaping population and metapopulation dynamics, community assembly, and species' global range dynamics, whose direct assessment may allow significant advances in ecology, evolution and biogeography (Jønsson et al. 2016).

Because habitat fragmentation may disrupt dispersal and consequently deeply impact the species persistence, landscape connectivity has gained increasing prominence in ecological studies and has become an essential element in conservation planning (Rudnick et al. 2012). While some metapopulation models and many connectivity metrics incorporate dispersal from an oversimplified view based on the assumption of matrix homogeneity, there is a general recognition that animal behavior (i.e., how an organism perceives and responds to landscape structure, Bélisle 2005; Baguette and Van Dyck 2007), and the nature of the intervening matrix have important effects on

dispersal and, therefore, should be incorporated into landscape connectivity assessments (Ricketts 2001; Revilla et al. 2004; Revilla and Wiegand 2008). In response to this call, studies developed in recent years have sought to evaluate connectivity from the organisms' perspective and have utilized a variety of algorithms to predict movement paths on resistance surfaces (representing how organisms perceive landscape elements). This type of approach has been particularly prominent in the conservation context since it is possible to map structures capable of facilitating (e.g., corridors and stepping stones) or preventing (e.g., barriers) animal movement across the landscape, essential information to guide current and future conservation initiatives (Cushman et al. 2013d).

Even though these models represent a breakthrough in relation to purely structural approaches, some of these models are based on frameworks developed initially in other disciplines, such as the models based on least-cost analysis and circuit theory. Thus, it is essential that users, especially beginners, have a prior knowledge of the models' structure and be aware of their limitations in representing animal movement. Our goal is to provide an overview of the most commonly used approaches to predict landscape connectivity based on the delimitation of movement pathways: the least-cost (LC) models, the circuit theory-based model (CTBM) and individual-based models (IBMs). Although there are already some recent general reviews of connectivity modeling (Rudnick et al. 2012; Zeller et al. 2012; Cushman et al. 2013d; Kool et al. 2013), we here presented a more detailed description of the models' structure and their current applications. We focused on discussing strengths and weaknesses of models when they are applied to identify important routes for dispersal movements, and suggest a research agenda to clarify the appropriate use and applications of the different methods and to guide their improvement. Although the revised models are currently used to assess

connectivity at different scales from within home-range movements to migrations, this review has as its main focus the application of the models to identify important areas for animal dispersal in terrestrial systems.

### **Resistance surfaces: the foundation of current connectivity models**

All LC methods used to predict landscape connectivity, as well as the CTBM and many IBMs are based on a landscape raster representation whose values indicate the resistance or difficulty imposed by environmental components on individual's movement (Fig. 1a; Zeller et al. 2012; Cushman et al. 2013; Etherington 2016). Resistance values are assigned to each landscape cell to reflect the organism's differential propensity to use a particular habitat type during its movement due to the physiological costs and/or mortality imposed by the different landscape elements being represented in the cells (Spear et al. 2010; Zeller et al. 2012). These landscape representations are commonly known as resistance surfaces, although there is a great variability of nomenclature equivalent to resistance such as cost, friction, impedance, or its inverse, such as permeability and conductivity (Spear et al. 2010; Zeller et al. 2012; Etherington 2016). The use of resistance surfaces allowed the transition from connectivity models based on homogeneous landscapes to those capable of incorporating the effect of different landscape characteristics on the species dispersal and gene flow (Spear et al. 2010; Zeller et al. 2012).

Although many different methods have been used to create resistance surfaces (see Zeller et al. 2012 and Cushman et al. 2013), in general the modeling process usually consists of: (1) selection of known or assumed environmental variables to affect the

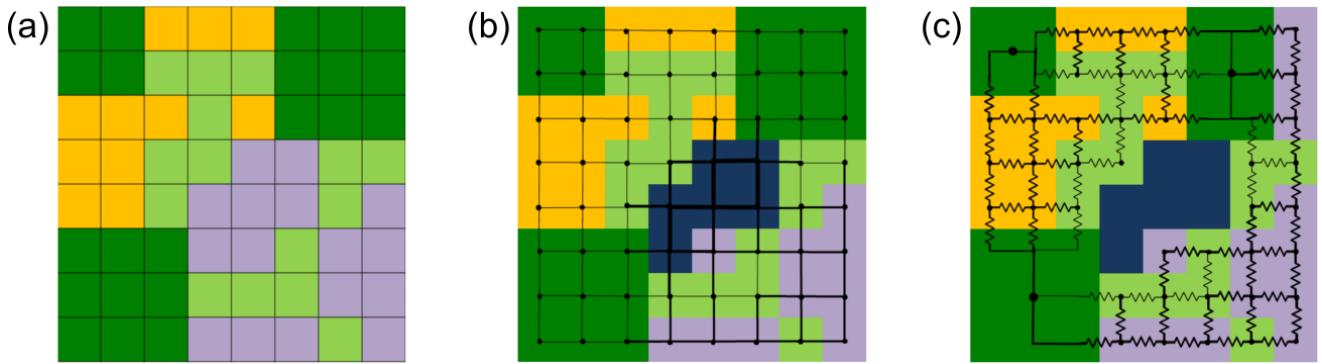
species movement; (2) selection of biological data (most commonly detection data, relocation data, pathway data, and/or genetic data) from which the values of environmental variables will be associated for estimation of resistance values; (3) application of an analytical approach to associate the biological movement data (shown in 2) with environmental factors (shown in 1). The final surface is obtained from the application of the estimated resistance values to the environmental layers (Zeller et al. 2012). Depending on the analytical approach selected, many competing surfaces may be created and confronted with biological data, and after the application of some model selection procedure, the best candidate is identified (e.g., Cushman et al. 2006; Zeller et al. 2012, 2018). Although unreliable and highly criticized, obtaining resistance surfaces from invalidated expert opinion is still frequent in connectivity studies (Zeller et al. 2012).

## How do the models work?

### *Least-cost models*

The least-cost (LC) modeling was first developed in the geographic transport context to find the optimal route (with the lowest cost) given all possible routes across landscapes (Etherington 2016). This technique consists of identifying the path with the lowest cost distance among all possible paths linking predefined source/destination locations (SD locations hereafter). The data required for this analysis is a resistance surface and the SD locations' coordinates. Most LC methods convert the resistance surface into a weighted lattice graph (Fig. 1b) where raster cells are represented by their centroids (nodes) connected by weighted edges, which are in turn determined as functions of both

Euclidean distance and cost units (Etherington 2016). A graph theory shortest-path algorithm (being the most common the Dijkstra's algorithm; Dijkstra 1959) is applied to the graph derived from the resistance surface to find the combination of edges with the lowest accumulated cost-distance linking a pair of SD sites. The LC distance is the sum of the edge weights along the LC path (i.e., its *accumulated-cost*; see Etherington 2016 for a detailed review).



**Figure 1** Many connectivity models are based on resistance surface where cell values represent the resistance imposed by landscape components to the individuals' movement (a). Least-cost models convert the resistance surface into a weighted-graph network in which nodes (cells' centroids) are connected by weighted edges according to the Euclidean distance and resistance values from the neighboring cells (b). In the circuit theory-based model, the edges are replaced by resistors (c). Dark green clusters represent habitat patches and other colors represent the intervening matrix whose components can facilitate (light green cells), hinder (purple and orange cells) or prevent the dispersal of individuals (dark blue cells). The width of edges and resistors represents the different resistance values associated with the elements of the landscape

Ecologists have extensively used LC analysis since its formal introduction by Adriaensen et al. (2003). Currently, LC models have been the most widely used to analyze landscape functional connectivity (Cushman et al. 2013d; Correa Ayram et al.

2016). Many variations from the classic LC analysis have been developed in an attempt to overcome some limitations of the original model when applied to animal movement; below we describe some of them (e.g., Compton et al. 2007; Cushman et al. 2009; Pinto and Keitt 2009; Landguth et al. 2012; Etherington 2016).

#### *The factorial LC path analysis and other improvements*

Because the LC path analysis has its roots in geographic transport, the prediction of a single optimum path between a defined pair of locations is justifiable when the goal is to save time and fuel. However, the initial LC framework seems to poorly match animal dispersal due to three main reasons. First, the specified pairs of SD locations among which the individual will disperse are rarely known. Moreover, prediction of the connectivity of populations may require modeling over hundreds or thousands of sites. Second, the model assumes that all individuals will follow the LC path (i.e., they have a clear destination as a goal, and a complete knowledge of the landscape routes to that destination, and always travel by the ‘cheapest’ one). This omniscience is not biologically realistic, making the results quite questionable. Finally, the LC path has a 1-pixel width, which is dependent on the resistance surface’s resolution, and proposing these narrow paths as corridors may be not suitable for many species.

To work around these problems, some authors have modified and implemented additional steps inside the classic LC path routine. A factorial application of LC path method computes the LC paths for all pairwise combinations among the SD locations, thereby providing a broader perspective of species population connectivity (Cushman et

al. 2009). For example, for 50 points the algorithm will identify the LC paths from one location to the 49 others and so on, totaling at the end 1,225 individual LC paths.

Considering multiple additional suboptimal routes or smoothing the LC paths using a probability density function have been used to deal with the unrealistic assumption of a single optimal path with a 1-pixel width (e.g., Landguth et al. 2012; Cushman et al. 2013c; Ribeiro et al. 2017). A swath of cells surrounding the LC path forming an LC corridor (Rudnick et al. 2012; Etherington 2016) avoids the unrealistic view of one very narrow permanent route.

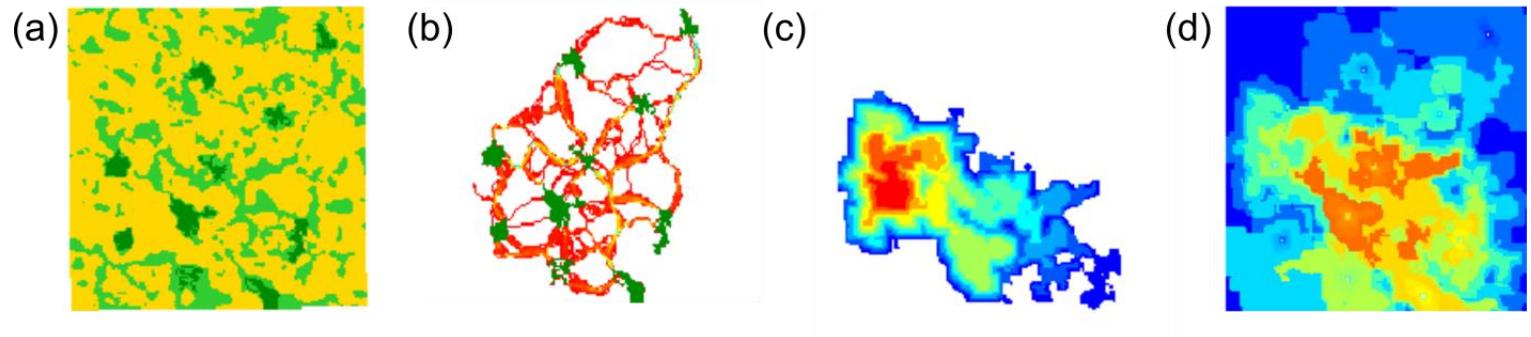
Pinto and Keitt (2009) extended Dijkstra's algorithm to design multiple dispersal routes through two methods: the conditional minimum transit cost (CMTC) and the multiple shortest paths (MSPs). The CMTC grid is created summing the cumulative cost grid for the target and the source, after that the cells with the lowest values in this grid are selected from an arbitrary threshold. The remaining group of cells is referred to as dispersal routes and the LC path is one of these routes (Pinto and Keitt 2009). The MSPs was developed from a stochastic version of Dijkstra's algorithm, first selecting a number between 0 and 1 from a random uniform distribution and deleting the weighed edges connecting two adjacent vertices that are greater than the selected number. After rebuilding the graph, the algorithm finds the LC path; this process can be repeated many times for each pair of SD location as many routes as the user wants (Pinto and Keitt 2009).

Cushman et al. (2009) used a factorial LC modeling and smoothed the final paths applying a parabolic kernel. To perform this, each LC path was transformed into a point

file and the kernels fitted over the points were summed (Cushman et al. 2009). Uniform kernels regardless of context using only a distance measure or, preferably, resistant kernels (detailed below) can be produced (Landguth et al. 2012; Cushman et al. 2013c). Although only one LC path is identified for each possible combination of SD location, the kernel-smoothed LC paths represent possible deviations from the optimal route due to stochastic behavioral choices of individuals and/or an incomplete knowledge about the adjacent environment (Cushman et al. 2009, 2013c). For example, (Cushman et al. (2013c) implemented factorial least cost corridor analysis which couples computation of all pair-wise paths in a system of nodes with resistant kernel buffering to provide a spatially synoptic and biologically realistic model of connectivity across a continuously distributed population in a heterogeneous landscape. In addition, the factorial least cost path approach as implemented in the software UNICOR (Landguth et al. 2012) includes incorporation of dispersal thresholds which limit the calculation of paths between nodes to a specified threshold representing the dispersal ability of the organism in question, which greatly increases the realism of the approach.

The method recently implemented by Ribeiro et al. (2017) adds two sources of stochastic variation in the LC simulations to obtain multiple paths (Fig. 2a). First, in this approach instead of fixed SD points, as in the methods above, the sources and destinations are habitat patches. To each simulation, the algorithm randomly selects pixels belonging to the SD patches between which the paths will be modeled. Still, in the same iteration, a new random map is yielded and multiplied by the resistance surface map; after these two steps, the LC path it is identified. This procedure is repeated for the same pair of SD patches according to the amount of user-defined iterations, resulting in a different LC path each round due to different selected points

and slightly modified resistance surfaces. A limitation of this approach is that it is focused on connectivity between patches, rather than between individuals, and populations are rarely limited to or constrained by particular patches.



**Figure 2** The resistance surface of a virtual landscape composed of three types of land cover with the following order of resistance: orange > light green > dark green. In (b) it is possible to see the density of multiple LC paths between all possible pairs of patches generated scholastically from the application of the method implemented by Ribeiro et al. (2017). In (c) a single resistant kernel was created from the centroid of one of the habitat patches and the cumulative resistant kernel surface resulting from the addition of all individual kernels (d). Software used: LSCorridors (Ribeiro et al. 2017) and the R package ‘gdistance’(van Etten 2015)

While all model variations shown above have made the LC approach more suitable to represent animal movement, they are focused on the identification of discrete structures such as corridors or linkage zones. Even though mapping of these structures may be important to define ecological corridors, in some situations a continuous and more synoptic view of connectivity may be required.

#### *Resistant kernels*

The resistant kernel approach arose from the union of two well-known methods, the dispersal kernel estimator and the LC path modeling (Compton et al. 2007). Through

standard dispersal kernels, it is possible to know what the probability of an individual dispersing to a given Euclidean distance (dispersal distance kernel) or to be found in a certain spatial location at the end of a dispersal event (dispersal location kernel; Nathan et al 2012). The dispersal location kernel is a probability density function fitted in the geographical space (x, y) describing the distribution of the post-dispersal locations of the dispersers in a population relative to a defined ‘start’ or ‘source’ point (Nathan et al 2012). A resistant kernel consists basically of the same framework of a dispersal location kernel modified to accommodate a functional distance measure (cost distance) instead of a structural one (Euclidian distance), and to consider multidirectional displacements instead of predefined SD points (Compton et al. 2007; Etherington 2016).

To apply the resistant kernel is necessary to have (1) a resistance surface depicting the cost imposed on the species movement by landscape elements; (2) the source locations representing the origin points of dispersers; (3) a dispersal function by which the cost distances will be converted into ecologically meaningful connection probabilities; and (4) a dispersal threshold representing an intrinsic condition of the species that limits its movement (Compton et al. 2007; Cushman and Landguth 2012).

The resistant kernel works as follows (Compton et al. 2007; Cushman et al. 2010; Cushman and Landguth 2012). First, the LC path starting at a source cell and ending at each cell surrounding it is identified using the resistance surface and then the accumulated cost of those paths are stored in the respective cell creating a map of movement cost. The model computes the optimal path only for adjacent cells to the source cell where the accumulate cost is less than the cost distance dispersal threshold for the studied species. Next, the accumulated-cost values maintained in each cell are

converted into an estimate of relative density using the defined dispersal function. The resultant density values represent the probability of a disperser leaving the source cell reaching any landscape cell. The expected probability of dispersing individuals at the source is the highest and it is down-weighted for the neighboring cells by the cumulative cost up to the dispersal threshold. The way in which the reduction of the probability of dispersing organisms occurs as the cumulative cost increases (e.g., linearly, exponentially or following a normal curve) is determined by the dispersal function. All the LC dispersal kernels are made individually (Fig. 2b) for each source cell and summed to yield a synoptic, all-directional dispersal map (i.e., a surface with the total expected density of dispersers or the expected movement rates at each pixel of the landscape, which is the most effective algorithmic way of representing the spatial incidence function of dispersal; Fig. 2c).

### *Circuit theory*

The development of an ecological connectivity model from electric circuit theory (McRae et al. 2008) is yet another of the many examples of how physical and mathematical models have helped us to understand animal movement. According to the physical concepts, a circuit consists of electrical elements connected together through which an electrical current flows (Bird 2014). The current  $I$  consists of the ordered movement of free electrons that tend to move in a particular direction when an electric field, a voltage  $V$ , is applied to a circuit (Bird 2014). Resistors are elements that conduct current but offer a resistance  $R$  to the flow of charge thus hindering the passage and electric current (Bird 2014). All of these elements can be associated through Ohm's law which states that the total current flowing in a circuit is directly proportional to the

applied voltage and inversely proportional to the effective resistance, mathematically represented by  $I=V/R$  (Bird 2014). The effective resistance, in turn, depends on the configuration of the resistors (in series or parallel) present in the circuit and their respective resistance values (Bird 2014). Circuits can be represented by graph models and the use of this mathematical tool for the study of electric circuits has played a key role in their structural properties consolidation since Kirchhoff's analysis (Klein and Randić 1993). The application of circuit theory to understand evolutionary and ecological processes was only possible thanks to the previously established theoretical relationship between electric circuits and random walk on analogous graphs (Doyle and Snell 1984; Klein and Randić 1993; Chandra et al. 1996).

Circuit theory can be used to model connectivity in both evolutionary and ecological contexts (McRae 2006; McRae et al. 2008). Initially, electrical networks were used to predict gene flow where the nodes in the circuit represent subpopulations and the resistors define the relative numbers of migrants exchanged between adjacent nodes (McRae 2006; McRae and Beier 2007). The link between population genetics and electric circuits was made by the isolation metric known as *resistance distance*, which is equivalent to the effective resistance between a pair of nodes and has a well-defined relation with the commute time (i.e., expected time for a random walker to travel between those two nodes and return; McRae 2006). In the ecological context (which will be our focus hereafter), electrical nodes in a circuit are used to represent landscape matrix cells and habitat fragments, and the resistors that connect them indicate functional connections such as dispersal. The resistance value offered to the current in the resistors represents the difficulty imposed by a landscape element (e.g., land cover) or a set of them to animal movement (Fig. 1c; McRae et al. 2008).

The application of circuit theory to model animal movement requires a raster representation of landscape, where different resistance values are assigned to different habitat types according to a resistance surface or, inversely, a conductance surface. Cells with finite resistance will be transformed into electrical nodes while cells with infinite resistance are dropped and used to represent complete barriers to movement (see McRae et al. 2008 for a detailed description). Cells belonging to habitat patches that are sources and destinations of individuals' movement have zero resistance and are converted into single nodes. Resistors are placed between each node and its four or eight neighboring nodes, with resistance values generally defined as the mean of the cells' resistance being connected (McRae et al. 2008). After the landscape has been converted into a large electrical circuit (Fig. 1c), to analyze the current flow between two habitat patches, one node is usually connected to a current source (source patch) and the other is connected to ground (destination patch). Instead of using a current source, it is possible to connect a voltage source to one or more destination patches and evaluate the voltage values across the remaining nodes. The Ohm's and Kirchhoff's laws are applied through the nodal analysis method to determine voltages at each node, and then the currents passing through individual resistors or nodes are calculated (McRae et al. 2008). As circuit theory is linked to animal movement via random walk, the current value flowing through a resistor is equal to the expected net number of times that individuals moving randomly starting at a source location or patch will cross that branch before reach a destination patch (McRae et al. 2008). In addition, the voltage value in any node is equivalent to the probability that a random walker starting at that node will successfully disperse to another node that is connected to a voltage source before reaching any node connected to ground (McRae et al. 2008).

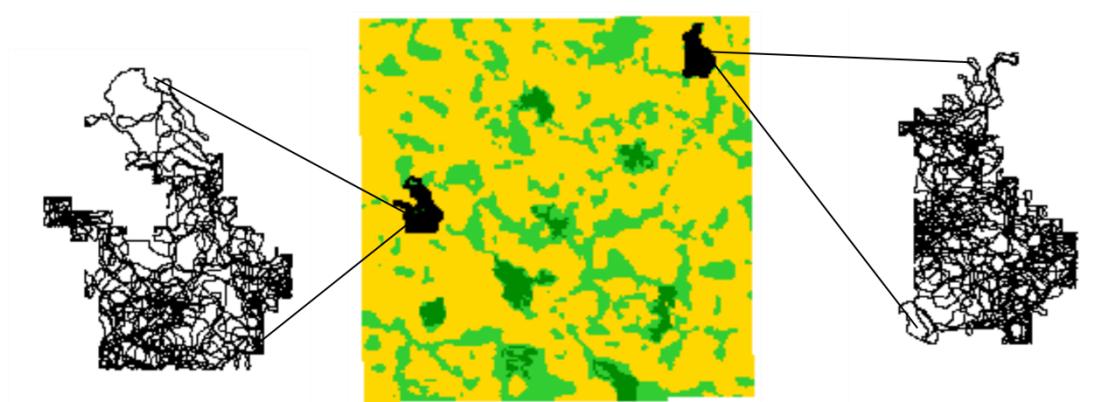
### *Individual-based dispersal modeling*

Although the models based on LC analysis and circuit theory are capable of spatially simulating potential movement paths, these approaches do not incorporate behavioral elements that drive individuals' movement in the real world. IBMs can overcome this limitation by explicitly simulating how the movement on the individual scale responds to landscape elements (Cushman et al. 2013d). IBMs, also known as agent-based models, have been used in ecological studies for more than four decades to address key questions related to population dynamics, community assembly, and food web ecology (DeAngelis and Grimm 2014). As bottom-up approaches, IBMs usually work following these logical steps: information about entities (often individuals) constituting systems (e.g., population, metapopulation, and communities) is collected and used to formulate hypotheses about their role or behavior; after that, computational programs are designed to simulate the potential behavior and interactions among the entities from the properties to be tested (used to construct the hypotheses); and, finally, the pattern resulting from the simulation is evaluated according to its capacity to reproduce emerging system-level properties or dynamics (Grimm and Railsback 2005; DeAngelis and Grimm 2014). For example, from empirical data of dispersing Iberian lynx, Revilla et al. (2004) defined a set of behavioral movement rules to compose an individual-based dispersal model, which was able to predict with some accuracy the population-level parameters estimated from data field. The calibration, selection or redefinition of IBMs can be accomplished using strategies such as the pattern-oriented modeling, through which the model complexity can be optimized based on multiple patterns observed in real systems, and the realism added to their structures may make them less sensitive to parameters' uncertainty (Grimm et al. 2005).

Hereafter we will refer to the IBMs constructed aiming to assess connectivity from dispersal simulation as individual-based dispersal models (IBDMs). The main advantage of using an IBDM to assess functional connectivity over other approaches is its potential to incorporate species-specific movement traits and the inter-individual variability based on dispersal and demographic data (Gardner and Gustafson 2004; Revilla et al. 2004; Cushman et al. 2013d; Kanagaraj et al. 2013). Generally, IBDMs have a common structure in which virtual dispersers are released from predefined locations and their movement paths are progressively formed step by step according to the interplay between a set of state variables or attributes characterizing the individual, movement rules used to simulate its behavior and the landscape structure. Information processing and decision-making (represented by the movement rules) by individual animals can be defined using a statistical model (e.g., non-linear regression models or finite mixture models) that in turn has been selected and parameterized from field data (e.g., Tracey 2006); or according to a weighted random walk which may (e.g., Kanagaraj et al. 2013) or not consider autocorrelation in movement (e.g., Allen et al. 2016). Movement rules incorporate elements that are chosen based on species' dispersal traits such as perceptual range, homing behavior, memory size and bias of movement away from the natal patch (Aben et al. 2014; Coulon et al. 2015). Each simulated animal is allowed only perform a maximum number of steps which may be a fixed parameter (e.g., Tracey 2006; Coulon et al. 2015) or defined based on a probability distribution (e.g., Kramer-Schadt et al. 2004; Kanagaraj et al. 2013). The stopping condition for the individual's movement path usually is based on one or more of the following events: the animal was able to reach another habitat patch different from the one it started (successful dispersal); the path intersected the landscape boundary; a mortality event occurs; or a maximum number of steps was exhausted before one of the

above situations happened (Gardner and Gustafson 2004; Tracey 2006; Palmer et al. 2011).

IBDMs can be designed to simulate animal movement in different types of landscape representations, which consequently determines how the movement rules work (Cushman et al. 2013d). Vector-based models represent the landscape element through discrete entities in form of points, lines or polygons (Tracey 2006; Cushman et al. 2013d). As the full extent of a polygon has a single value, generally the vector-based models are more adequate to represent the movement of organisms that experience the landscape in a more homogeneous way (i.e., the dispersers do not respond to fine-scale spatial heterogeneity). The movement routes can be based on turn angles and relative distances to certain landscape objects (Tracey 2006). If the landscape elements affecting the animal movement are perceived as continuous spatial variation rather than discrete, then raster-based models are more appropriate to translate the effect of these elements on the animal routes (Tracey 2006; Cushman et al. 2013d). As a result, most IBMDs are raster-based models and the paths are usually formed step by step from the connection of a cell to one of its neighboring cells (Fig. 4).



**Figure 4** Two movement pathways created from the application of a spatially explicit

individual-based model to the same virtual landscape shown in Fig. 2 and 3. Software used: R package ‘SiMRiv’ (Quaglietta and Porto 2018)

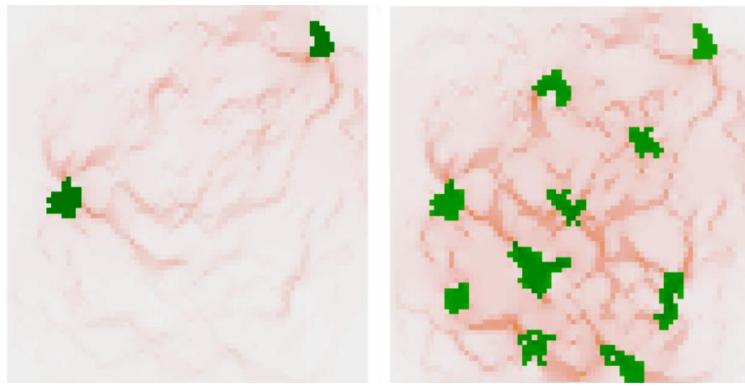
Despite individual-based dispersal models share a similar general framework, they can present different levels of complexity depending on the constituent parameters and dynamics. To illustrate in detail the structure of an IBDM developed to estimate habitat connectivity, we describe the *stochastic motion simulator* (SMS; Palmer et al. 2011) due to its simplicity but great flexibility to be applied to a variety of species (Aben et al. 2014; Moorhouse et al. 2014; Coulon et al. 2015; Marrotte et al. 2017). The SMS is an example of raster-based IBDM able to incorporate landscape heterogeneity through the use of a resistance surface (Palmer et al. 2011), the same required in the LC and circuit-based analyses presented previously. The movement is modeled according to two parameters: the animal’s *perceptual range* describing the radius of perception in which the movement decision can be affected by the landscape elements; and the *directional persistence* reflecting the strength of correlation in the movement (i.e., the tendency of the animal to follow a correlated random walk). The user can optionally define a third variable indicating the type of method to be used to evaluate the cost of the cells captured by the perceptual range (Palmer et al. 2011). Virtual individuals begin their movements from predefined locations and are only able to perform a finite number of steps during their movement paths. The decision of movement to one of the eight neighboring cells depends on its probability of selection, which in turn is inversely proportional to its effective cost weighted by the directional persistence. The cell’s effective cost is determined by its own cost and the cost of neighboring cells captured by the perceptual range. Although in its original version SMS requires the definition of only two or three parameters, it is possible to incorporate other movement traits and additional steps to take into account the species-specific biology including memory size,

homing behavior and auditory attraction to breeding sites (Aben et al. 2014; Coulon et al. 2015).

## **How is connectivity assessed through the models?**

The resistant kernel approach can be applied to evaluate the connectivity within and between populations (Compton et al. 2007). Because this model provides a continuous picture of the connectivity across the landscape, it does not identify discrete structures such as corridors or linkage zones. Due to this, some studies have combined resistant kernel with factorial LC path analysis (Cushman et al. 2013b, 2018; Mullins et al. 2015; Moqanaki and Cushman 2017; Hearn et al. 2018; Khosravi et al. 2018). This integration allows mapping and assessing broad scale population connectivity considering the configuration of different elements: generally core area, fracture zone (locations where connectivity is potentially reduced by barriers or cumulative dispersal cost) and/or barriers from resistant kernel (Cushman et al. 2013b), and dispersal corridors form the factorial LC paths. Core areas can be defined as contiguous units with resistant kernel values above a certain percentile (e.g., 90th). Similarly, fracture zones are identified as the locations with resistant kernel values below a certain percentile and greater than zero (Cushman et al. 2013b). All cells with zero (no movement) in the final cumulative kernel map are considered as barriers. Core areas and fracture zones together are usually classified as the total connected habitat for a species, while all cells with zero kernel density are usually classified as non-connected (Cushman and Landguth 2012; Wasserman et al. 2012; Cushman et al. 2013b; Krishnamurthy et al. 2016). For models that generate multiple paths, the resulting routes can be overlapped to generate a density map indicating the number of paths passing through each landscape pixel (Fig. 2a).

Current values provided by the CTBM can be used to identify areas with the highest visit rates during the movement of individuals (McRae et al. 2008). From the mapping of current density along the landscape, it is possible to visualize and identify movement patterns and, consequently, the most important routes for connectivity throughout the study area (Fig. 3). The higher the current value in a landscape cell, the greater its net passage probability for individuals moving randomly from a source to a destination. The current values also allow the identification of *pinch points*, generally narrow areas that have a high current value because they condense many potential paths (McRae et al. 2008; Pelletier et al. 2014). These areas can have a great impact on maintaining dispersal since they can constitute almost obligatory passages due to the high resistance in surroundings and few alternative paths. The same general functionality is obtained by the factorial least cost path implemented with resistant kernel buffering, but with much lower computational demands (e.g., Cushman et al. 2013c). Connectivity can also be assessed using resistance distance as a measure of effective distance between patches or locations (McRae et al. 2008). It is worth noting that unlike the LC distance that reflects both the Euclidian distance and the cumulative costs faced by dispersers during their movement, the resistance distance is related to the availability of multiple alternative paths and the resistances through them (McRae et al. 2008). Thus, the more paths with low resistance exist between two nodes, the smaller the resistance distance between them (McRae et al. 2008).



**Figure 3** Current density maps showing the net movement probability for random walkers moving between two habitat patches or among all possible pairwise combination of patches. Software used: Circuitscape (McRae et al. 2016)

A variety of connectivity measures can be produced from an IBDM's output. Most commonly, inter-patch connectivity is described as a function of the relative numbers of successful dispersers (e.g., Tracey 2006; Kanagaraj et al. 2013; Coulon et al. 2015). The spatial identification of corridors can be performed overlapping of the individuals' movement paths across the simulations (Allen et al. 2016). In addition, a spatial layer of the probability of matrix use and dispersal habitat can be produced by counting the number of times each cell was visited by the dispersers (Kanagaraj et al. 2013). The spatial incidence function can be computed by summing the total locations visited by all individuals in all time steps, and is conceptually equivalent and highly correlated to the predictions of the cumulative resistant kernel, when the IBDM is based on cost-weighted random walks.

### What are the main applications of the models in conservation planning?

In addition to the commonly performed analysis of connectivity pattern to propose or evaluate corridor effectiveness (e.g., Puyravaud et al. 2017; Naidoo et al. 2018), the

models reviewed here have been used to predict how population connectivity and individuals movement will respond to potential land-use change (e.g., Moorhouse et al. 2014; Cushman et al. 2016; McClure et al. 2017; Hearn et al. 2018) and climate change scenarios (Wasserman et al. 2012). For example, McClure et al. (2017) coupled circuit theory with Brownian bridge movement models to estimate habitat quality and connectivity for puma movement across the state of Arizona under different scenarios of conversion of vegetative land cover into impermeable structures such as pavement and building. Cushman et al. (2016) evaluated nine alternative scenarios of future landscape development and conservation in southern Africa across a range of dispersal abilities to evaluate vulnerability of lion population connectivity to landscape change with resistant kernel analysis. Wasserman et al. (2012, 2013), as the first to evaluate effects of climate change on population connectivity, evaluated how warming climate will affect connectivity and genetic diversity of American marten, also using resistant kernel modeling approaches.

Area prioritization for connectivity conservation can be done using the results derived from the application of CTBM (e.g., resistance distance) or a LC model (e.g., the mean of expected relative density of dispersing individuals in core areas from resistant kernels) as input in graph network algorithms (Avon and Bergès 2016; Khosravi et al. 2018) or based on ranking of corridor or core area strength (Cushman et al. 2013c, 2018). In the same way, landscape graphs can be designed using IBDM's output. Relative thresholds of successful transfers among habitat patches, which are converted into nodes, are usually used to determine the existence of connections among them, represented by the placement of edges (Lookingbill et al. 2010; Morzillo et al. 2011). One of the great advantages of using IBDMs to construct landscape graphs compared to

other models is the projection of directed graphs that allow the representation and evaluation of movement asymmetrically (Morzillo et al. 2011).

Another very common application of the models is the evaluation of road/highway impacts on population connectivity and the effectiveness of mitigating measures. Cushman et al. (2013c) applied the factorial LC path modeling coupled with resistant kernels to analyze the effectiveness of wildlife crossing structures for black bear movement and prioritize locations to improve permeability for the species based on corridor-highway intersections. Using an IBDM for simulate population dynamics of a virtual species, Ceia-Hasse et al. (2018) compared the relative importance of the two main negative effects of roads (direct road mortality versus barrier effect) and their interaction with dispersal on population isolation, persistence and size. The effect of road mortality on connectivity and the possible success of reintroduction initiatives for the Eurasian lynx in Germany (where no empirical data were available) were assessed through an IBDM calibrated with dispersal data of individuals from Switzerland (Kramer-Schadt et al. 2004).

More recently, connectivity models have been applied to predict the spatial pattern of disease occurrence based on host animal movement. For example, Kaszta et al. (2018) used cumulative resistant kernels to calculate the contact risk between cattle and buffaloes in South Africa, an important assessment for the foot and mouth disease control since the buffalo is the primary source of infection for susceptible livestock in the region. Combining an IBDM with circuit theory, Rees et al. (2013) showed that the effectiveness of vaccination to control raccoon rabies depends on landscape spatial heterogeneity. Marrotte et al. (2017) used the density of white-footed mouse pathways

(transmitter of Lyme disease) provided by SMS simulations to predict high contact areas of the species in a landscape in southern Quebec.

## **What are the main assumptions and limitations of models when representing animal dispersal?**

### *Dispersal phases*

Both LC (but not resistant kernel) and circuit-based models are only capable of simulating the transfer phase of dispersal. Using a pairwise framework, the models assume that emigration and immigration occur from predefined sources and destination patches/locations. This may be realistic for animals engaging in foraging through a known environment or conducting seasonal migration, but is patently inconsistent with dispersal of individuals through novel environments where they do not have clear destinations. Although they have the potential to model a wide range of processes, most IBDMs do not explicitly model dispersal as a complex three-phase process, and just as the other models focus on the representation of the transfer phase (but see Bocedi et al. 2014). One of the main applications of connectivity models is the identification of areas or elements that may offer greater chances of success for individuals' movement, but if the other two dispersal phases (emigration and immigration) are not guaranteed, the proposed connector structures may have questionable functionality. After all, there is no point in having well-connected areas and not making sure that they are able to provide dispersers and/or ensure their establishment. Therefore, a more realistic representation of the dispersal process explicitly accounting for its three stages is needed, and will allow us to produce more reliable predictions about species' dynamic population and,

consequently, more efficiently inform the efficient management strategies (Travis et al. 2012). One model that can represent all three phases of dispersal is CDPOP (Landguth and Cushman 2010), which models individual-based dispersal, mating, mortality, and gene flow across a costs and mortality risk surface. This model simulates the transfer phase as a cost-weighted dispersal process, and also simulates dispersal cost and mortality risk of the locations where dispersing individuals settle. By enabling simulation of dispersal, selection, mating and mortality across large populations and long-time periods in complex landscapes, this model provides realistic dispersal dynamics within a comprehensive individual-based population and genetics model.

### *Landscape resistance to dispersal*

Landscape resistance values are often estimated from the habitat suitability based on detection data (Zeller et al. 2012; Cushman et al. 2013d). However, this strategy may lead to misleading interpretations for species that exhibit different patterns of habitat selection during their home range and dispersal movements because occurrence data usually represent within-home range habitat use patterns (Cushman et al. 2013d). Recent studies using movement data have reinforced this potential source of error. For example, Elliot et al. (2014) parameterized demographic-specific resistance surfaces using telemetry data from African lions and showed that path selection as well as the connectivity pattern varied widely among dispersers, adult males and adult females. Using kinkajous' home range movement and natal and breeding dispersal, another study yield different connectivity maps from these movement categories and concluded that matrix landscape is less resistant to the movement of individuals during their natal and breeding dispersal than for individuals performing home range movements (Keeley et

al. 2017). It is becoming firmly established that resistance surfaces are likely to be most reliable when developed from dispersal movement data directly (e.g., Elliot et al. 2014) or from genetic data, which captures the multi-generational effect of dispersal across a resistant landscape (e.g., Cushman et al. 2006; Shirk et al. 2010). In the absence of these, habitat utilization models developed from point selection functions may perform adequately in some cases (e.g., Zeller et al. 2015, 2018, Mateo-Sánchez et al. 2015a, b). A number of examples have shown that expert opinion is an unreliable basis for developing resistance surfaces and should be avoided whenever empirical data are available (e.g., Shirk et al. 2010).

#### *Source locations*

All the models presented here require the definition of source locations. Ideally, the source locations used in the connectivity models should accurately represent the sources of dispersers (i.e., potential populations). Specifically, connectivity is a function of three things: (1) the density and distribution of the source population, (2) the resistance patterns in the landscape, (3) the dispersal ability and behavior of the dispersing organisms. For connectivity models to provide biologically accurate predictions, they must be built on realistic source points that reflect the actual distribution and density of individuals in the population.

From the application of CTBM in its original format and factorial LC path analysis, connectivity is often assessed in a pairwise fashion. From this perspective, we assume not only to know the points where the dispersers start their movements, but also all their potential destinations. In other words, before performing the connectivity analysis, we

are already assuming all the possible links between the source-target sites, which is a drawback of strictly pair-wise methods like circuit theory. A number of connectivity approaches are based on predicting connectivity between particular patches in a landscape. There are several strong disadvantages of this, most notably that the size and location of patches are often a very poor proxy for the actual population distribution and abundance (Cushman et al. 2008). Another disadvantage of assuming that dispersal occurs between certain habitat patches without a previous assessment of their potential to sustain populations is a possible mismatch between movement scales. One could assess the connectivity between habitat patches belonging to the home range of one or more individuals linked to daily movements and mistakenly assume to be assessing population connectivity via dispersal (Mimet et al. 2016).

In contrast, resistant kernels and IBDMs do not require an *a priori* identification of destinations. Specifically, the resistant kernel approach simulates least-cost dispersal from source points, reflecting the density and distribution of the population, to all locations in the landscape accessible to those individuals, based on the resistance of the surrounding landscape and the dispersal ability of the species. As noted above, this creates a biologically realistic estimate of the spatial incidence function of dispersal, in terms of the probability or density of movements through each and every location in the landscape. Summing the locations of all individuals in all time steps in cost-weighted random walk IBDMs creates an equivalent measure of the spatial incidence function of dispersal. In these methods point-to-point or patch-to-patch connectivity is a property that emerges from dispersal assessment considering only starting points.

Because the location and amount of SD nodes within the study area can influence the current density estimates driven by CTBM, new omnidirectional alternatives have been proposed to overcome this often unwanted property (Koen et al. 2014; Pelletier et al. 2014). For example, Koen et al. (2014) suggested that current flow should be estimated between nodes randomly placed around the perimeter of a buffered resistance surface, then removing the buffer to obtain a final current density map. The placement of source locations in the perimeter of the study area can also be applied to factorial LC path analysis (Cushman et al. 2009). These omnidirectional approaches are most appropriate when there is no *a priori* reason to place nodes in specific sites or when it is intended to have an overview of connectivity throughout the study region (Koen et al. 2014). The use of techniques that avoid the arbitrary placement of nodes can also be valuable for assessing the connectivity of species in which the delimitation of habitat patch may not be meaningful, such as those with continuously distributed populations.

#### *Animal's perception of the landscape*

As discussed above, many improvements have been implemented in LC analysis in recent years mainly aiming to overcome the unrealistic assumption that all individuals will always follow the optimal path between two locations. Studies using the classic single LC paths (factorial or not) assume that animals have perfect knowledge of the landscape, have specific destinations, and always make their decisions in order to optimize the movement to those destinations (i.e., reduce the cost-weighted distance). Both resistant kernel and the other LC approaches presented here break the assumption of omniscience in different ways. In the resistant kernel model, movement is not goal orientated and, consequently, the dispersal is treated diffusely since all paths around the

source with an accumulated cost lower than the species dispersal threshold are possible. Although approaches that adopt kernel-smoothed LC paths consider that individuals will imperfectly follow LC paths, a greater probability will still be attributed to the optimal paths, and the possible deviations will still be centralized in their vicinity. So, this approach still assumes that individuals have near perfect knowledge of the landscape because they are still more likely to follow the optimal paths. The use of multiple low-cost paths created from stochastic variations assumes that individuals can disperse via different routes, some of which may deviate considerably from the LC paths. The most important conceptual difference between the LC path and resistant kernel approach is that in the path model individuals have an *a priori* destinations and the model finds optimal routes between them while in the resistant kernel approach organisms disperse optimally based on cost away from source points but without *a priori* destinations, with probability of final location a function of cumulative cost from the source point.

When we use CTBM, we are assuming that the studied species follows a resistance-weighted random walk from specified source to *a priori* destination locations. From the models' perspective, animals behave like random walkers between sources and destinations, showing a preference for low-resistance habitat and having no long distance perception (McRae et al. 2008; Cushman et al. 2013d). Although all paths from a source location to a destination location are possible, those with low resistance (i.e., higher current values) are more likely to be taken since they have higher net passages probabilities to the walkers (McRae et al. 2008; Cushman et al. 2013d). The movement decisions are taken probabilistically according to the resistance values imposed by the surrounding habitat and no local directional bias is considered (McRae et al. 2008).

Because these decisions are only influenced by the resistance in the four or eight neighboring cells, the model assumes that the perceptual range is invariably equivalent to 1-cell size. As each movement step is taken independently of the others, any possible effect that the individual's spatial memory may have on movement is ignored (McRae et al. 2008).

In IBDMs, the cell-to-cell movements are usually the result of a cost-weighted random choice based on the adjacent cells' movement probabilities, which are attributed according to the habitat characteristics of those cells. Although dispersal is modeled as a probabilistic event driven by animal's habitat type preferences, as in circuit theory and resistant kernels, IBDMs can still make the shift from one cell to another dependent on the degree of autocorrelation in the movement, mortality, food availability, conspecific interactions, perceptual range and other parameters (e.g., Gardner and Gustafson 2004; Kramer-Schadt et al. 2004; Watkins et al. 2015; Krishnamurthy et al. 2016). Most IBDMs consider that an individual will move to a cell according to its perception of the environment in the eight cells surrounding its current location, also assuming a 1-cell size perceptual range (e.g., Gardner and Gustafson 2004; Revilla and Wiegand 2008; Kanagaraj et al. 2013; Allen et al. 2016, but see Pe'er and Kramer-Schadt 2008; Palmer et al. 2011). However, there is no algorithmic or theoretical limitation to extending perceptual range in IBDMs to a larger range (e.g., CDPOP; Landguth and Cushman 2010).

Most connectivity models developed to date do not incorporate the species' perceptual range in the movement decision-making process. For example, as implemented currently, neither LC path or resistant kernel approaches incorporate organisms'

perceptual distance, and of the LC models reviewed here, only the one implemented by Ribeiro et al. (2017) explicitly considers the species' perceptual range. However, as the ability of animals to perceive and respond to different landscape features (e.g., forests, water bodies and cities) can change connectivity quantitatively and qualitatively, the incorporation of this element in the models should receive high priority to obtain a more realistic dispersal representation (Pe'er and Kramer-Schadt 2008).

### *Dispersal threshold*

Both LC models and IBDMs are able to incorporate dispersal thresholds that are used to limit the length of potential paths that the organisms may follow. For LC path and resistant kernel approaches, the maximum dispersal distance can be specified based on the Euclidean distance or converted to a maximum cumulative cost value (Compton et al. 2007; Cushman and Landguth 2012; Landguth et al. 2012). The movement threshold in IBDMs is defined in terms of maximum number of movement steps or cumulative cost that may represent the entire dispersal process (e.g., Palmer et al. 2011; Allen et al. 2016) or a fraction of it, and in this last case the threshold is renewed following a temporal mark (e.g., days) until it reaches a certain period of time such as a year (e.g., Kramer-Schadt et al. 2004; Kanagaraj et al. 2013). In contrast, CTBM does not take into account any measures representing the species' dispersal ability, which is a major limitation of circuit theory approaches to connectivity. Therefore, all possible paths between a pair of nodes can be followed by individuals regardless of the distance or cost between them and, consequently, contribute to connectivity.

### *Time*

Only a few IBDMs are able to explicitly consider time during dispersal modeling. Since Kramer-Schadt et al. (2004) showed that patch connectivity may be also dependent on the simulated time period, the time window during which the dispersal is modeled may be important, especially for those models operating on an intraday time scale.

### *Mortality during dispersal*

None of the LC models reviewed is capable of directly incorporating mortality during dispersal. In contrast to LC paths, which are “reflective” models (e.g., paths are reflected around obstacles to their *a priori* destination), resistant kernels are “absorptive” (e.g., resistant kernel value decreases cumulatively with accumulated cost from the dispersal source), which in some systems and for some species can reflect mortality losses during dispersal, while in others it can simply reflect the relative probability of final destination of dispersal. The difference between the two approaches would be reflected in whether the total kernel volume is constant or is down weighted by cumulative cost, the latter reflecting losses (mortality) during dispersal, and the former reflecting purely the dispersal phase without any modeled mortality. Although it is conceptually possible to model mortality in CTBM, it does not seem to be a very trivial task (McRae et al. 2008). The main concern is related to the definition of probability of mortality so that the model does not overestimate death events. To simulate the probability of a random walker dying along the way, grounded resistors can be added on each node with resistance reflecting the probability of death as individuals pass through them (McRae et al. 2008). However, even if the probability of

mortality is high in a given node, individuals can still visit it several times since they are moving randomly, inflating the mortality rates. This is because individuals are not allowed to have memory or ability to perceive these high-risk points and, consequently, they are incapable of avoiding them (McRae et al. 2008). When incorporated this way, mortality is assumed to be constant independent of any individuals' condition (e.g., age or sex). Stochastic mortality depending on habitat quality defined based on human disturbances (Kanagaraj et al. 2013) or due to starvation and predation (Gardner and Gustafson 2004) can be associated with each movement step or time step within IBDMs and may be age-dependent (Watkins et al. 2015). This arguably is one of the main strengths and advantages of IBDMs, as incorporating both the effect of the landscape on dispersal (e.g., resistance) and mortality (e.g., risk) is essential to reliable predictions of the population-level implications of any landscape condition or change. Because dispersal is costly and often involves relatively high risk of mortality (Bonte et al. 2012), neglecting dispersal mortality may overestimate dispersers success and, consequently, landscape connectivity. In addition to the risk of mortality due to increased exposure to predators, energy costs and/or associated with the movement through inhospitable environments, it is important to identify and include human-induced dispersal costs that can impose additional risk mortality (Bonte et al. 2012). For example, even including baseline mortality, most of the patches were connected for lynx according to the IBDM developed by Kramer-Schadt et al. (2004), but adding realistic levels of road mortality produced an opposite scenario. This study reinforces the idea that in some landscapes, especially those intensely disturbed by human actions, the connectivity patch system may not only depend on the distribution of dispersal habitat or animal's vagility.

### *Individual variation*

Animal dispersal is driven by multiple factors, being often both condition-dependent and phenotype-dependent (i.e., some phenotypic differences are related to different dispersal propensity and individuals may adjust their dispersal tactics based on external factors such as habitat quality; Clobert et al. 2009). Because individual variability in dispersal behaviors has been widely documented for many species (Bowler and Benton 2005; Clobert et al. 2009) and can substantially impact connectivity estimates (Palmer et al. 2014), it is essential to incorporate this source of variation into analysis of dispersal and connectivity linkage design (Baguette et al. 2013).

All the models analyzed here that consider stochastic variation to produce multiple alternative routes incorporate some inter-individual variability, but stochastic variation does not enable separation of effects of particular organism characteristics on movement or connectivity. Additionally, it is possible to consider variation across individuals explicitly. For example, instead of considering only average individuals when describing the dispersal threshold in LC models and IBDMs, it would be interesting to use a range of values also allowing for the occurrence of less frequently observed long-distance dispersal events. Cushman et al. (2010, 2016) did something like this for salamanders and African lions, respectively, evaluating how a range of dispersal distances affect predictions of connectivity, and Elliot et al. (2014) showed how individual differences related to demographic groups affected connectivity of African lions, all using the resistant kernel approach. IBDMs may additionally incorporate variability in the parameters used to define dispersal behavior. All models that use resistance surfaces may also incorporate inter-individual variability in resistance values

to reflect different dispersal strategies such as that presented by bolder individuals, which may take greater risks during dispersal by crossing matrix components generally avoided by other individuals (Palmer et al. 2014).

### **Which model best explains real-world movement data?**

Improvements in tracking technologies integrated with remote sensing data have enabled the start of "a golden age of animal tracking science" (Kays et al. 2015). Despite this, there are still few studies comparing the predictive performance of connectivity models using independent dispersal data (Zeller et al. 2018). Given the immense and increasing interest in connectivity and dispersal modeling, there are few topics in landscape ecology and conservation biology more urgent than evaluating the relative performance and utility of alternative connectivity modeling methods, and under which situations and for which questions each is best suited. Here we present a brief summary of their main findings. The comparative validation of connectivity models has great implications mainly for conservation research since they can offer different solutions to the same problem (Avon and Bergès 2016). Besides that, validation techniques allow us to determine how well suggested corridors can capture the species dispersal process (Zeller et al. 2018).

Cushman et al. (2014) compared the performance of the neighborhood average landscape resistance (a local connectivity approach) against the predictions provided by factorial LC path and resistant kernel (synoptic connectivity approaches) in predicting highway crossing locations of American black bear. They found that the synoptic methods outperformed the local landscape resistance, indicating the species' movement

choices when crossing highways are influenced by landscape structure in broader scales than the local one. This study also showed that although factorial LC paths predicted the locations of crossing events slightly better than the resistant kernels, the latter model has a greater capacity to offer simultaneously high predictive performance and moderate sensitivity to differences in resistance values. Using the same system and data, Cushman (pers. comm.) also showed that both LC paths and resistant kernels outperformed circuit theory based approaches for predicting the locations of black bear highway crossing locations.

Several studies comparing the concordance of dispersal data with the results provided by circuit models and LC analysis showed a tendency of the former to outperform the latter. However, these studies used the classic version of the LC approach in which only a single LC path is identified (Jackson et al. 2016; McClure et al. 2016). Recently, Zeller et al. (2018) used a variety of data types from pumas (presence-only, GPS collar and genetic data) and different methods (SDMs, PSF, PathSF and landscape genetic framework) to build 32 resistance surfaces which through cost distance and circuit theory models were applied. From a comparative evaluation of the performance of each resistance surface/connectivity model combination in predicting independent puma dispersal data, they found that the cost distance algorithm used (which shares a great similarity with resistant kernels) outperformed circuit-based algorithm for GPS collar and genetic data.

In addition to dispersal, some papers have shown, comparatively, how well circuit theory-based model and LC analyses predict movement data at other scales. For instance, LaPoint et al. (2013) indicated that none of the models was able to predict well

within home-range movement corridors for fishers. Using migration data, McClure et al. (2016) showed that the LC path model predicted paths for elk slightly better when compared to the CTBM. Similar results were also observed for pronghorn migration (Poor et al. 2012) and wildebeest migration (Bond et al. 2017).

Comparing the performance of the dispersal rates derived from SMS with three other connectivity estimates (Euclidean distances, cumulative costs from LC path analysis and resistance distances from CTBM), Coulon et al. (2015) showed that SMS provided better estimates to predict genetic connectivity for a tropical forest and a temperate amphibian than the distance metric provided by the other models.

## Synthesis and Future Directions

The effectiveness of conservation efforts to mitigate the impacts of rapid global changes on biodiversity is strongly linked to our ability to adequately understand and represent the ecological processes underlying population dynamics. Given the negative impacts resulting from increasing habitat loss and fragmentation, landscape connectivity has been identified as a critical element for species persistence. The value of population connectivity is directly related to its critical function in sustaining dispersal and other movement types. Hence, the success of conservation measures focused on improving connectivity will depend on how well the models can capture the actual process of species dispersal. In this review, we describe the models most commonly used to predict connectivity and identify linkage structures in the landscape, highlighting their applications, main assumptions and limitations in representing the dispersal process.

The models discussed here represent animal dispersal through different perspectives. The new LC approaches break the assumption that the species have complete knowledge of landscape and disperse only by using optimal routes. Some of these models introduce stochasticity to simulate the possible variation of the routes followed by dispersers; other models smooth the LC paths to represent individuals' stochastic behavioral choices. Many of these methods include dispersal thresholds to more realistically reflect biological limitations on dispersal distances. The resistant kernel model depicts the dispersal in a diffuse form where all paths starting from a source location that imposes costs lower than the species capacity can be traveled, producing theoretically optimal measures of the dispersal incidence function. Through circuit theory, the dispersers are depicted as random walkers capable of traversing any possible paths between two locations. Routes with lower resistance are more likely to be followed by dispersers and no dispersal threshold is imposed. Individual-based dispersal models are the only ones with sufficient flexibility to incorporate species-specific movement behaviors and explicitly model the process of movement decisions and factors that may influence dispersal. Because all the models reviewed here are based on resistance surfaces, it is first necessary to ensure that these structures are reliable (i.e., represent the actual costs imposed by the different landscape elements to animal dispersal).

As dispersal is an organism-level process that involves three stages and multiple costs and risks, it may be heavily influenced by the inter-individual variation and the interaction among individuals. Therefore, an IBDM approach is likely to be most able to realistically model complex interactions of dispersal behavior with complex landscape patterns, temporal variability and inter-individual variation. Despite this, the individual

based models produced to date rarely incorporate inter-individual variation in life-history traits and behaviors. Although the volume of movement data in spatial and temporal resolution has increased in recent years, there are still few studies comparing the predictive power of models and the best data type to represent dispersal, and those able to do so generally consider a limited number of species and restricted geographical locations. In the near future, we expect that the increased availability of animal movement data will enable studies with more generalizable conclusions about the ability of different types of models and data to capture the dispersal process.

As connectivity is dependent on the interactions between species and landscape characteristics, we suggest that the choice of model should ideally result from the consideration of three factors: the complexity of the system (studied species plus focal landscape), the assumptions underlying the models in relation to animal movement and the study's objectives. It is essential that the target species' biology is known or estimated with precision, especially dispersal traits, so that a preliminary evaluation of the model's ability in representing the studied species' dispersal behavior is possible. We suggest that whenever possible, researchers should opt for approaches that can represent movement behavior more realistically, in addition to incorporating factors known to influence the species' dispersal success. When the use of these models is impracticable and/or the information on dispersal behavior is very limited or not available, estimating the connectivity from different models and confronting their results with empirical dispersal data will bring substantial gain for models' evaluation. In this scenario, performing sensitivity analyzes or incorporate uncertainty into the parameter estimates is also essential for evaluating the results robustness. We suggest a focused research agenda to explore the behavior, accuracy and similarities among

connectivity modeling methods (e.g., Cushman et al. 2014; Zeller et al. 2018). Specifically, we recommend studies that use simulations of animal movement, based on known and specified relationships between landscape resistance, mortality risk and other costs to generate movement paths, which then can be compared to the predictions of alternative connectivity modeling approaches. This will enable robust determination of the effectiveness of alternative connectivity modeling methods, much as simulation modeling has been instrumental in evaluating and improving methods in landscape genetics (e.g., Cushman and Landguth 2010; Shirk et al. 2012, 2017; Cushman et al. 2013a).

Lastly, although connectivity studies are often dissociated from population analysis, the integration of population dynamics and dispersal behavior models (e.g., Watkins et al. 2015) may provide an even broader and more realistic view of how landscape connectivity can be impacted by potential environmental changes and management strategies and what consequences this can bring to the species persistence. For example, individual-based models like CDPOP (Landguth and Cushman 2010) that incorporate realistic dispersal dynamics in resistant landscapes with differential mortality risks. Further expanding the spatial scale, dispersal models can also be coupled to niche-population models to explore theoretical and applied questions about species' spatial dynamics.

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## **Capítulo 2**

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### Evaluating analytical tools for designing multispecies habitat network

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## **Evaluating analytical tools for designing multispecies habitat network**

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## RESUMO

**1.** A perda e a fragmentação de habitat têm comprometido a viabilidade a longo prazo das populações de animais selvagens em todo o mundo. Portanto, o estabelecimento de redes de áreas protegidas capazes de fornecer habitat e conectividade é essencial para a persistência de múltiplas espécies. Como as redes de habitats podem ser projetadas a partir de métodos diferentes, é crucial saber se a escolha de ferramentas analíticas pode afetar o desempenho dessas estruturas espaciais em atender as demandas específicas das espécies-alvo. **2.** Aqui, nós criamos cenários de conservação otimizados para 11 mamíferos utilizando modelos de ocorrência e predizendo a conectividade a partir de dois modelos (teoria de circuitos e um algoritmo de caminho de custo mínimo). Em seguida, projetamos redes para múltiplas espécies usando duas abordagens de priorização: (a) somando os mapas de conectividade de habitat para todas as espécies e identificando áreas com grande valor de conservação (abordagem Interseção) e (b) aplicando o algoritmo Zonation usando a regra de remoção de células área-núcleo. Também exploramos o potencial da abordagem espécies focais como um atalho de conservação. **3.** Avaliamos a congruência espacial das áreas prioritárias indicadas pelas diferentes redes considerando múltiplas espécies (mapas compostos) ao longo de três limiares de conservação. Verificamos a correlação nas áreas comuns entre cada mapa composto e todos os cenários de uma única espécie. Também avaliamos a eficácia relativa de áreas prioritárias indicadas pelas redes compostas em abranger aquelas identificadas através de cenários projetados para espécies únicas. **4.** Em geral, as redes compostas resultantes de diferentes abordagens indicaram áreas prioritárias com baixa sobreposição espacial. A rede composta por todas as espécies cuja conectividade foi acessada através da teoria de circuito e a estrutura final montada através do método Interseção teve a maior capacidade de reter de forma semelhante os critérios de conservação para todas as espécies. A utilidade da abordagem espécies focais como um atalho de conservação foi dependente do método utilizado. Em alguns casos, o desempenho de redes de espécies focais mostrou um viés em favor de espécies com baixa capacidade de dispersão. **5. Síntese e aplicações.** Nossa estudo demonstrou que a escolha da abordagem utilizada para projetar redes de habitats para múltiplas espécies pode ser decisiva para a conservação das espécies-alvo. Sugerimos que as ferramentas analíticas sejam selecionadas de acordo com os objetivos de conservação, ao invés de arbitrariamente, assumindo equivalência entre os diferentes métodos.

**PALAVRAS-CHAVE:** teoria de circuitos, dispersão, abordagem espécies focais, conectividade da paisagem, modelagem de caminho de custo mínimo, conservação de múltiplas espécies, priorização espacial, Zonation

## ABSTRACT

**1.** Habitat loss and fragmentation have jeopardized long-term viability of wildlife populations around the world. Therefore, the establishment of protected areas networks capable of providing habitat and connectivity is essential for the persistence of multiple species. As multispecies habitat networks have been designed using different methods, it is crucial to evaluate whether the choice of analytical tools can affect their performance in meeting target species' specific demands. **2.** We built single-species-optimized scenarios for 11 mammals using occurrence models and predicting connectivity from two models (circuit theory and a least-cost algorithm). Then, we designed multispecies networks using single species requirements from two different prioritization approaches: (a) summing the predicted connectivity and habitat maps for all species and identifying areas with great value (Intersection approach) and (b) applying the Zonation algorithm using the core-area cell removal rule. We also explored the potential of the focal species approach as conservation short-cut. **3.** We evaluated the spatial congruence of the priority areas indicated by the different multispecies networks along three conservation thresholds. We verified the correlation in the common areas between each composite map and all single species scenarios. We also evaluated the relative effectiveness of priority areas indicated by multispecies networks to encompass those identified through single species scenarios. **4.** In general, multispecies networks resulting from different approaches indicated priority areas with low spatial overlap. The composite network formed by all species features through the Intersection method and circuit theory model had the greatest ability to similarly retain the conservation criteria for all species. The utility of the focal species approach as a conservation shortcut was dependent on the method used. In some cases, the performance of focal species networks showed a bias in favor of short-dispersal species. **5. *Synthesis and applications.*** Our study demonstrated the choice of approaches used to design multispecies habitat networks may be decisive for the conservation of target species. We suggest that the analytical tools should be selected according to the conservation objectives, rather than arbitrarily, by assuming equivalence between the different methods.

**KEYWORDS:** circuit theory, dispersal, focal species approach, landscape connectivity, least-cost modeling, multispecies conservation, spatial prioritization, zonation

## INTRODUCTION

Human-induced land use changes have strongly impacted wild populations, making them smaller, subdivided and, therefore, more vulnerable as habitat loss and fragmentation advance through natural landscapes (Fahrig 2003; Fischer and Lindenmayer 2007). Faced with this scenario of increasingly imminent extinction, protecting a collection of well-connected habitat patches capable of providing sufficient habitat for the long-term persistence of many species (i.e., a multispecies network of protected areas) seems to be one of the most powerful conservation strategies to mitigate the impacts of human activities on biodiversity (Albert et al. 2017). The design of multispecies networks requires a broad methodological framework necessary to define the conservation strategy, ranging from the selection of target species to the final conservation map construction (Albert et al. 2017). All methodological steps can be carried out through different approaches and two essential decisions are to choose the connectivity model and the strategy used to convert single-species data into a map of multispecies conservation priorities (e.g., Brodie et al. 2015; Krosby et al. 2015; Albert et al. 2017).

There are many ways of quantifying the importance of landscape elements for species dispersal (Rudnick et al. 2012; Kool et al. 2013; Dickson et al. 2018). Currently, the most used connectivity models are based on resistance surfaces, which are raster representations of landscapes where each cell receive a value according to the resistance or cost imposed by the landscape elements within the cell (e.g., habitat quality, altitude, climate suitability) on species movement (Zeller et al. 2012; Etherington 2016). In the circuit theory-based model (hereafter, CS model), the landscape is represented as a giant

electrical network where cells are converted into electrical nodes linked to each other by resistors whose values are defined according to the resistance surface (McRae et al. 2008). Circuit theory is related to movement ecology via random walk and the current values along cells are equivalent to net movement probabilities for individuals randomly moving through the landscape (McRae et al. 2008; Dickson et al. 2018). Thus, the maps of cumulative current flow can be used to identify pathways that are more likely to be used by individuals of a particular species (i.e., the most important areas for connectivity) during their movement (e.g., Dutta et al. 2016). The least-cost modeling (hereafter, LC models) emerged in the context of transport geography to find the ideal route (the least-cost one), considering all possible routes between landscapes (Etherington 2016). After its introduction in ecology, the LC model has become one of the most widely used methods for evaluating connectivity and many modifications of the initial framework have been proposed (Etherington 2016). From LC model, it is possible to prioritize areas for connectivity by identifying landscape pixels that are crossed by a greater number of paths (e.g., Ribeiro et al. 2017).

One of the most common approaches for the development of multispecies maps is to individually generate habitat networks for each target species (i.e., single-species-optimized networks) and build a consensus map of conservation priority based on their overlap (hereafter, Intersection approach) (e.g. Cushman and Landguth 2012; Crosby et al. 2015; Khosravi et al. 2018). Alternatively, the conservation solution for multispecies from single-species networks can be obtained from the Zonation software (Moilanen et al. 2005), a multispecies prioritization tool that allows to delineate near-optimal connected reserve networks considering the spatial conservation values of the landscape pixels for multiple species simultaneously (e.g., Early and Thomas 2007; Albert et al.

2017; Correa Ayram et al. 2018). The priority conservation map provided is produced according to the order of iterative removal of landscape cells that have the lowest marginal conservation value, which is determined by the input biological features (Moilanen et al. 2014). This hierarchical prioritization of the landscape can be done using different cell removal rules that determine the cells' marginal values based on different conservation conception and, consequently, define the order in which cells will be discarded (Moilanen et al. 2014).

Since connectivity and habitat mapping to individual target species can be time consuming, especially in larger regions, one alternative for developing multispecies networks that requires less analytical effort is the focal species approach (Lambeck 1997; Nicholson et al. 2013). This conservation shortcut is based on the selection of a small group of species whose requirements for persistence are able to define landscape attributes that satisfy the needs of the non-target, co-occurring species (Lambeck 1997). Focal species are generally identified through ecological characteristics indicating that they are the most demanding species in terms of area and dispersal (Lambeck 1997; Nicholson et al. 2013). As different approaches can result in different conservation solutions for the same problem (Avon and Bergès 2016), it is essential to test how the efficiency of multispecies networks can be determined by methodological decisions. Thus, comparative performance analyses of the different approaches used to identify priority areas for multispecies are essential for informing and guiding methodological decisions and improve conservation planning.

Here, we designed multispecies habitat networks by combining two connectivity models (CS and LC models) and two prioritization/design approaches (Intersection and

Zonation approaches). Then, we verified their performance in representing the individual spatial requirements of the target species. More specifically, we projected single-species and multispecies habitat networks for 11 mammals in a large region of the Atlantic Forest to answer the following questions: (1) Are multispecies networks designed from different connectivity models congruent with each other? (2) Does the choice of methodological strategy (connectivity model and prioritization/design approach) influence the ability of the multispecies network to encompass the individual spatial needs of its target species? (3) Is the performance of networks based on the focal species approach similar to scenarios derived from the full set of target species? (4) Is the representation of the target species in multispecies scenarios dependent on their dispersal ability? (5) Does the efficiency of conservation priority areas vary according to the methodological strategy applied?

## METHODS

### **1. Selecting the study area and the target species**

We designed multispecies habitat networks using the requirements of 11 mammal species (see Appendix 2- Table S1) distributed in a wide area of the Atlantic Forest (~207,015 km<sup>2</sup>) (see Appendix 1- Figures S1). We included in our analysis only species with: (1) at least 30 presence points along Atlantic Forest fragments; (2) at least 10 expert opinions attributed to resistance values; (3) a broad range with high spatial overlap with the other species' range. The final species present different levels of dispersal ability, matrix utilization and sensitivity to human disturbance, constituting a sample encompassing the regional diversity of mammals and their requirements. We

selected occurrence data collected from studies developed between 1999 and 2017 in the Brazilian Atlantic Forest from the databases available in Lima et al. (2017) and Bovendorp et al. (2017). We used the species distribution maps (IUCN 2018) to access the Atlantic Forest region common to all species geographical ranges. After delimiting our study area, we created the species-specific resistance surfaces by reclassifying the land use and land cover map at a resolution of 30m from MapBiomas dataset (MapBiomas 2018) according to the median of the values assigned by field and research experts to the land cover classes for each species (see Supplementary Information- Appendix 1).

## **2. Modeling the species occurrence**

To estimate the probability of occurrence of the target species along forest patches, we constructed species-specific multiple logistic models using six variables describing habitat patches (identified from the presence/absence points) and the landscape structure around them: patch area, patch climatic and topographic suitability, distance to urban infrastructure, matrix resistance, immediate landscape cohesion, and percentage of surrounding core area (Supplementary Information-Appendix 1). Because matrix resistance, immediate landscape cohesion, and percentage of surrounding core area are scale dependent, here we explored in greater detail the spatial scale of species' response to those variables. We ran simple logistic regression models in four species-specific scales equivalent to species daily movement distance and 25%, 50%, and 100% of the species' dispersal distance. Due to the layer resolution used to extract the landscape variables, for species with dispersal distance of less than 600 m (see Appendix 2- Table S1), we used only the scales represented by daily distance and 100% of dispersal

distance. For these species daily distance represented between 60-70% of the natal dispersal distance. Next, we identified the response scale of the variable as the scale that obeyed the largest absolute regression coefficient (e.g., Zeller et al. 2016). The species' dispersal capacity (Sutherland et al. 2000) as well as the daily movement distance (Carbone et al. 2005) were derived from allometric relationships using body mass (Smith et al. 2003) and diet (Wilman et al. 2014).

We developed a multi-scale, multiple logistic regression models for each species using as predictors the independent and the scale-dependent variables at their respective response scale. Because small sample sizes can bias model building with multiple parameters, here we restricted the maximum number of variables in the final models to three. For each species, we performed all possible combinations of three predictors using the six variables. We verified the correlation between the parameters using Pearson correlation test and retained only poorly-correlated variables ( $r < 0.7$ ). We compared the different models used to predict species occurrence through the Akaike Information Criterion corrected for small sample sizes (AICc). We used the best model in predictive accuracy to predict species occurrence probability along the forest patches located in the study area. Due to the large number of small habitat patches in the study area, we arbitrarily limited the models' prediction for forest patches with area equal or greater than 10 ha ( $N = 29,900$ ). Thus, the final habitat patch map for each species presents a unique set of forest fragments with different probability of occurrence values (ranging from 0 to 1) determined by the selected variables in the best multiple logistic regression model. The final map was truncated based on a threshold where the receiver operator curve (ROC) is closest to the perfect fit. We use the map of forest fragment with predicted occurrence as reference to model connectivity (see above). However, the

continuous map (ranging from 0 to 1) was also used as a conservation criterion (habitat quality) to produce the multispecies networks.

### **3. Modeling connectivity**

We used two connectivity models to quantify the importance of the pixels in the study area for the target species' dispersal. Although the two models are based on resistance surfaces, their algorithms represent the dispersal process through distinct perspectives, showing different performance in predicting empirical dispersal data or genetic connectivity (Coulon et al. 2015; Zeller et al. 2018) and, consequently, providing discordant conservation solutions in some situations (Avon and Bergès 2016).

The circuit theory-based model was applied using an omnidirectional adaptation that is independent of the placement of source-target points or patches, demanding only species resistance surface (Pelletier et al. 2014). Using the method described in Pelletier et al. (2014), we first partitioned the resistance surface of the species into a series of small square blocks of 500 x 500 pixels (the tiles) and, in a loop structure, we applied to each tile individually the next steps. First, we determined a buffer radius equal to 500 pixels from the tile's edge, which was filled using resistance surface data. Next, the current was passed across the buffer incorporating the tile in orthogonal directions (i.e., south-north and east-west) through two independent runs using as input/output regions areas having 1-pixel wide arranged in parallel and located in the buffer boundaries (see Figure 2 in Pelletier et al. 2014). After the buffer extraction, we added the two current density raster blocks for each tile. Thereafter, we gathered all the final tiles to obtain the current density map of the entire study area. Finally, from the final mosaic of each

species, we selected only the current density values within buffers established from the edges of all patches present on the species habitat patch map. Buffer radius was defined according to species dispersal capacity. We executed this omnidirectional fashion of the circuit model using the software R and Circuitscape (Shah et al. 2008).

There are many methods to model connectivity derived from the classic least-cost path analysis. Here we used the LC model implemented in the software LandScape Corridors (LSCorridors) that simulates multiple movement paths considering different sources of random variation (Ribeiro et al. 2017). Beyond the resistance surface, LSCorridors requires as input a raster map indicating the pairs of source-target patches between which the movement of individuals is assumed. At each simulation, the algorithm selects different target and source points within a particular pair of patches to be connected, thus representing different departure and arrival points of the movement routes (Ribeiro et al. 2017). In addition to the random target locations, a second source of stochastic variation is added to the path simulations through a variability parameter that modifies the resistance values, which may represent uncertainties associated with the definition of the resistance surface. LSCorriors offers four route simulation methods that differ from each other in the way they incorporate landscape context into simulations (Ribeiro et al. 2017). Here, we used the MP method, which considers the information for each pixel separately, to simulate 30 possible routes for each pair of target-source patches using the default value of the variability parameter (equal to 2) for all species. We defined pairs of target-source patches individually for species integrating different spatiotemporal scales of connectivity through the metapatch concept (Zetterberg et al. 2010; Mimet et al. 2016): short-range connectivity that is

defined by the species' daily movement distance and the long-range connectivity represented by the species' dispersal distance (Supplementary Information-Appendix 1).

From the simulated routes resulting of the LSCorridors, we constructed a density map for each species showing how many movement trajectories cross each landscape pixel according to the connectivity model. In these path density surfaces, as well as in the current density map derived from Circuitscape, pixel values were standardized to range from 0 to 1, and the higher the pixel value, the greater the probability that the cell will be used during the dispersal of individuals for a given species.

#### **4. Designing single-species and multispecies networks**

We assembled two species-specific networks for each species by adding the habitat quality map to each connectivity surfaces and rescaling pixel's value to vary from 0 to 1. After obtaining the single-species-optimized scenarios, we built multispecies networks using two different approaches which were applied equally for the connectivity models. In the Intersection approach, we summed all species-specific networks to form a composite conservation scenario and standardized the final raster to vary from 0 to 1. We used Zonation software v.4 (Moilanen et al. 2005) as an alternative way to design multispecies networks. Zonation is a decision support tool conceived to identify areas important to maintain habitat quality and connectivity for multiple species considering different biodiversity features. Here, we defined as biological features the single-species habitat quality maps and connectivity surfaces (totaling 22 input layers), attributing equal weights to each species and feature layer. We used the core-area removal rule and the edge removal rule; this last parameter

determines that cells are removed from the edges of the landscape remaining instead of anywhere, saving computing time (Moilanen et al. 2014).

To implement the focal species approach, we first identified the species with the shortest mean dispersal distance (the dispersal-limited species), the species that had the largest absolute regression coefficient for the variable patch area (the area-limited species) and the species that presented the highest sum of resistance values for urban infrastructure, agriculture, and pasture (the matrix-limited species). According to these criteria, *Akodon montensis*, *Leopardus wiedii*, and *Oryzomys russatus* were selected as the dispersal-limited, area-limited, and matrix-limited species, respectively. Next, we designed multispecies network considering only the spatial requirements (species-specific networks) of the three focal species from Intersection and Zonation methods, and rescaling the final map to a 0 to 1 range in the first case.

## **5. Determining the efficiency of multispecies networks**

After designing the multispecies networks, we evaluated the degree of spatial agreement between them by calculating the overlap percentage between the priority areas indicated by each network along three conservation thresholds: 17% (Aichi Biodiversity Target 11), 10%, and 5%. We used Spearman rank correlation coefficient for measuring the similarity between each single-species-optimized scenario and its corresponding area within the different multispecies networks. The average correlation coefficient at the species-level and its standard deviation were used as network performance measures. A multispecies network with high average and low standard deviation indicates that its final structure is able to efficiently cover the individual demands and does so in a

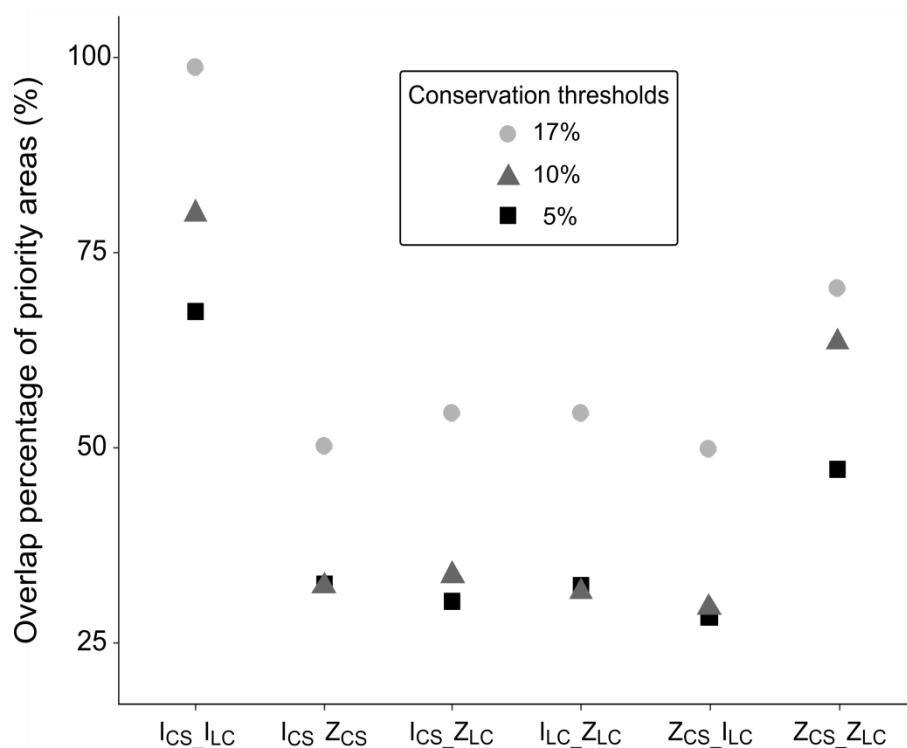
similar way throughout the species. To identify if there is any potential bias in the capacity of the multispecies networks encompassing the species requirements along movement traits, we regressed the rank correlation coefficient computed between the multispecies and single-species networks against the species' dispersal ability. We compared the performance of this relationship for each network with what would be expected by a null model, through an error-effect ratio. We replicated the null model 1,000 times and ran the regression for each replicate of the randomized network predictions, recording the  $R^2$  for each randomization. We then calculated a statistical effect-error ratio (Ellis 2010), in which the statistical effect is represented by the  $R^2$  of the observed relationship, and the statistical error is the standard error of  $R^2$  (Efron and Tibshirani 1993), estimated as the standard deviation of the null  $R^2$ . The ratio between the observed  $R^2$  (effect) and the standard error of local  $R^2$  (effect) follows a z-distribution and is a standardized measure of how much the observed effect is greater than the statistical error. Standard statistical interpretation argues that an effect at least two times larger than the error (i.e., an effect-error ratio of 2) represents substantial evidence that this effect would not have been obtained by sampling error with a 95% confidence level (Rangel et al. 2015). In order to verify the efficiency of priority areas selected from the different multispecies networks in covering the areas with the highest conservation value for each target species, we calculated the percentage of the single species networks retained at the intersection between the priority areas identified only using single species scenarios and the priority areas indicated by the different multispecies scenarios across several thresholds. A spatial overlap equal to the threshold from which it was calculated, it means that the identified areas are completely coincident. For example, obtaining a 10% overlap when 10% of the networks are selected as priority areas means that if we protect 10% of the multispecies network with

the highest conservation value, we are also representing 10% of the areas with the highest priority considering the individual spatial needs for a given species. A value of spatial overlap less than its threshold indicates that the species is under-represented and a higher value indicates otherwise. All spatial and statistical analyzes were performed in the R 3.5 environment (R Core Team 2018b)

## RESULTS

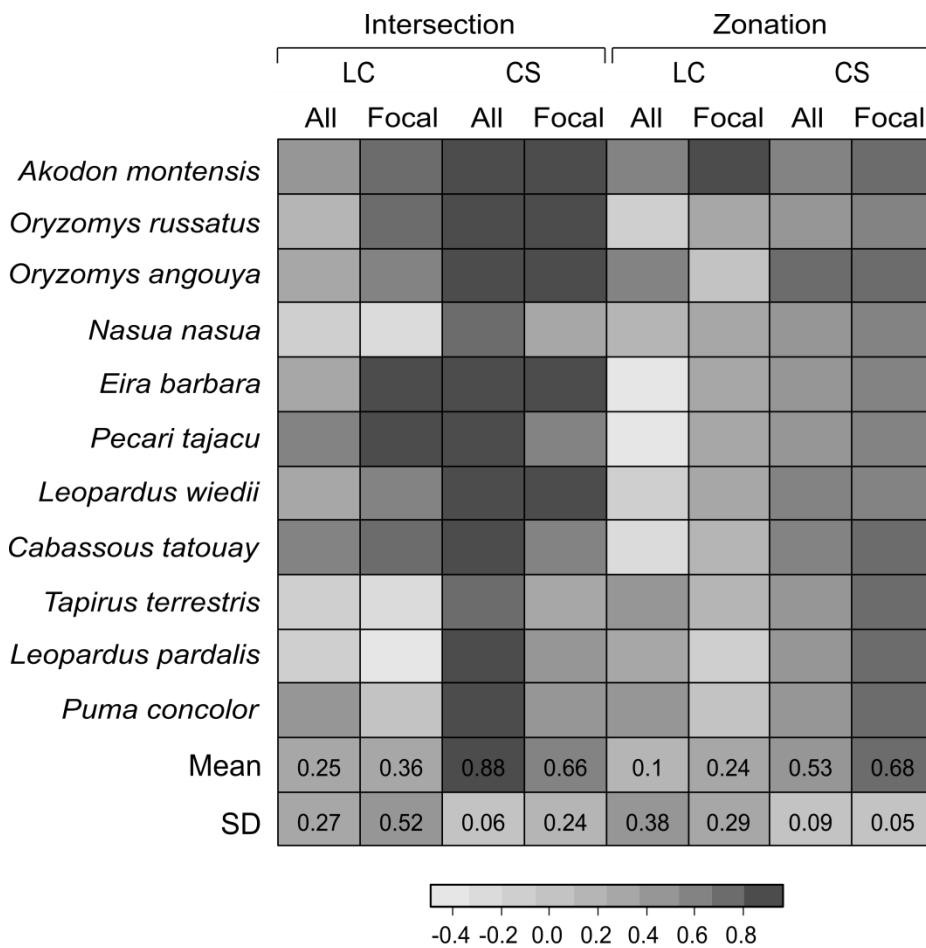
Nine of the eleven multi-scale, multiple logistic regression models explaining target species occurrence had area under the receiver-operator characteristic curve (AUC) values between 0.70 and 0.90, indicating moderate accuracy (see Appendix 2- Table S1). The target species were sensitive to different combinations of the variables used to describe the forest fragments and the surrounding landscape. Only *Nasua nasua* and *Oryzomys angouya* had their presence affected by the same variables, but at different response scales. While the first species was negatively related to the resistance around the patch in a radius equivalent to 25% of its dispersal distance, the second species responded negatively to the resistance in an area limited by its daily movement distance. Five of the eleven species were affected at different scales by the physical connectedness of the forest fragments around the patches, but two of them responded negatively to these structural connectivity (*Tapirus terrestris* and *Akodon montensis*), showing to be favored by the discontinuity of forest fragments in immediate landscapes to focal patches. Among the scale-independent variables, patch climatic and topographic suitability and area were the most frequent, present in the best model for six and five species, respectively (see Appendix 2- Table S1).

Overall, conservation priorities identified in the multispecies networks resulting from different prioritization methods had low correspondence (Figure 1 and Appendix 2-Figure S2). This spatial disagreement was observed even for those networks in which dispersal was predicted from the same connectivity model. For instance, the congruence between CS networks designed from Intersection and Zonation approaches ( $I_{CS}/Z_{CS}$ ) was only 32% for the 5% and 10% thresholds. The same result was also observed for networks whose connectivity pattern was determined by LC modeling (Figure 1). Even by modeling species dispersal through different algorithms, as the conservation thresholds increased, we observed a considerable increase in the overlap percentages between the networks derived from the same prioritization method. When we overlapped the top 17% priorities of the Intersection networks ( $I_{CS}/I_{LC}$ ), the identified areas were virtually identical (overlap percentage equal to 98.6%).



**Figure 1** Pairwise spatial agreement between priority areas identified from different multispecies habitat networks designed from two prioritization methods (Z – Zonation, I – Intersection) and two landscape connectivity models (CS – Circuit theory-based model, LC – Least-cost model implemented through *LSCorridors* software). Conservation priorities were selected considering cells in the top 5%, 10%, and 17% of the study area.

Accounting for the capacity of the multispecies networks to encompass the individual target species' habitat requirements, we found that the multispecies scenarios showed average rank correlation coefficients between 0.1 and 0.88 (Figure 2), indicating that the network performance varied from very low to high according to the methodological strategy used. In general, the composite networks projected from the CS model presented higher average spatial similarity with the single species networks than the LC networks. The same result was also observed from Intersection networks in relation to the Zonation networks. Among all multispecies scenarios, the Intersection CS network showed the greatest capacity to retain similarly of most of the target species' spatial demands (average correlation coefficient =0.88, SD=0.06). The networks of 9 of the 11 target species showed negative correlation with at least one of the four LC networks projected from the requirements of all species or only of the focal species, indicating the existence of regions with conflicting conservation values. The full multispecies Zonation LC network had the worst performance presenting divergences with optimized scenarios for five species (Figure 2).

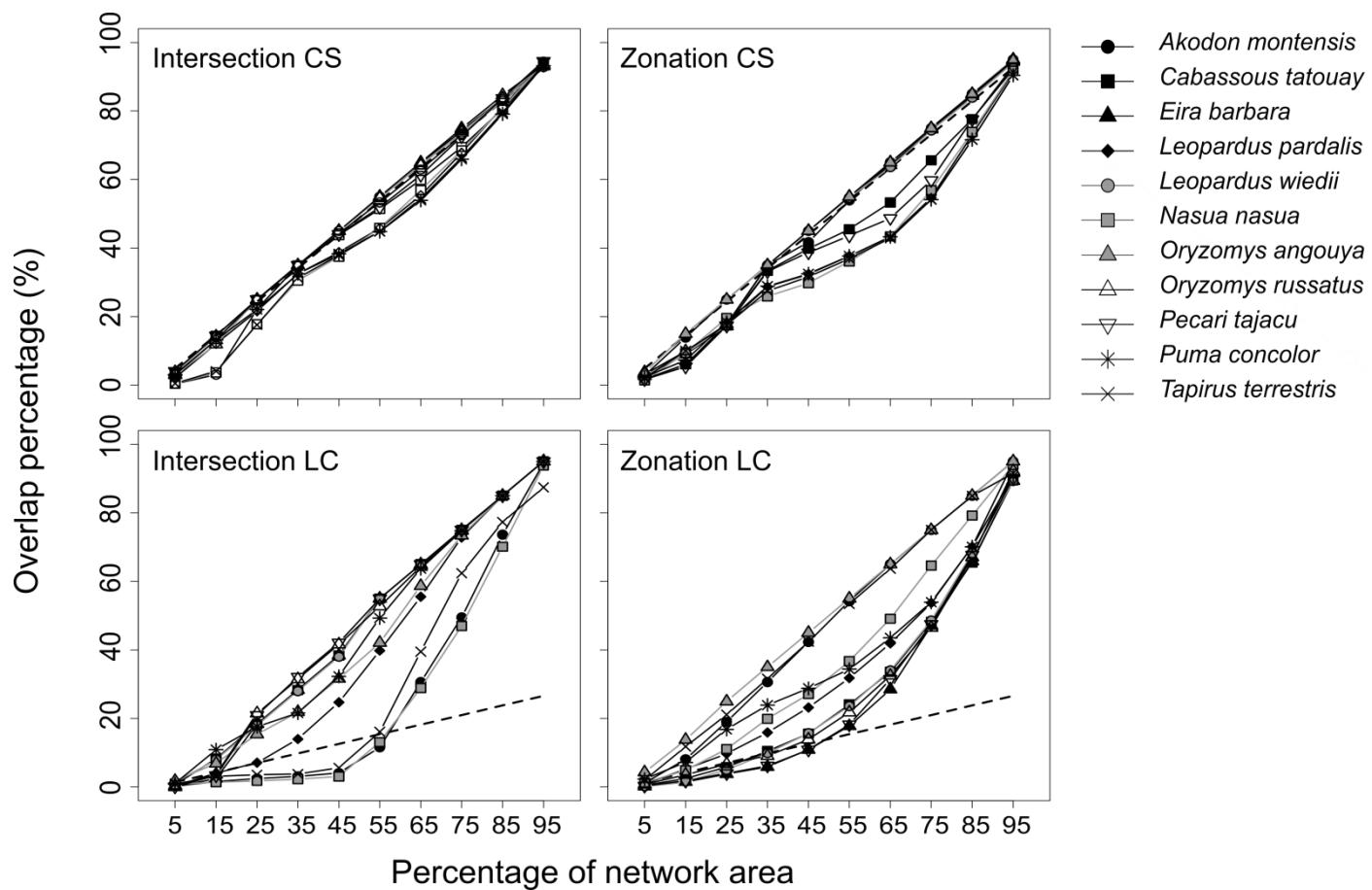


**Figure 2** Performance of multispecies networks (columns) composed of habitat quality and connectivity criteria for all target species (All) and using the focal species approach (Focal) to encompass the individual spatial needs of the target species (rows). The pairwise spatial overlap between the composite networks and single-species-optimized scenarios was measured using the Spearman rank correlation coefficient. The higher the coefficient, the greater the similarity between scenarios. All networks were standardized to range from 0 to 1 before correlation tests. (Z = Zonation, I = Intersection, CS = Circuit theory model, LC = Least-cost model)

We found that the Intersection LC network projected using only focal species presented an average performance 44.7% higher than the network considering all target species (Figure 2). In contrast, for the Intersection CS network there was a 24.8% reduction in the average correlation coefficient if we replaced the full multispecies network by the one derived from the focal species approach. In both cases, the use of the surrogate

strategy reduced the similarity with which conservation criteria were retained for all species (i.e., there was an increase in the standard deviation). Regardless of the connectivity model, networks resulting from Zonation software application using focal species presented higher average performance and lower standard deviation than the full species networks. We observed a negative relationship when the species dispersal capacities were regressed against the Spearman rank correlation coefficients for focal species networks. We found this relationship had an effect at least two times higher than would be expected considering the error for three focal species networks: Intersection CS and LC, and Zonation LC. Thus, species that disperse at shorter distances have their habitat networks better represented than long-distance dispersal species in multispecies networks designed from these approaches.

Among all the composite scenarios, priority areas identified from the Intersection CS and Zonation CS networks had high correspondence with the priority areas identified in the individual scenarios of practically all species (Figure 3). For example, the selection of 25% of the Intersection CS network area with the highest conservation value encompassed, in average, 23% ( $\pm 3\%$ ) of the area with greater potential to maintain habitat and connectivity for all target species. This spatial agreement of the priority areas was also observed for some species when we evaluated the LC networks, but it was at the same time totally contrasting to other species depending on the prioritization method used. For example, while protecting 45% of the area with the highest conservation value in Intersection LC network means to protect only 5% of the priorities for *Akodon montensis* and *Tapirus terrestris*, using Zonation LC network we increase this perceptual to 42% at the same conservation threshold (Figure 3).



**Figure 3** Performance curves for conservation prioritization based on different multispecies networks (i.e., the percentage of spatial demands of each species represented in the multispecies schemes along different prioritization thresholds). For a given multispecies scenario at the 5% threshold, for example, we ranked all pixels of this composite network according their conservation values as well as the pixels of the single species networks, selected the cells in the top 5% of both networks and computed the percentage of the single species networks retained at the intersection. The spatial overlap was done using the single species networks projected from the same connectivity model used in the multispecies models. The dashed line refers to the percentage of the study area represented in the selected area of multispecies networks along the area thresholds. (CS = Circuit theory model, LC = Least-cost model)

## DISCUSSION

The effectiveness of a protected areas network is related to its ability to simultaneously meet the demands required by the long-term persistence of multiple species (Nicholson et al. 2006; Beier et al. 2008; Albert et al. 2017). However, the great challenge is how to develop a spatial structure capable of providing habitat and connectivity to a set of species that should preferably present contrasting life histories and movement characteristics (Nicholson et al. 2006; Albert et al. 2017). In this study, we used different strategies to design wildlife linkages and prioritize multispecies habitat networks for a diverse set of mammals in a broad region of the Atlantic Forest. By assessing the performance of these composite spatial structures on representing the individual requirements of the target species, our work demonstrated that the ability of multispecies habitat networks to encompass important areas for the conservation of target species vary widely according to the methodological approach used.

We found that the application of different prioritization methods can lead to widely divergent conservation solutions (Figure 1). At 5% and 10% conservation thresholds, the overlapping of the priority areas provided by the Zonation and Intersection approaches was only about 30%, a result observed independent of the connectivity model. We believe that this mismatch in the spatial distribution of priority areas occurred mainly because of the different conceptions of how conservation value is determined along the study area. Applying the Zonation algorithm using the core-area cell removal rule, as was done here, implies that the cells' removal order will be dictated by the highest value of the most valuable biological feature (Moilanen et al. 2014). Here, we do not assign different weights to habitat quality and connectivity layers, we

assume that it is equally important to protect all these features. According to this approach, a cell has a high conservation priority if it has very high value for at least one of the two biological features and for at least one species. Prioritization based on the core-area Zonation produces solutions capable of providing habitat and/or connectivity with quality independent of the quantity of benefited species. In contrast to this high-quality prioritization, the Intersection approach assigns high value to cells that have the highest conservation value for most species. Through this additive approach, areas capable of retaining the conservation criteria for most species are prioritized, even though they are not very efficient from the species-specific perspective. This approach is very similar to that applied using Zonation through the additive benefit function as cell removal rule (Moilanen et al. 2014). Here we decided to sum the maps and find the areas with the highest values instead of using the additive benefit function in Zonation because the first is a more common practice between the analysis of connectivity planning (e.g., Cushman and Landguth 2012; Crosby et al. 2015; Khosravi et al. 2018).

The connectivity model choice to form a multispecies network was also a determining factor of its ability to represent individual species requirements. Because the connectivity models presented here have their own fundamentals and mathematical background, when choosing a given model we are assuming important differences in animal dispersal behavior. The application of circuit theory to model movement paths, as well as gene flow, was due to well-defined pre-established relationships between elements of electric circuits and random walks in analogous graphs (McRae et al. 2008; Dickson et al. 2018). Consequently, by using circuit theory, we assume that organisms move randomly, making their decisions only from their immediate surroundings and, therefore, it has been suggested that the model is particularly appropriate for predicting

natal dispersal routes (McRae et al. 2008; Dickson et al. 2018). In contrast, the classical least-cost analysis assumes that the dispersers have full knowledge of the landscape since considering all possible routes between two locations they will always follow the one that offers the least total resistance (Etherington 2016). Although this tendency to follow optimal travel routes may be adequate for modeling some species migration (Poor et al. 2012; Bond et al. 2017) or even predicting patterns of movements across known areas, assuming that individuals will follow optimal paths during natal dispersal can be a great mistake. In recent years, numerous modifications of the classic least-cost analysis have been proposed in an attempt to overcome the deterministic view of movement process consequent of its framework (Etherington 2016; Ribeiro et al. 2017). The algorithm used here, for example, incorporates two sources of stochastic variations in the least-cost modeling which may represent both the stochastic variation inherent in dispersal process and the uncertainty in the parameter definition (Ribeiro et al. 2017). Although most users have applied the CS and LC models as alternative strategies for assessing connectivity, some studies use them as complementary approaches (e.g., Howey 2011; Dutta et al. 2016).

Some species-specific scenarios showed a negative correlation with the multispecies networks for which connectivity was modeled using LC algorithm (Figure 2), indicating the existence of areas with conflicting conservation values. These incompatibilities may have originated due to two main factors. First, our habitat quality models showed that the occurrence of target species was limited by different landscape characteristics at different scales (Appendix 2- Table S1), and this heterogeneity led to the selection of unique sets of habitat patches from which the connectivity was evaluated individually for each species. Second, inconsistencies in the connectivity patterns of target species

may have arisen because of their contrasting movement strategies, since the set of species has been chosen to maximize the diversity of movement ecologies. While it is desirable for multispecies networks to be efficient for the largest and most diverse set of species possible, the existence of conflicts in the species-specific representation may be unavoidable when the network is designed to simultaneously meet the wide range of life-history and movement traits (Breckheimer et al. 2014; Brodie et al. 2015). Because species exploit habitats differently at specific scales, multispecies habitat networks will hardly be as effective as the spatial structures designed to meet the species needs exclusively. This trade-off between single- and multi-species in connectivity planning was evaluated by Brodie et al. (2015) who argued that multispecies networks are more efficient when designed to support connectivity for ecologically similar species rather than when built from a very diverse group. In a recent work, Meurant et al. (2018) showed that both the quantity and the selection criteria of surrogate species are important to determine schemes' performance to prioritize habitat and connectivity for multiple species. In addition to factors that can naturally lead to habitat incompatibilities between co-occurring species (e.g., different habitat preferences, competition, and predation), recent human-induced habitat modifications can create or intensify disparities in landscape use among species and, consequently, their ability to indicate habitat and connectivity to each other (Breckheimer et al. 2014; Diniz et al. 2018). Because habitat incompatibilities among species are not uncommon and can affect the performance of conservation solutions (Brodie et al. 2015; Beaudry et al. 2016), we recommend to address this factor explicitly in multispecies networks planning.

Our results indicated that the utility of the focal species approach as surrogate strategy may be dependent on the adopted methodological strategy. While the scenario resulting

from prioritization through the Zonation algorithm using only the focal species' biological features outperformed the scenario of all species, independent of the connectivity model, for the Intersection method this happened only when LC model was used. The value of the focal species approach as a conservation short cut was also demonstrated by Nicholson et al. (2013) once they showed that reserve system based on three focal species (the most area-limited, least fecund, and dispersal-limited species) was able to minimized the expected species loss in a larger group of 10 species from which the focal species were selected. Despite its potential as a conservation surrogate, our results point out that the use of the focal species approach may disproportionately benefit species with lower dispersal ability.

Our study demonstrates that some of the analytical tools most commonly used to design multispecies habitat networks are not interchangeable. These tools should be selected in a way that is strongly aligned with the conservation objectives, rather than being arbitrarily selected by assuming equivalence between them. The way in which multispecies networks are structured can determine how efficient they will be in representing the target species' specific demands and which species will be best represented. We hope that future studies expand the range of procedures to be evaluated in multispecies habitat network.

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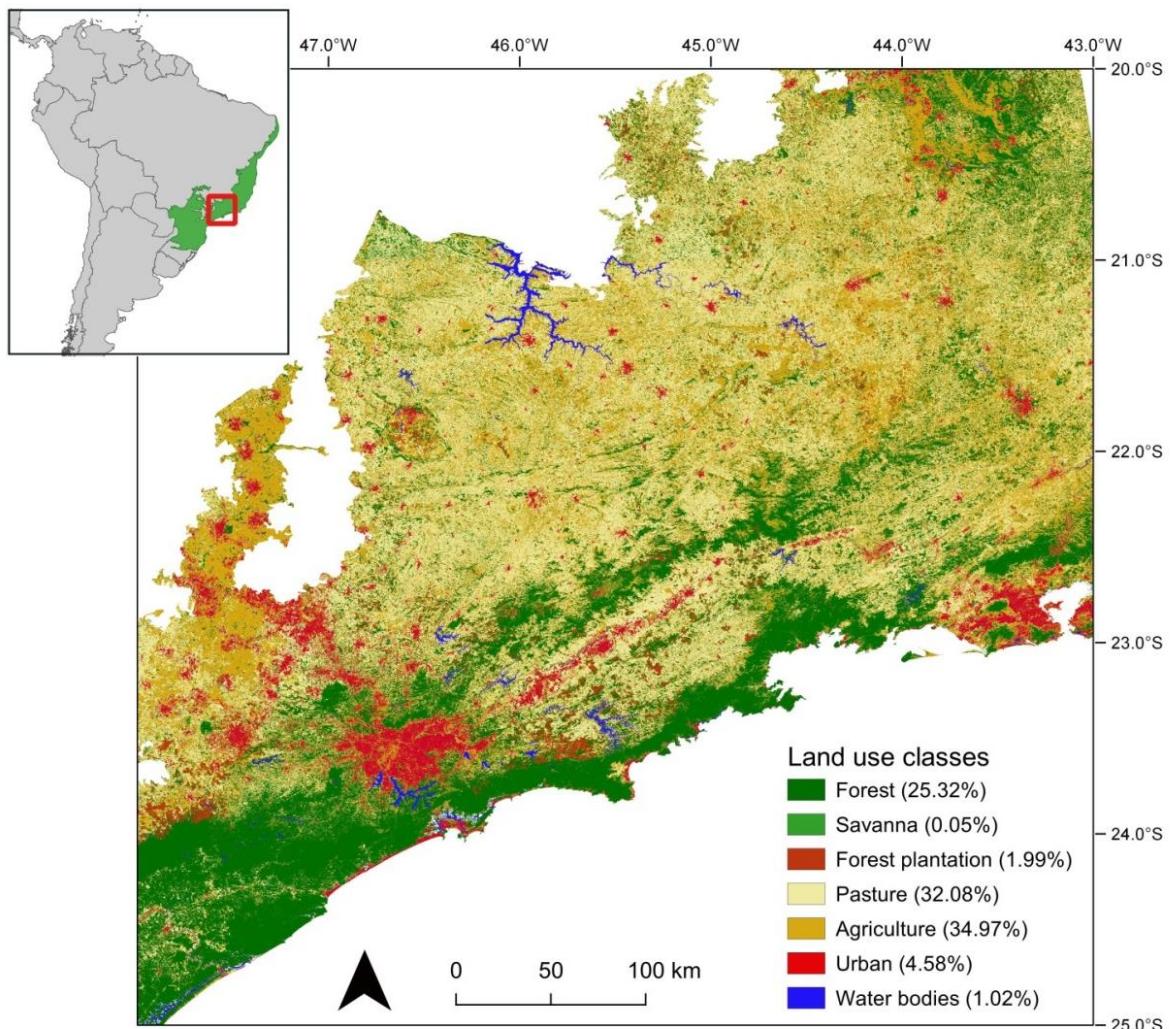
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## Supplementary Material 1: Evaluating analytical tools for designing multispecies habitat network

### Appendix 1 – Methods



**Figure S1** Land cover/use in the study area ( $\sim 207,015 \text{ km}^2$ ). The values in parentheses indicate the percentage of the study area occupied by each class.

### Selecting species presence and absence points

We used presence data from studies developed in the Brazilian Atlantic Forest. Because the land cover and land use maps used in this study (MapBiomas, collection 2.3) are available to our study region from 2000 to 2016, we used presence data recorded only

between 1999 and 2017. We identified the absence points for the species within each database following a species-specific procedure. First, we selected all study sites that did not obtain any record of the species and excluded all points outside its range (IUCN 2018). Next, we identified the minimum sample effort required to capture the species using all data collected in surveys conducted from 1999 to 2017. Afterwards, we selected as points of absence all the sites studied within the species range of that had a sampling effort equal to or greater than the minimum effort able to detect the species, but which, however, were not successful in their capture or observation. For species in which the proportion between presence and absence data was discrepant ( $<0.45$  or  $>0.55$ ), we equated the number of points between the two groups by randomly sampling the excess set. The absence data is assumed in the logistic models that are used to predict species occurrence over the landscape.

### **Assessing species-specific resistance surfaces**

Resistance surfaces can be constructed through expert opinion, detection data, relocation data, pathway data, or genetic data (reviewed by Zeller et al. 2012). Although measures of resistance derived from empirical approaches are preferable rather than expert opinion, in some situations this latter approach may be the most appropriate. We have decided to use expert opinion for two main reasons. The detection data used here were mostly recorded along forest fragments and using them to construct resistance surfaces could underestimate the importance of matrix for species movement. The absence of other movement data for most species has prevented us from using more refined approaches.

We were able to gather the opinion of 59 research experts in mammal field work on the resistance values presented by the eight land cover classes to the species movement (values varying from 1 to 100, with higher values indicating higher resistance). On average, we obtained the response of 12 specialists per species and included in this study only species with 10 or more opinions. We created the resistance surfaces for the species by reclassifying the land use and land cover map according to the median value assigned by the specialists for each class.

## **Modeling the climatic and topographic suitability**

Here, we modeled the climatic and topographic suitability of species by modeling species distribution through an Ecological Niche Model (ENM) that accounted for bioclimatic variables and altitude. We extracted the climatic information for our study region using the 19 bioclimatic and altitude variables available in the WorldClim database (Hijmans et al. 2005). The 19 bioclimatic and altitude variables were reduced into principal components (PCs) of a principal component analysis (PCAs). We created an ENM for each species using Maxent, a modeling procedure that only requires presence data to fit the model (Phillips et al. 2006). Among presence-only algorithms, Maxent has a good performance (Elith et al. 2006) and is one of the most used algorithms. For each species the model was built with species presence points and the PCs. To reduce sampling bias in the presence points we used a geographical filter into the occurrence data, removing excessive points which are close to each other (See de Oliveira et al. 2014). The models were calibrated using 70% of the occurrence points as the training sample, and the remaining 30% as the testing data. Here, we used AUC to evaluate the model. On the one hand, an AUC value of 0.5 indicates that model's prediction is equal to a random model. On the other hand, AUC values larger than 0.7 are considered accurate, with values between 0.7 and 0.9 indicating moderate models and values larger than 0.9 excellent models in their accuracy power. After running the models, we extracted species mean suitability for each forest patch. This variable represents the suitability of species in each location given the topographic and climatic conditions. The species suitability is then assumed as a predictor variable in the logistic models to give a more complete information of species requirements when predicting species occurrence at landscape scale (Hasui et al. 2017).

## **Extracting variables from the presence/absence points**

After selecting the presence and absence points for each species, we used the following strategy to obtain the variables used in the multiple logistic models. First, we identified the year when the presence or absence records were obtained (for data that were collected in surveys that lasted more than one year we determined the median of the period as the year of study). We calculated the parameters using the land cover maps at

a resolution of 30m from the MapBiomas database (MapBiomas 2018) corresponding to the year of study for each record. For each presence or absence point we arbitrarily established a buffer with a radius of 300 m (equivalent to 10 cells in the raster) and selected the forest patch with the largest area contained in it as a focal fragment. For each identified patch we accessed the following variables:

1. *Patch area*: number of pixels in the focal patch
2. *Climatic and topographic suitability of patch*: the average climate and topographic suitability for each focal patch using the information extracted from the species distribution models (see the section above).
3. *Distance to urban infrastructure*: the minimum distance in meters between the focal patch and the nearest pixel of urban infrastructure (e.g., cities and roads).
4. *Matrix resistance*: resistance offered by the matrix types surrounding the focal forest fragment to the species movement. The matrix resistance index (MRI) was calculated using the following formula:

$$MRI = \frac{\sum(RV_s * A_s)}{A_b}$$

where  $RV_s$  is equal to the resistance value of landcover type  $s$ ;  $A_s$  is the area occupied by landcover type  $s$ ; and  $A_b$  is the total area of the buffer around the forest fragment  $b$ . The resistance values of landcover types for the movement of each species were attributed based on expert opinion (see the section *Assessing species-specific resistance surfaces*). The MRI is a modification of the Matrix Permeability Index presented in Goulart et al. (2015); however, instead of using permeability values, we used the median resistance values offered by the landcover types (assigned by the specialists to each species). The higher the value of the index, the greater difficulty the species will have in crossing the matrix around the fragment. If the buffer was totally covered by forest (which has cost equal to 1 for all species of this study) or by any other class of landcover with resistance value equal to 1 (the lowest value between the types of landcover surveyed), the MRI value would be equal to 1. In this highly permeable scenario, the movement of individuals would be highly favored by the minimum resistance offered by the environment, and the extent of movement would depend only on their maximum dispersal distance.

5. *Immediate landscape cohesion*: a measure of the forest fragments' physical connectedness in the immediate area to focal patches limited by a buffer

extension. The cohesion index varies from 0 to 100, with higher values indicating greater aggregation in the distribution of forest fragments. The cohesion index is equal to 0 if there is a single non-background cell in the buffer.

6. *Surrounding core area*: relative amount of core area habitat (defined from a 1-pixel edge, equivalent to 30m) within a buffer around the focal patch.

Matrix resistance, patch cohesion index, and percentage of core area were calculated at different scales defined according to the daily movement distance and the maximum dispersal of the species. The three scale-dependent variables in their respective response scales, along with the remaining three scale-independent variables, were used to construct the logistic regression models.

### **Finding the source-target locations to apply the least-cost model**

We designed spatial arrangements by establishing links between forest patches that had high probability of species occurrence. In this step we use the framework based on the metapatch concept proposed by Zetterberg et al. (2010) and slightly modified by Mimet et al. (2016). This approach can integrate the different spatio-temporal scales involved in connectivity. In fragmented landscapes, such as the landscapes studied here, many species need to move along small, scattered habitat patches, instead of one, large, contiguous habitat patch, to reach the different types of resources required during their life cycles. In this context and from metapatch concept, the links among habitat patches are determined based on nested scales (Zetterberg et al. 2010). On a smaller scale different patches can integrate the home-range of one or more species' individuals if they are connected through daily movement. All habitat patches connected by daily distance belong to a metapatch population. The second scale is broader and considers that the different metapatch populations within a region can be connected through the dispersal process (Zetterberg et al. 2010; Mimet et al. 2016).

We decoupled the daily movements within the home ranges and the population (intra-population movements) of the dispersal movements (among populations) for each species using the average daily distance and median dispersal distance obtained through the allometric relationship mentioned in the main text. As was done in Mimet et al. (2016) we use two different strategies to construct the graphs for species with low and

high capacity of movement. For species with more limited dispersal and less spatial requirements, the extension of landscapes would have the capacity to maintain many populations. Therefore, for these species we defined the links between the metapatch populations according to the two spatio-temporal scales mentioned above. We considered all patches belonging to a population if the Euclidian distance between their edges had a length equal to or less than the species' daily movement distance. For highly mobile species we only use dispersal scale to find the pair of target-source patches, thus avoiding that few or even unique populations were identified in the landscapes (Mimet et al. 2016). The patches potentially connected by Euclidean distance determined by the species' dispersal distance in the final graphs were defined as source-target locations from which the movement of both species with low and high mobility was modeled considering matrix heterogeneity.

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## Supplementary Material 2: Evaluating analytical tools for designing multispecies habitat network

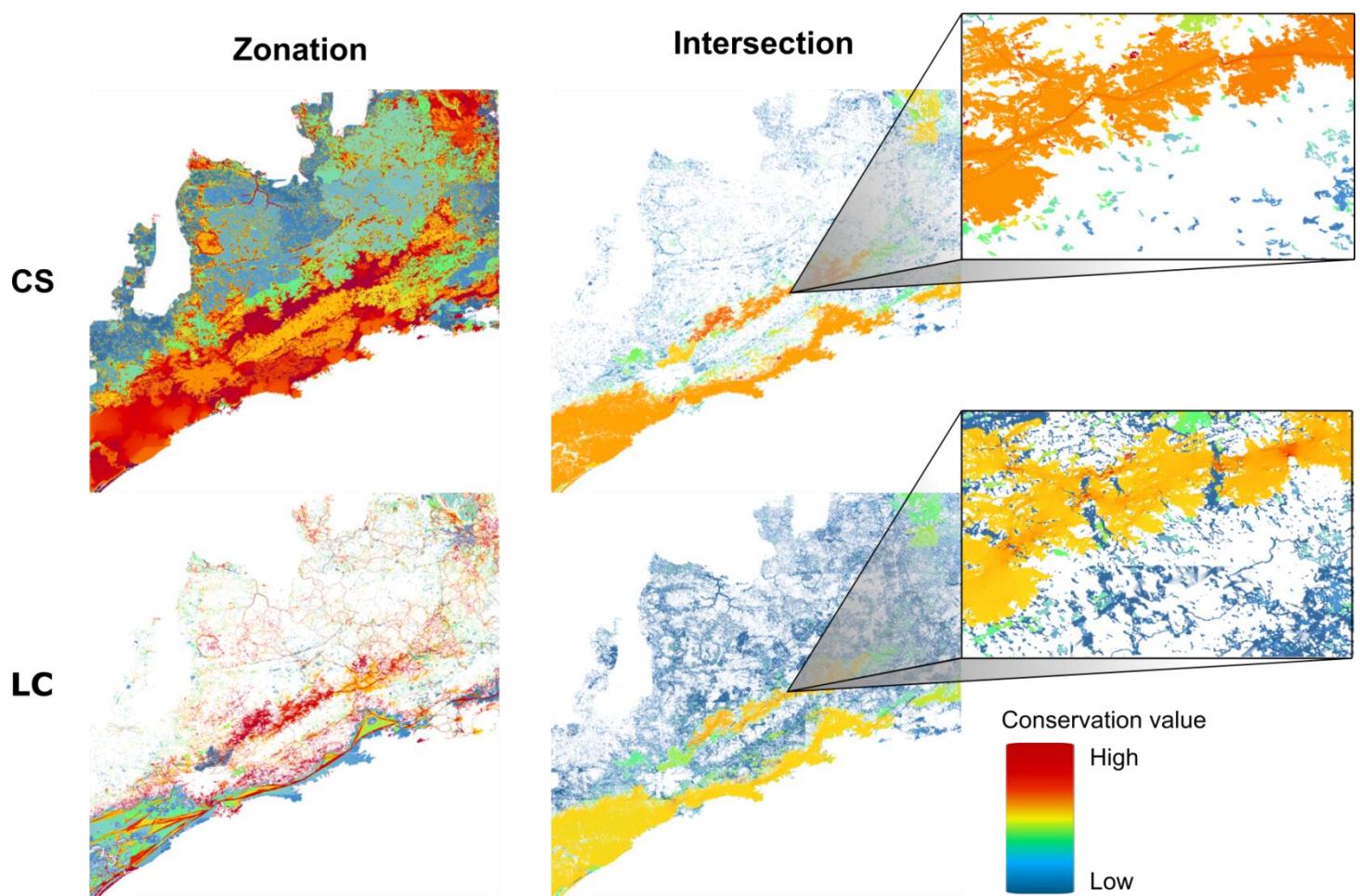
### Appendix 2 - Results

**Table S1** Variables retained in the best multi-scale, multiple logistic regression models used to predict the occurrence of 11 mammals species along forest remnants of the Atlantic Forest. Model comparisons were performed by Akaike information criteria corrected for small sample sizes (AICc) and the area under the receiver operating characteristic curve (AUC) is showed to provide a measure of model performance.

The plus or minus sign before each variable indicates its positive or negative effect on species occurrence. For three scale-dependent variables (cohesion, core area and resistance), prior to model selection, we identified the spatial scale of species' response based on their daily movement distance (DD) and 25%, 50% and 100% of their dispersal distance. For species whose best model retained any of these variables, the effect scale is shown as subscripted.

Species	Dispersal <sub>km</sub>	Best model variables	AICc	wAIC	AUC
<i>Akodon montensis</i>	0.22	(-) Area (+) CTS (-) Cohesion <sub>DD</sub>	169.49	0.38	0.77
<i>Cabassous tatouay</i>	15.35	(-) Area (-) DUI (-) Resistance <sub>DD</sub>	67.64	0.09	0.73
<i>Eira barbara</i>	3.03	(+) Area (-) Resistance <sub>25%</sub> (+) Cohesion <sub>DD</sub>	101.67	0.23	0.83
<i>Leopardus pardalis</i>	31.26	(+) DUI	155.80	0.06	0.58
<i>Leopardus wiedii</i>	9.82	(+) Area (+) CTS	76.28	0.33	0.86
<i>Nasua nasua</i>	2.98	(+) CTS (-) Resistance <sub>25%</sub>	79.73	0.32	0.76
<i>Oryzomys angouya</i>	0.46	(+) CTS (-) Resistance <sub>DD</sub>	90.41	0.18	0.82
<i>Oryzomys russatus</i>	0.32	(+) CTS (-) Core area <sub>DD</sub> (+) Cohesion <sub>100%</sub>	134.61	0.86	0.82
<i>Pecari tajacu</i>	7.56	(+) Area (+) DUI	111.35	0.15	0.75
<i>Puma concolor</i>	60.00	(+) CTS (+) Cohesion <sub>DD</sub>	122.50	0.07	0.67
<i>Tapirus terrestris</i>	25.85	(+) DUI (+) Core area <sub>100%</sub> (-) Cohesion <sub>100%</sub>	67.65	0.25	0.82

Variables: Area = patch area, CTS = patch climatic and topographic suitability, DUI = distance to urban infrastructure , Resistance = matrix resistance, Cohesion = immediate landscape cohesion and Core area = % of surrounding core area. The detailed description of each variable can be found in the *Supporting Information*



**Figure S2** Multispecies networks designed using different prioritization methods (Zonation and Intersection) combined with two landscape connectivity models (CS – Circuit theory-based model, LSC – Least-cost path model implemented through *LSCorridors* software). From the zoom of the Intersection networks (right panels) it is possible to visualize pinch points (i.e., critical locations for connectivity due to their high current densities) on the map where the connectivity was modeled using circuit theory and the cells with high density of paths on the map where the connectivity was modeled using the least-cost model.

# Capítulo 3

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Can we face different types of storms under the same umbrella? Efficiency and consistency of connectivity umbrellas across different patchy landscape patterns

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# **Can we face different types of storms under the same umbrella? Efficiency and consistency of connectivity umbrellas across different patchy landscape patterns**

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## **RESUMO**

*Contexto* A abordagem guarda-chuva aplicada à conectividade da paisagem baseia-se no princípio de que a conservação ou restauração dos habitats de dispersão de algumas espécies também pode facilitar o movimento de outras. As características das espécies, por si só, não parecem ser suficientes para identificar boas espécies guarda-chuvas para conectividade, mostrando a necessidade de se investigar a influência de fatores adicionais sobre essa propriedade.

*Objetivos* Nós testamos se o potencial de uma espécie como guarda-chuva para a conservação da conectividade pode ser influenciado pela composição e configuração da paisagem.

*Métodos* Nós simulamos rotas de movimento para oito espécies hipotéticas em paisagens artificiais com diferentes níveis de fragmentação, quantidade de habitat e permeabilidade da matriz. Determinamos a eficácia do guarda-chuva de conectividade das espécies virtuais calculando as interseções par-a-par dos habitats importantes para seus movimentos em todas as paisagens.

*Resultados* O desempenho do guarda-chuva de conectividade de todas as espécies foi afetado pela interação entre o nível de fragmentação e a quantidade de habitat das paisagens. No geral, o desempenho das espécies melhorou com a redução da fragmentação e o aumento da quantidade de habitat. Na maioria das paisagens e considerando o mesmo limiar de dispersão, espécies capazes de se mover mais facilmente através da matriz mostraram maior desempenho guarda-chuva do que aquelas para as quais a matriz ofereceu maior resistência.

*Conclusões* O guarda-chuva de conectividade não é uma característica estática que depende apenas dos traços das espécies, mas sim uma propriedade dinâmica que também varia de acordo com os atributos das paisagens. Portanto, não recomendamos a transferência espacial de espécies guarda-chuvas de conectividade identificadas em uma paisagem para outras que possuam níveis divergentes de fragmentação e quantidade de habitat.

**PALAVRAS-CHAVE:** espécies guarda-chuvas de conectividade, fragmentação, perda de habitat, permeabilidade da matriz, transferibilidade espacial, espécies virtuais

## ABSTRACT

*Context* The umbrella approach applied to landscape connectivity is based on the principle that the conservation or restoration of the dispersal habitats for some species also can facilitate the movement of others. Species traits alone do not seem to be enough to identify good connectivity umbrella species, showing the need to investigate the influence of additional factors on this property.

*Objectives* We test whether the potential of a species as a connectivity umbrella can be influenced by landscape composition and configuration.

*Methods* We simulated movement routes for eight hypothetical species in artificial patchy landscapes with different levels of fragmentation, habitat amount and matrix permeability. We determined the effectiveness of the connectivity umbrella of the virtual species using pairwise intersections of important habitats for their movements in all landscapes.

*Results* The connectivity umbrella performance of all species was affected by the interaction of fragmentation level and habitat amount. In general, species performance increased with decreasing fragmentation and increasing habitat amount. In most landscapes and considering the same dispersal threshold, species able to move more easily through the matrix showed higher umbrella performance than those for which the matrix offered greater resistance.

*Conclusions* The connectivity umbrella is not a static feature that depends only on the species traits, but rather a dynamic property that also varies according to the landscape attributes. Therefore, we do not recommend spatial transferability of the connectivity umbrella species identified in a landscape to others that have divergent levels of fragmentation and habitat quantity.

**KEYWORDS:** connectivity umbrella species, fragmentation, habitat loss, matrix permeability, spatial transferability, virtual species

## INTRODUCTION

As anthropogenic pressures continue to grow, the long list of species needing conservation action increases with each new IUCN Red List assessment (IUCN 2017). Nevertheless, the resources available for biodiversity conservation are often insufficient to meet the individual needs of all threatened species (Wiens et al. 2008). Even if this problem could be solved, the knowledge gaps in demography, distribution and life-history for many Data Deficient species (IUCN 2017) could prevent effective individual management. Facing resource and knowledge constraints, conservation biologists and wildlife managers have the difficult task of choosing which species or group of species will be the focus of immediate conservation action. In order to solve this problem, a conservation shortcut frequently used is the surrogate species approach. This method uses certain species or a restricted group of species to represent other species or aspects of the environment (Wiens et al. 2008; Caro 2010; Hunter et al. 2016)

In an attempt to prioritize patches to be included in reserve networks, it is necessary to determine the minimum size of protected areas and thresholds for landscape configuration and composition to achieve effective species protection (Margules and Pressey 2000). The great challenge is how to define these parameters for the purpose of maximizing the use of habitat networks for a large number of species, since we do not even know the basic biology for many of them. Some authors have suggested the umbrella species approach to solve these conservation tasks (see Roberge and Angelstam 2004 for a critical review). The label of ‘umbrella species’ can be attributed to “species whose conservation confers a protective umbrella to numerous co-occurring species” (Fleishman et al. 2000). This approach is based on similarity in habitat use by

sympatric species. If we can efficiently represent the habitat needs of one or a few umbrella species, then other co-occurring, non-target species that have similar requirements will also be protected (Roberge and Angelstam 2004). Traditionally, umbrella species have been used for conservation of primary habitats to indicate the location, size and shape of the reserves (Roberge and Angelstam 2004; Caro 2010). Although the umbrella approach has also been expanded and has encompassed landscape connectivity for some time now (e.g. Lambeck 1997; Minor and Lookingbill 2010; Cushman and Landguth 2012), only recently Breckheimer et al. (2014) defined formally a good connectivity umbrella species as “a species for which conservation or restoration of its dispersal habitat also facilitates dispersal of other target species”.

Since habitat loss and fragmentation have become ubiquitous factors in natural landscapes around the world, the necessity to incorporate habitat connectivity into conservation planning has become unquestioned (Rudnick et al. 2012). The ability of individuals to move among habitat patches is fundamental to maintain important processes, including the search for foraging and reproductive resources through daily movement, as well as maintaining genetic diversity via dispersal (Morales et al. 2010; Saastamoinen et al. 2018). Given the need to sustain these processes, corridor identification has become a common agenda in conservation planning and literature (Bennett 2003; Gilbert-Norton et al. 2010). Ecological corridors are more efficient if they can accommodate the movement of as many species as possible. Yet, movement data are usually difficult to obtain, limiting the corridor identification to a select group of species (often large-bodied, charismatic species) for which the protection of important areas to connectivity is assumed to benefit many other species (e.g. Noss et al. 1996; Silveira et al. 2014)

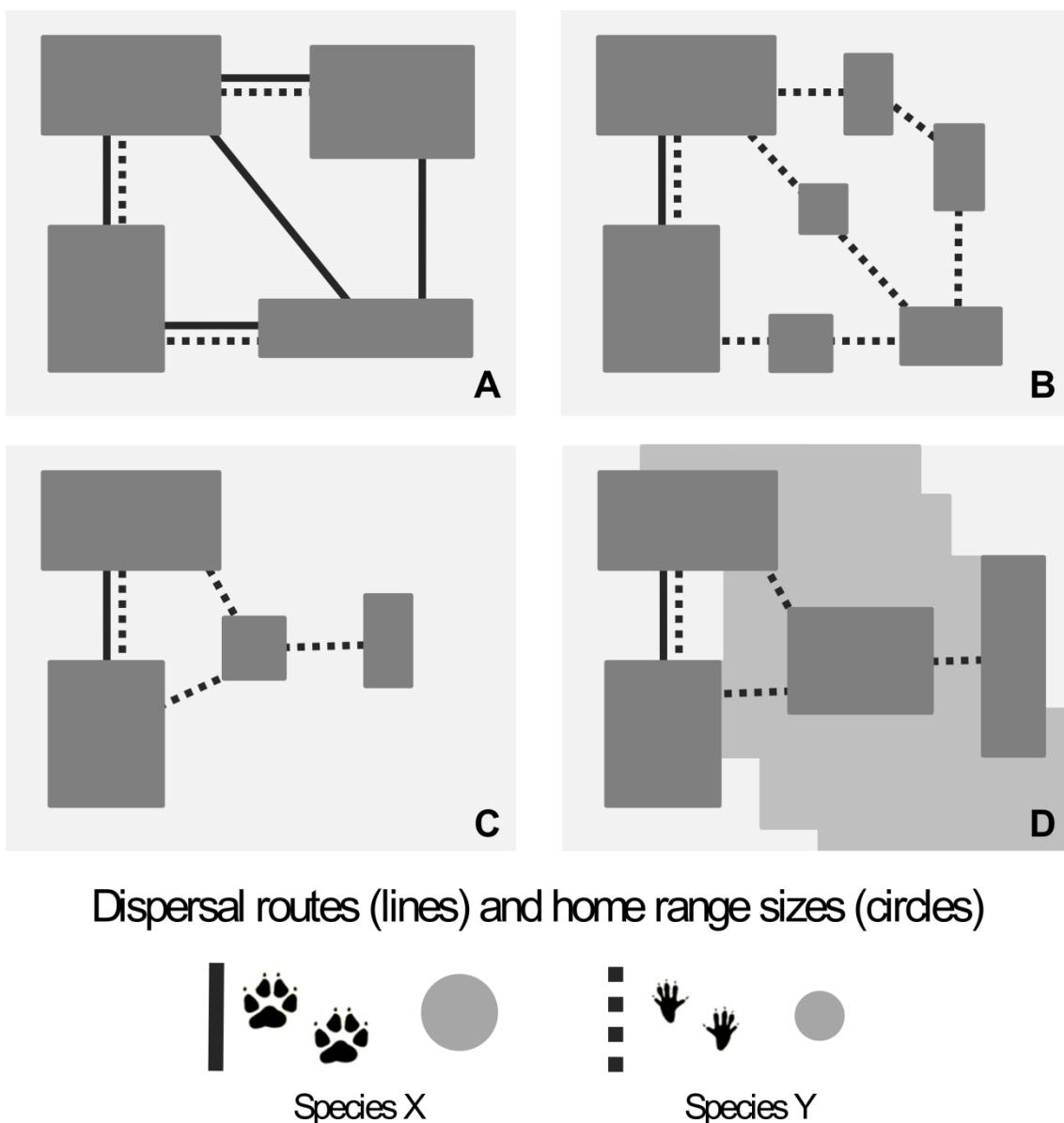
It is expected that all species have the ability, to a greater or lesser extent, to represent primary and/or dispersal habitat of other species, but the central point of the umbrella approach is to find which species are most efficient at performing this task (Fleishman et al. 2001; Breckheimer et al. 2014). Whereas we know what is necessary for a species to be labeled as a good umbrella for connectivity (Breckheimer et al. 2014), there is still no consensus on what characteristics are associated with the umbrella capacity of species. For instance, large-bodied species, such as large carnivores, are expected to be better dispersers and to need large areas to maintain their populations viable. Due to these characteristics, species with large body size are generally assumed to be good umbrella species; however, many studies have shown the opposite (Beier et al. 2009; Minor and Lookingbill 2010; Cushman and Landguth 2012; Breckheimer et al. 2014). Minor and Lookingbill (2010), for example, showed that connectivity for small mammals with low dispersal abilities cannot be predicted by connectivity for large-bodied, far-ranging mammals. Contrary to the earlier, Cushman and Landguth (2012) evaluated the connectivity umbrella performance for a wide range of hypothetical organisms and found that species with large dispersal abilities were more effective in indicating the connected area for the other species.

The low apparent predictive power of species characteristics in determining the efficiency of species as umbrellas for connectivity may be better explained by the need of additional information about composition and configuration of the studied landscapes. Divergent landscape patterns may emerge from different land use changes or historical patterns along the distribution of a species, causing it to have distinct habitat requirements to persist in contrasting landscapes. For instance, in the Brazilian Amazon, the fishbone pattern results from a complex interaction of roads and

deforestation, and is shaped by the regular distribution of small properties along the roads (e.g. see Fig. 2 in De Oliveira Filho and Metzger 2006). Another common deforestation pattern in this region is known as independent settlement and, unlike the first, is characterized by small properties irregularly distributed along the landscape (e.g. see Fig. 2 in De Oliveira Filho and Metzger 2006). These patterns may differ profoundly in terms of matrix nature (i.e. composition and structure of the landscape element surrounding habitat patches), amount of riparian vegetation and remaining habitat as well as spatial arrangement. Thus, a species that occurs in both landscapes, for example, may exhibit different patterns of occupancy and movement, which may render its ability to represent the dispersal habitat of other species dependent on the landscape context (Fig. 1). Therefore, matrix resistance, remaining habitat amount and spatial arrangement may represent important components to determine the choice of umbrella species for connectivity studies, as well as the success of this approach. Nevertheless, to date, studies evaluating the effectiveness of connectivity umbrella species have focused only on species traits, and have not performed comparative analyses of this property across different landscape patterns (Beier et al. 2009; Minor and Lookingbill 2010; Cushman and Landguth 2012; Brodie et al. 2015)

In this work, we investigated the effect of landscape composition and configuration on the connectivity umbrella performance of different virtual species. We expected that the potential of a given species as connectivity umbrella depends not only on its profile of landscape use, but is a dynamic property influenced by landscape features. For this, we identified and overlapped the movement routes for eight virtual species with different spatial requirements (dispersal distance, minimum home range size and landscape matrix use) across simulated landscapes with different levels of fragmentation, habitat

amount and matrix permeability. Here we are not focused on identifying the most efficient connectivity umbrella species considering the different landscape patterns; rather, we are interested in verifying whether and how the ability of different species in indicating movement pathways of other species can change when distinct landscape patterns are considered, discussing how this can impact the conservation planning based on single-species approaches.



**Figure 1** Species occupancy and dispersal along landscapes can be affected in different ways by habitat structure. Thus, it is expected that the effectiveness of species as potential connectivity umbrellas depends on the landscape context, as shown in the

diagram above. Continuous lines illustrate the movement pathways for a far-ranging species (species X) whose occurrence is limited by large habitat patches (dark gray rectangles), while dashed lines represent the movement of a species with lower dispersal ability that requires smaller areas for its establishment (species Y). The matrix class represented by the light gray color can be transposed by the two species, while the matrix class delimited by the medium gray region imposes a low resistance to the species Y movements and constitutes a barrier for the species X. Far-ranging species with occurrences restricted to large patches are efficient connectivity umbrellas in landscapes that correspond to its requirements (A). However, their efficiency is questioned in other landscapes due to the different levels of fragmentation (B), habitat amount and spatial arrangement (C) or matrix permeability (D)

## METHODS

### Landscape patterns

We used the SIMMAP 2.0 (available at <http://www2.montes.upm.es/personales/saura/>) that applies a stochastic simulation method called modified random clusters (MRC) to create landscape patterns in raster format (Saura and Martínez-Millán 2000). The MRC spatial patterns are more realistic due to their patchy and irregular appearance, characteristics present in many real landscapes (Saura and Martínez-Millán 2000). A great advantage of the MRC method is that habitat amount and fragmentation can be systematically and independently varied (Saura and Martínez-Millán 2000). The SIMMAP creates landscapes based on initial probability  $p$ , number and amount of the simulated classes (percentage of the landscape area covered by each class), map linear dimension  $L$ , minimum mapped unit  $m$  and neighborhood criterion. The parameter  $p$  determines the degree of fragmentation or patch aggregation level of the simulated

landscapes. With decreasing values of  $p$  (hereafter patch aggregation level), we can generate more fragmented landscapes with smaller and more numerous patches, and spatial patterns with opposite characteristics using higher values of this parameter; patch aggregation level  $\approx 0.5928$  corresponds to the percolation threshold for the 4-neighborhood criterion (Saura and Martínez-Millán 2000).

We generated 3-classes landscape patterns with  $L$  equal to 200 pixels and  $m$  equal to 1 (minimum pixel size of existing patches). For all virtual species, one class represented the primary habitat, class with the lowest resistance to movement and suitable habitat for the potential establishment of home ranges, and the other two were considered as different matrix components - one more and the other less permeable. We simulated landscapes using 10%, 30% and 50% of habitat; these same values were used to define the percentage of the remaining pixels covered by the most permeable matrix class. For each level of habitat amount, we used three patch aggregation values (0.1, 0.3 and 0.5) to generate landscapes with different degrees of fragmentation. We performed 10 replicates for each combination of the above-mentioned parameters (27 in total), resulting in 270 landscapes analyzed. A replica of each spatial pattern is shown in Supplementary Material Fig. S1.

### **Virtual species**

We defined the virtual species based on three key characteristics of landscape use: ability to move through the matrix, dispersal threshold and minimum home range size (Table 1). First, we constructed two landscape-resistance models to represent species for which the matrix imposed different ecological costs during their movement. Cost (or

resistance) values depict habitat preferences, physiological cost and/or mortality for individuals of a given species moving through a particular environment (Zeller et al. 2012). In both models the primary habitat had resistance equal to 1 cost unit. In the low resistance model, the matrix classes offered cost values of 2 and 3, representing species less sensitive to the landscape classes outside primary habitat; and had cost values of 10 and 20 in the high resistance model, simulating species for which the matrix imposed greater resistance. Therefore, we tested the effect of matrix permeability on umbrella connectivity performance using both amount of the most permeable matrix class and resistance models. Next, we selected four dispersal capacities to represent species with: low dispersal (10 cost units), intermediate dispersal (50 and 100 cost units) and high dispersal (200 cost units). If we consider that our virtual landscapes have a resolution of 100 m, for example, these dispersal thresholds would be equivalent to 1 km, 5 km, 10 km and 20 km, respectively. As in both resistance models the primary habitat has cost value equal to 1, keeping in mind the 100 m resolution, dispersal thresholds can be interpreted as follows: if a landscape was covered entirely by the primary habitat, the 1 km species could move 10 cells in any direction from the departure points; 5 km and 10 km species could advance 50 and 100 cells, respectively; and 20 km species would be able to cross the whole landscape horizontally or vertically from any cell.

**Table 1** Description of the eight virtual species used in this study, followed by an example of mammal species with similar characteristics. See the section *Virtual Species* for more details. The real species' dispersal distances may not exactly coincide with those used to define our virtual species, but the exemplified species are good examples of low, intermediate and high dispersal species. For real species, matrix resistance refers to that imposed by anthropogenic areas such as open agricultural land and urban areas. We have provided only mammals as examples because here we used the relation between home range and dispersal distance of this group and previous work evaluating

umbrella species has been biased towards mammals, but it is important to note that other taxa may also be used as umbrella species (Branton and Richardson 2011; Breckheimer et al. 2014)

Virtual species	Dispersal distance	Home range size	Matrix resistance	Real example	Reference
L1	1 km	small	low	<i>Potos flavus</i>	Keeley et al. (2017)
L5	5 km	medium	low	<i>Canis lupus</i>	Byrne et al. (2018)
L10	10 km	medium - large	low	<i>Tapirus terrestris</i>	Tobler et al. (2009)
L20	20 km	large	low	<i>Puma concolor</i>	De Angelo et al. (2011)
H1	1 km	small	high	<i>Oryzomys russatus</i>	Umetsu and Pardini (2007)
H5	5 km	medium	high	<i>Genetta genetta</i>	Carvalho et al. (2016)
H10	10 km	medium - large	high	<i>Leontopithecus rosalia</i>	Moraes et al. (2018)
H20	20 km	large	high	<i>Ailuropoda melanoleuca</i>	Pan et al. (2014)

Finally, we used the home range size as a threshold to determine the species occurrence in the primary habitat patches (hereafter referred to as ‘occurrence threshold’). We defined the occurrence threshold corresponding to the four dispersal capacities (1 km, 5 km, 10 km and 20 km) using the equation of the regression line between home range and dispersal distance for mammals, which has a positive slope and was derived from the compilation made by Minor and Lookingbill (2010) (from the data used by Bowman et al. 2002 and Corry and Nassauer 2005). We chose to use the relation for mammals because most studies evaluating the efficiency of species as potential connectivity umbrellas used mammals as models (e.g. Beier et al. 2009; Minor and Lookingbill 2010; Cushman and Landguth 2012; Brodie et al. 2015).

The four levels of dispersal capacity and their respective occurrence thresholds, combined with the two resistance models, resulted in a set of eight virtual species representing different landscape use profiles (Table 1). Here we considered species that

use the same class of primary habitat to simplify the analysis, but the connectivity umbrella approach can also be used for species having different breeding and foraging habitats (Breckheimer et al. 2014).

### **Movement routes and effectiveness of the species' connectivity umbrellas**

Home range size was used as a cut-off point to establish in which primary habitat patches the species could occur. Therefore, all patches greater than or equal to the minimum home range requirement for a particular species were considered the source and target points from which the movement routes were identified using the Conditional Minimum Transit Cost (CMTC) method (Pinto and Keitt 2009). The CMTC method is based on graph theory and results from a modification of Dijkstra's algorithm, which in turn is used in least-cost path models. However, instead of returning only a path of least resistance, as obtained in the classical least-cost analysis, CMTC identifies several paths with similar costs (Pinto and Keitt 2009). The various minimum cost paths identified, being the least-cost path one of them, form together the potential movement routes for a given species between a group of source and target locations (Pinto and Keitt 2009).

We identified the movement routes for the eight hypothetical species in each landscape based on matrix resistance model and thresholds for dispersal and occurrence. After finding the movement routes using the CMTC method, we ranked all landscape cells according to their importance for connectivity, and then we selected 10% of the cells containing the highest values for each species within each landscape. We calculated umbrella performance for a given species using pair-wise intersections of the cells in the top 10% of the landscape for its dispersal compared to the top 10% for the dispersal of

co-occurring species. The mean spatial overlap, used as a response variable, ranged from 0 (no overlap) to 1 (maximum possible overlap). In our analysis, a species could have an umbrella performance equal to zero for two reasons: either its movement paths do not spatially coincide with the routes of any other species or the species does not occur in any habitat patch.

We used factorial ANOVA via permutation tests to examine the main effects and interactions of the three factors representing landscape attributes (fragmentation, habitat amount and matrix permeability) on the connectivity umbrella performance of the eight hypothetical species. We carried out permutation tests because the assumption of normality has not been reached even though we have tried various types of transformations of the variable response. All analyses were performed in R 3.1.2 environment (R Core Team 2018a) and values of  $p < 0.05$  were considered significant.

## RESULTS

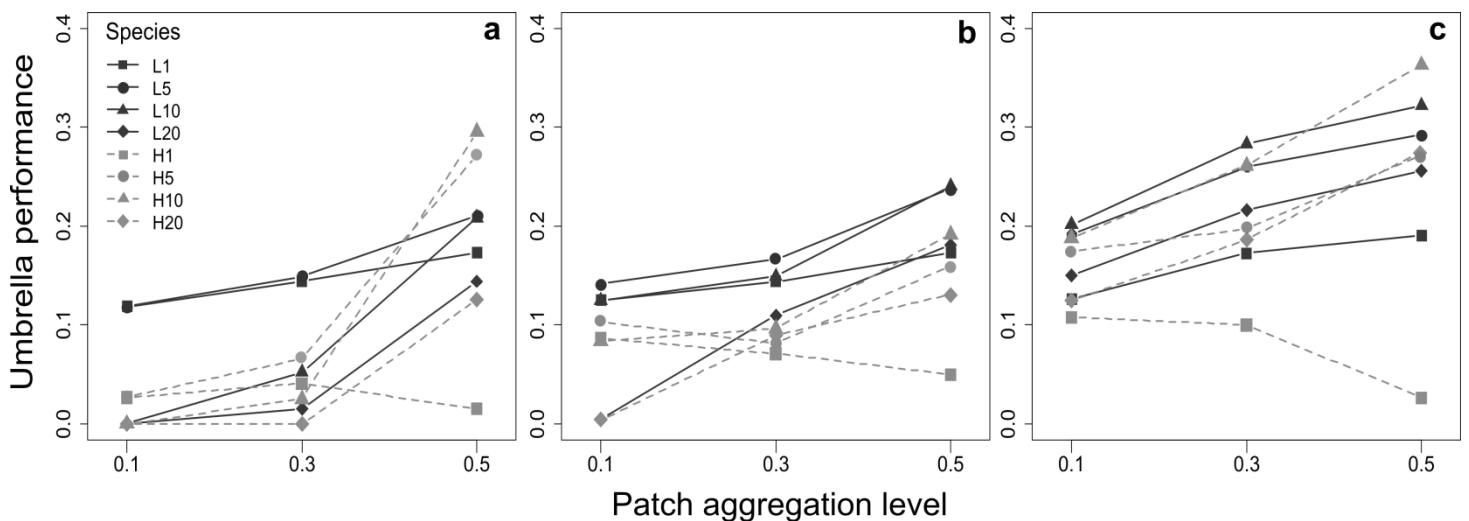
All eight hypothetical species presented umbrella performance (i.e. the ability to represent the movement routes of co-occurring species) dependent on the interaction of fragmentation level and habitat amount (Table 2). The three-way ANOVA test indicated no significance for the main effect of the amount of hospitable matrix or for its interactions (Table 2). Most hypothetical species presented higher umbrella performance with decreased fragmentation (higher levels of patch aggregation) and increased habitat amount (Fig. 2). In most landscapes and considering the same dispersal threshold, the L species, for which the matrix offered lower resistance, presented better umbrella performance than the H species, which were relatively more

intolerant to matrix use (Fig. 2). Not surprisingly, species with higher dispersal capacities and, consequently, higher habitat requirements had the lowest patch occupancy rates. These species were not able to occur practically in any patch in more fragmented landscapes with 10% and 30% of habitat (Supplementary Material Fig. S2).

**Table 2** Results of the three-way ANOVA used to evaluate the effects of fragmentation (FR), habitat amount (HA) and proportion of the most hospitable matrix class (MP) on the connectivity umbrella performance of eight hypothetical species. Each horizontal division of the table shows the result for species with the same dispersal threshold distinguished by their low (LS) or high (HS) ability to use the matrix during movement (shown in the columns). The symbol ‘\*’ indicates the statistic significant factors at the 0.05 level

Dispersal	Factors	df	LS <sub>F</sub>	LS <sub>P value</sub>	HS <sub>F</sub>	HS <sub>P value</sub>
1 km	FR	2	153.44	<0.001*	10.88	<0.001*
	HA	2	18.42	<0.001*	13.54	<0.001*
	MP	2	1.85	0.160	2.29	0.194
	FR:HA	4	3.48	0.042*	2.44	0.009*
	FR:MP	4	1.74	0.144	0.80	0.537
	HA:MP	4	1.35	0.256	0.23	0.921
	FR:HA:MP	8	1.88	0.065	1.40	0.192
	Residuals	243				
5 km	FR	2	199.65	<0.001*	61.48	<0.001*
	HA	2	179.45	<0.001*	35.79	<0.001*
	PM	2	0.29	0.756	0.85	0.436
	FR:HA	4	4.76	0.001*	10.58	<0.001*
	FR:MP	4	0.86	0.480	0.46	0.776
	HA: MP	4	0.69	0.607	0.92	0.457
	FR:HA:MP	8	1.15	0.327	0.48	0.872
	Residuals	243				
10 km	FR	2	213.85	<0.001*	153.06	<0.001*
	HA	2	312.96	<0.001*	118.75	<0.001*
	MP	2	0.13	0.879	0.55	0.581
	FR:HA	4	14.62	<0.001*	16.20	<0.001*
	FR:MP	4	0.22	0.926	0.45	0.764
	HA:MP	4	0.04	0.997	0.63	0.640
	FR:HA:MP	8	0.10	0.999	1.40	0.199
	Residuals	243				

20 km	FR	2	169.01	<0.001*	64.770	<0.001*
	HA	2	209.42	<0.001*	92.162	<0.001*
	MP	2	0.04	0.959	0.254	0.782
	FR:HA	4	9.73	<0.001*	3.072	0.018*
	FR:MP	4	0.71	0.588	1.351	0.253
	HA:MP	4	1.01	0.404	0.667	0.616
	FR:HA:MP	8	0.57	0.804	0.593	0.788
	Residuals	243				



**Figure 2** Average connectivity umbrella performance of eight hypothetical species characterized by different dispersal abilities (1, 5, 10 and 20 km) and for which the matrix classes impose low (L species) or high resistance (H species) to movement in landscapes with three degrees of fragmentation (depicted through the patch aggregation level) and 10% (a), 30% (b) and 50% (c) of habitat. Increasing values of the patch aggregation level indicate landscape patterns less fragmented. The umbrella performance for a given species was defined as the average spatial overlap between cells in the top 10% of the landscape for the species connectivity and the cells in the top 10% for the co-occurring species connectivity

The species characterized by the low resistance model and 1 km dispersal threshold (L1 species) presented little variation in its umbrella performance in relation to the different

levels of fragmentation and habitat amount. There was practically no difference in this species performance between landscapes with 10% and 30% of primary habitat independent of the fragmentation degree (Fig. 2a, b). Increasing the matrix resistance 10-fold at the 1 km threshold caused a drop in umbrella performance as the landscapes became less fragmented (Fig. 2). The performance of the H1 species was 91%, 71% and 86% lower than that presented by the L1 species in landscapes with 10%, 30% and 50% of habitat, respectively, and patch aggregation level equal to 0.5 (Fig. 2).

Overall, at least one of the species with intermediate dispersal capacity (L5, L10, H5 and H10) was among the most efficient umbrella species in all landscapes (Fig. 2). In the low resistance model, species such as L5 or L10 showed similar increases in their umbrella performance in landscapes with 30% and 50% of habitat (Fig. 2b, c). In landscapes with 10% of habitat and patch aggregation levels equal to 0.1 and 0.3, the L5 species showed an equivalent performance to the L1 species and both were the most efficient umbrella species in these types of landscapes; while in landscapes with the same habitat amount, but with the lowest level of fragmentation (patch aggregation level= 0.5), the H5 and H10 species had the highest performance. In most spatial patterns, intermediate dispersers more intolerant to cross the matrix (H5 and H10) presented a reduced performance in relation to those species with the same dispersal capacity (L5 and L10) for which the matrix imposed less resistance; however, the former species presented umbrella scores approximately 30% and 40% higher (for 5 km and 10 km, respectively) compared to the latter in less fragmented landscapes (patch aggregation level= 0.5) with 10% of habitat (Fig. 2a).

In the more fragmented landscapes (patch aggregation levels equal to 0.1 and 0.3) with 10% of habitat, 20 km species had an umbrella performance approximately equal to

zero independent of the ability to move through the matrix (Fig. 2a). The same was observed for the performance of these species (L20 and H20) in landscapes with the highest fragmentation level and 30% of habitat (Fig. 2b). On the other hand, the umbrella performance of the L20 species was slightly comparable or exceeded the capacity of all other species with less ability to move through the matrix in landscapes with 30% of habitat and aggregation level equal to 0.3 (Fig. 2b). Besides, the L20 species had a superior performance in comparison to the H1, H5, H20 and L1 species in landscapes with the same fragmentation degree and 50% of habitat (Fig. 2c).

## DISCUSSION

Our study confirmed that the connectivity umbrella performance of species is affected by landscape attributes, more specifically by the interaction of fragmentation level and habitat amount. Therefore, the connectivity umbrella is not a static property determined only by species traits, but it is also influenced by landscape characteristics. Functional connectivity is dependent on both landscape context and organisms' needs. Species may respond differently to habitat loss and fragmentation due to their different life history traits, such as dispersal capacity, niche breadth and reproductive rate (e.g. Öckinger et al. 2010; Keinath et al. 2017). Therefore, it is not entirely surprising that one species' ability to encompass the spatial demands of other species changes among landscapes with different levels of disturbance.

The efficiency of an umbrella species under the classic definition may be transferable among taxonomic groups or landscapes with similar regional climate, biogeographic past and land-use history (Betrus et al. 2005). Banks-Leite et al. (2011) used the

umbrella index proposed by Fleishman et al. (2000) to evaluate the efficacy of species-based indicators to reflect changes in bird community integrity in fragmented landscapes with different proportion of forest cover (10%, 30% and 50%). They found that species-based indicators had a low transferability between the studied landscapes, probably due to the different degrees of habitat loss. Going in the same direction, our results provide evidence that the connectivity umbrella performance of a species in a particular landscape may not be transferable to other landscapes with divergent composition and configuration of primary habitat. This means that the result of the connectivity umbrellas selection may change according to the degree of fragmentation and habitat amount of the focal landscapes and, consequently, the final subsets of selected species will probably vary among the different spatial scenarios. Therefore, we suggest that there is no single best umbrella species for connectivity within an ecosystem because different species can be selected depending on the studied landscape. Because functional connectivity also has a temporal component (Auffret et al. 2015), it is also very likely that there is no temporal transferability of the connectivity umbrella in landscapes that maintain increasing rates of habitat loss and fragmentation over time. In other words, a given species can be a good connectivity umbrella in the present, but if the landscape changes substantially, its efficiency in representing the requirements of other species becomes questionable.

The matrix composition has a significant role for connectivity of terrestrial animal populations in patchy landscapes (Watling et al. 2011), influencing processes ranging from movement rates (Eycott et al. 2012) to metapopulation dynamics (Vandermeer and Carvajal 2001). In our study, the effect of matrix permeability on connectivity umbrella performance of species was evaluated using both the proportion of the most permeable

matrix class and different resistance models, the last variable representing species with different abilities to move through the matrix. The results showed that the amount of hospitable matrix had no effect on the umbrella performance for any species. On the other hand, when we compared species with the same dispersal thresholds but with contrasting abilities to move in the matrix, we verified that the species characterized by the high resistance model had in general lower performance (Fig. 2). This finding accords with the results from Cushman and Landguth (2012) that species with more specialized dispersal requirements performed poorly in representing the generalists' dispersal habitats.

Surprisingly, we found that the H1 species presented decreases in its umbrella performance as the fragmentation degree decreased regardless of the habitat amount (Fig. 2). We believe that this may have happened because this species has the lowest dispersal threshold (10 cost units) and the matrix cells in the high resistance model (with cost unit equal to 10 or 20) acted as barriers to its movement. Faced with this insurmountable matrix, the movement of this species could benefit from habitat cells scattered acting as stepping stones in the most fragmented landscapes. For example, scattered trees have the potential to facilitate animal movement, improving landscape connectivity (Fischer and Lindenmayer 2002; Lindenmayer and Laurance 2017). However, it is worth noting that the matrix resistance can influence the effectiveness of stepping stones and corridors (Baum et al. 2004).

Our results suggest that, in general, at least one of the species with intermediate dispersal capacity (5 km and 10 km) was among the best performing umbrella species in the simulated landscapes. We believe the hypothetical intermediate dispersers combine

the advantageous characteristics present in the species with more extreme requirements. The 1 km species can exist in many habitat patches, but their movement is rather limited. At the other extreme, the 20 km species are restricted to large habitat patches, but they have greater movement ability. Intermediate species may occur in more patches than the 20 km species without having a dispersal as restricted as the 1 km species. This combination of traits favors both occurrence and movement, making intermediate species able to better exploit the landscape and, consequently, cover the habitat and dispersal needs of other species. Despite this, in more fragmented landscape with 10% and 30% of habitat remaining the species characterized by the 1 km dispersal threshold and the low resistance model had an equivalent performance. Recently, Correa Ayram et al. (2018) used 40 species of terrestrial mammals to design multispecies corridors and found that the connectivity model for species with intermediate dispersal ranges (250–1500 m) had greater spatial overlap with the scenario considering all species compared to the scenarios designed using groups of species with short ( $> 250$  m) and wide dispersal ranges ( $> 3000$  m). This study was carried out in a highly fragmented landscape with 54% of anthropic land covers.

Although we were not focused on identifying the most efficient umbrella profile associated with each spatial pattern, this would be a powerful approach to be explored by subsequent studies. If, in fact, there are umbrella species profiles for connectivity associated with certain spatial patterns, then the use of a variety of them could make the design of protected area networks more robust to potential changes in the landscape. Our results showed that less matrix-intolerant species with lower dispersal ability can provide a wider umbrella than many other species in more fragmented landscapes with a low habitat amount. This result agrees to some extent with Nicholson et al. (2013) that

showed that a reserve system designed for a highly fragmented system using only an area-limited species, a dispersal-limited species (*Rattus fuscipes* with mean dispersal distance of only 100 m) and a species with low fecundity could provide protection for all studied species (10 in total). This study evidences the conservation value of species having low dispersal ability as part of multispecies umbrellas.

Independent of the resistance model, our analysis indicated that hypothetical species with greater mobility were not the best connectivity umbrella species in any landscape. In more fragmented landscapes with 10% of primary habitat, these species had umbrella scores equal to zero, most likely due to their absence or low occurrence in the smaller patches of these landscapes (Supplementary Material Fig. S2). Some studies have shown that large-sized species, generally thought to have high dispersal capacity and large home range, may not be effective connectivity umbrellas for some other species (Minor and Lookingbill 2010; Breckheimer et al. 2014; Wang et al. 2018). The long-term persistence of large mammals is probably more limited by large habitat areas than by the connectivity between them (Minor and Lookingbill 2010). Consequently, in highly fragmented landscapes with severe habitat loss, the extinction of these species can be a matter of time, if no conservation action is taken. Therefore, perhaps using these species to guide conservation planning is not a good choice in these highly disturbed scenarios. However, this does not imply that large body species are not good species for other conservation tasks in these landscapes, such as species used in flagship campaigns (Smith et al. 2012).

We evaluated the relative performance of individual species in indicating areas important for the connectivity of other species. However, like other authors, we strongly suggest that the design of protected area networks or wildlife linkages should be based

on the requirements of multiple focal species, since it is very unlikely that any single species could cover the needs of an entire community (Lambeck 1997; Beier et al. 2009; Minor and Lookingbill 2010; Baguette et al. 2013) even though some of them have great appeal for conservation. For example, as some potential corridors identified for the iconic giant panda may not be functional for other co-occurring mammals, a conservation planning based on a multispecies perspective, including the giant panda instead of being exclusively designed for it, may have greater value for biodiversity conservation (Wang et al. 2018). A multispecies umbrella composed of a diverse group of species capable of representing the habitat demands of a range of taxa present in the studied ecosystem will probably be more efficient in achieving conservation goals than approaches using unique species requirements (Lambeck 1997; Fleishman et al. 2000; Baguette et al. 2013). For multispecies corridors planning, it has been suggested that connectivity scenarios should be designed using restricted subsets of ecologically similar species (e.g. carnivores or herbivores) (Brodie et al. 2015).

Even though studies evaluating umbrella species are strongly biased toward birds and mammals in terrestrial systems (Branton and Richardson 2011), this shortcut may have great value for the conservation of marine and freshwater ecosystems (Gilby et al. 2017; Kalinkat et al. 2017). We suggest that following studies use empirical data to also investigate the potential of non-mammal and non-bird species as umbrellas in multispecies approaches, since researchers have shown that less intuitive groups such as frogs, butterflies (Breckheimer et al. 2014) or tortoises (Johnson et al. 2017) may have better umbrellas than species previously thought to have.

We used only three traits related to landscape use to define our virtual species: dispersal threshold (translated as cost threshold), minimum home range size (defined as a function of the dispersal threshold) and resistance model (represented by two cost schemes). Although these traits seem very simplified, they are in agreement with other studies (e.g. Minor and Lookingbill 2010; Cushman and Landguth 2012). We hope that future analyzes can test the sensitivity of the connectivity umbrella to other life history traits and landscape features, as well as to show how some life-cycle traits can influence this property. For species exhibiting contrasting variations during different life stages in characteristics that influence the design of movement routes, such as habitat preference and movement strategies, it is expected that their performance as connectivity umbrellas will be life stage-dependent. For example, adult lions of both sexes may perceive the landscape more fragmented and less permeable than male natal dispersers, resulting in significant differences in landscape connectivity patterns depending on the demographic category considered (Elliot et al. 2014). In aquatic ecosystems, differences in habitat requirements and movement patterns during the life-cycle stages of many species may be even more contrasting. Therefore, it is expected that these differences to significantly alter the results of the selection of umbrella species when considered in the analysis. For example, because coral reef fishes exhibit different movement patterns during the adult, juvenile and larval stages which may vary among and within species (Green et al. 2015), taking into account the life-cycle traits causing these differences is essential for a robust assessment of species' potential as connectivity umbrella species.

Our findings have important implications for the connectivity planning based on the umbrella species approach. Even though we believe in the potential of a multispecies umbrella, the choice of the species should be made cautiously based not only on the

species traits but also on landscape attributes. We also suggest caution in the generalizations made about the connectivity umbrella efficiency of a species evaluated in one or a few similar landscapes. In the face of severe habitat loss, fragmentation and many other threats, the spatial transferability of the connectivity umbrella property is not advisable among very divergent landscape patterns. Although our results showed that certain species have excelled as connectivity umbrellas in some spatial patterns, we strongly believe that no single species identified as an umbrella species in a particular scenario is capable of representing the dispersal habitats of so many others in landscapes with varying levels of disturbance. In other words, we seriously doubt that there is an ideal umbrella that can handle any type of storm.

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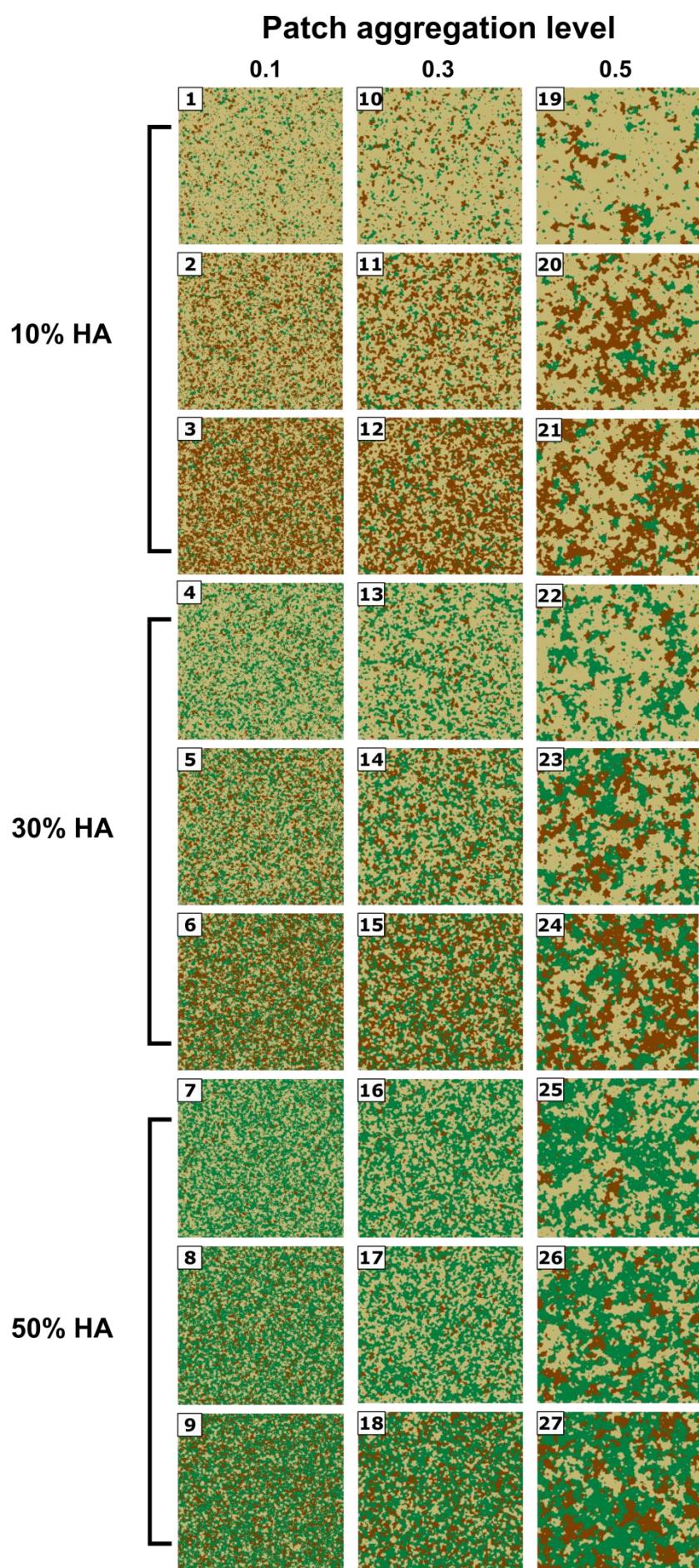
Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. *Landsc Ecol* 27:777–797

## **Supplementary Material: Virtual landscapes and patch occupancy**

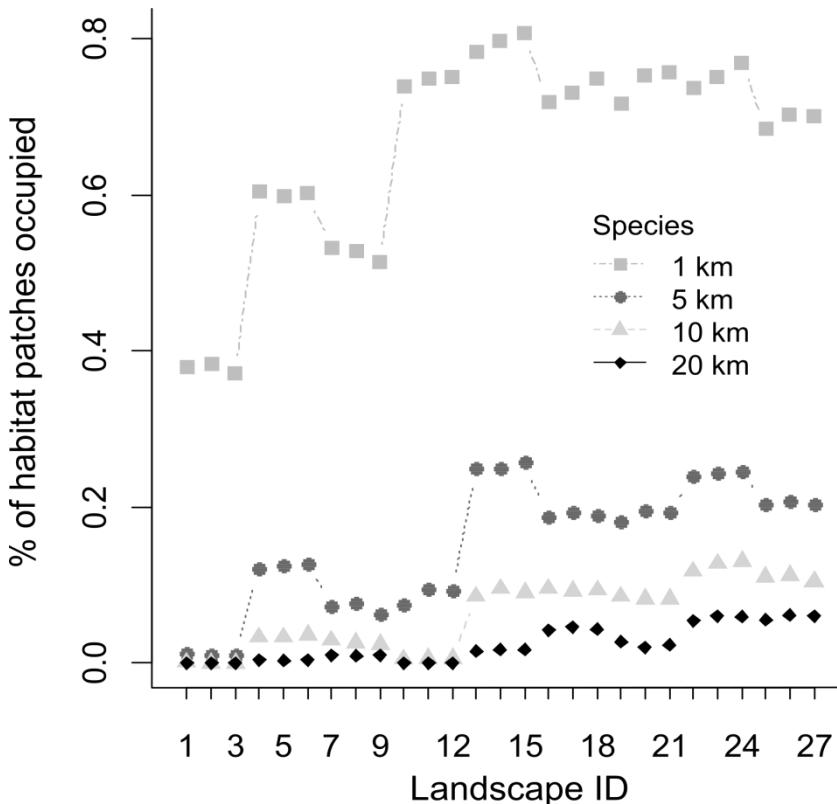
Can we face different types of storms under the same umbrella? Efficiency and consistency of connectivity umbrellas across different patchy landscape patterns

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**Figure S1** A replica of each landscape pattern created from the MRC method using three classes: primary habitat (green), more hospitable matrix class (brown) and less hospitable matrix class (sand color). We created 27 types of landscapes using three levels of habitat fragmentation (represented by the patch aggregation level, with smaller values indicating more fragmented landscapes), three percentages of habitat amount (HA, specified on the left side by the brackets) and three percentages of the more hospitable matrix class (the first three landscapes arranged horizontally in each block delimited by brackets have 10% of the more permeable matrix class, the second and third trio in each block show landscapes with 30% and 50% of same class, respectively)



**Figure S2** Average percentage of habitat patches occupied by each hypothetical species across the 27 types of simulated landscapes. The set of habitat patches occupied by a species, from which the movement routes were designed, was identified using only the size of the species' home range as a cut-off point, which in turn was defined as a function of its dispersal capacity using the regression equation provided by Minor and Lookingbill (2010). Although it is expected that species with higher dispersal capacities will have a high occupancy rate, their requirements for large areas are not compatible with the size of most habitat patches in the landscapes. The numbers on the horizontal axis correspond to the landscape identification in Fig. S1

# **Capítulo 4**

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## **Performance of different species-based surrogates to design habitat networks**

Paper prepared to be submitted in April 2019 to the journal Biological Conservation

## **RESUMO**

Como as decisões de conservação são comumente feitas utilizando substitutos ecológicos baseados em espécies, é essencial estabelecer critérios para a definição de abordagens substitutas capazes de fornecer soluções de conservação confiáveis. Aqui, nós avaliamos o desempenho de diferentes estratégias substitutas usando modelos de qualidade de habitat e conectividade projetados para 11 espécies de mamíferos em uma ampla região da Mata Atlântica. Para isso, avaliamos separadamente o potencial de diferentes espécies em representar habitat e conectividade para um grupo diversificado de outras espécies (desempenho guarda-chuva). Nós selecionamos a espécie que executou bem as duas tarefas de conservação simultaneamente e a definimos como a espécie guarda-chuva para nosso estudo. Em seguida, comparamos a eficácia da rede de habitats da espécie guarda-chuva com o desempenho de redes projetadas a partir de esquemas substitutos considerando múltiplas espécies, usando como referência o cenário combinando as demandas de todas as espécies. Os esquemas substitutos usando múltiplas espécies foram definidos a partir de diferentes perspectivas: maximizando a similaridade e a diversidade entre as espécies de acordo com três características ecológicas (nível trófico, capacidade de dispersão e sensibilidade à matriz). O desempenho das redes de habitat derivadas a partir dos diferentes esquemas foi medido através da média e desvio padrão da similaridade em relação aos cenários otimizados para as espécies individualmente. Nós mostramos que nem sempre uma boa espécie guarda-chuva para a conservação da conectividade também será para a conservação do habitat primário, e vice-versa. Além disso, a rede da espécie guarda-chuva foi muito variável na representação das demandas das outras espécies, mesmo que a espécie guarda-chuva tenha mostrado um bom desempenho em representar separadamente tanto a conectividade quanto a qualidade do habitat das outras espécies. Esquemas baseados na similaridade tiveram desempenho limitado e inconsistente entre as categorias de todas as três características ecológicas. Os esquemas baseados na diversidade tiveram uma eficiência comparável à da rede combinada de todas as espécies, independentemente da característica ecológica considerada. Nossa trabalho traz importantes perspectivas para a seleção de espécies substitutas para a conservação da rede de habitats.

**PALAVRAS-CHAVE:** conectividade, semelhança ecológica, conservação de múltiplas espécies, espécie guarda-chuva

## ABSTRACT

Since conservation decisions are commonly made on the basis of species-based surrogates, it is essential to establish criteria for the definition of surrogate approaches capable of providing reliable conservation solutions. Here, we evaluated the performance of different surrogate strategies using habitat quality and connectivity models designed for 11 mammal species in a broad region of the Atlantic Forest. We evaluated separately the potential of different species to represent habitat and connectivity for a diverse group of other species (performance umbrella). We selected the species that performed well both conservation tasks simultaneously and elected it as the umbrella species. Then, we compared the effectiveness of the umbrella species habitat network with the performance of networks designed from multispecies surrogate schemes, using the all-species-combined scenario as reference. Multispecies surrogate schemes were defined from different perspectives: maximizing the similarity and diversity among species according to three ecological characteristics (trophic level, dispersal capacity and matrix sensitivity). The performance of the habitat networks derived from the different schemes was measured by the average similarity and standard deviation in relation to the single-species-optimized scenarios. We found that not always a good umbrella species for connectivity conservation will also be for the primary habitat conservation, and vice versa. In addition, networks based on the single-species surrogate, even the species presenting good average performance as umbrella for both connectivity and habitat quality, was very variable in the representation of other species. Schemes based on similarity had limited and inconsistent performance across the categories of all three ecological characteristics. Diversity-based schemes have comparable efficiency to the all-species network independent of the ecological characteristic considered. Our work brings important insights to the selection of surrogate species for habitat network conservation.

**KEYWORDS:** connectivity, ecological similarity, multispecies conservation, umbrella species

## INTRODUCTION

Uncontrolled human exploitation of ecosystems has made habitat loss and degradation virtually ubiquitous factors in the list of major threats to species (IUCN 2018). Faced with an imminent biodiversity loss scenario, the establishment of protected areas has been identified as one of the main conservation tools capable of ensuring the persistence of remaining species (Saout et al. 2013). Although conservation planning based on only one species is still common in conservation literature (Caro 2010), the use of single-species surrogates (e.g., umbrella species, flagship species) has been widely criticized in recent years (e.g., Beier et al. 2009; Cushman and Landguth 2012). Although the value of some species as conservation proxy has already been proven (e.g., Caro 2003; Thornton et al. 2016), there is no single species capable of efficiently meeting the needs for a varied group of background species.

Species are limited by unique sets of environmental and eco-evolutionary factors and these differences reflect on their demands for foraging, dispersal, and reproduction, as well as their responses to human-induced changes (Breckheimer et al. 2014; Osborne et al. 2015). Therefore, the idiosyncrasies in species conservation demands can make management based on a species to be neutral or even conflicting with management for other species (Simberloff 1998; Breckheimer et al. 2014). Developing conservation plans taking into account multiple species with contrasting ecological characteristics has been suggested as more effective (Lambeck 1997; Nicholson et al. 2006; Beier et al. 2008). However, since no conservation scenario is likely to be as effective as that designed to meet the demands of a single species, the problem of conflicting

management also permeates the construction of multispecies habitat networks (Brodie et al. 2015; Beaudry et al. 2016).

Habitat conflicts may inevitably arise when the identification of conservation priorities is made for a diverse set of multiple species and at wide spatial scales (Beaudry et al. 2016). However, assessing incompatibility between species can be challenging since a set of species may present very different spatial patterns of primary habitat, such as breeding and foraging, but have congruent dispersal routes, and vice versa (Breckheimer et al. 2014). Thus, multispecies approach likely present a trade-off between the diversity of species needs being addressed and the effectiveness of the final habitat network in representing the individual demands for their component species (Brodie et al. 2015). Therefore, a key question for the success of multispecies conservation solutions is how to select surrogate species so that the final combination of their habitat and connectivity requirements will satisfactorily represent the individual needs for all species considered. For connectivity conservation, different solutions have been found. While Brodie et al. (2015) showed that multispecies connectivity scenarios may be more effective when they are built by grouping ecologically similar species, Meurant et al. (2018) demonstrated that prioritization schemes based on the systematic selection of a few species representing the diversity of habitat and/or movement needs is probably the best strategy to capture the demands of a broader species pool.

Here, we evaluated the efficiency of scenarios for habitat quality and connectivity conservation designed from surrogate schemes based on one and multiple species. We aim to answer three questions: (1) Does the capacity of a species to encompass the spatial requirements of the primary habitat of other species also extend to areas

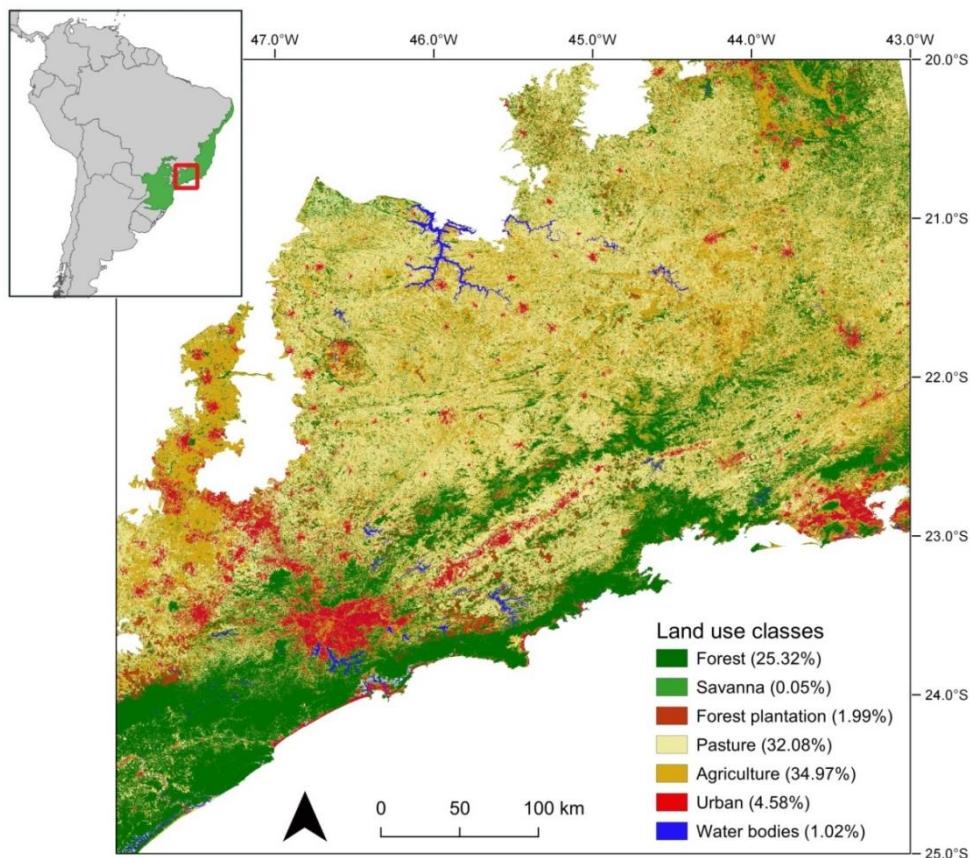
important for connectivity? (2) Do multispecies networks outperform a network designed from a single-species umbrella approach? (3) Which criterion for the projection of multispecies networks produces a more efficient spatial solution: similarity or diversity? We expect that: (1) the potential of a species to be primary habitat umbrella does not predict its ability to be a connectivity umbrella, and vice versa; (2) multispecies networks have superior performance in similarly retaining the demands of the target species relative to the network designed for a single umbrella species; (3) networks formed by grouping ecologically similar species will be more efficient in representing the needs of their component species than networks grouping species with divergent ecological characteristics.

## METHODS

### Study area and target species

The habitat networks for 11 mammal species were designed in the Atlantic Forest region equivalent to the intersection area of the geographical ranges of all species (IUCN 2018). Our study area included lands in a rectangular region of approximately 207,000 km<sup>2</sup> (Figure 1) with natural covers occupying 25% of its extension, being dominated by anthropic land covers (mainly pasture, agriculture, and urban area). Target species were selected according to the availability of occurrence data (Bovendorp et al. 2017; Lima et al. 2017) and in order to maximize the representation of the ecological characteristics (trophic level, dispersion capacity, and matrix sensitivity) from which the surrogate schemes were formed (Table 1). To construct target species' occurrence and connectivity maps along the study area, the land cover/land use mapping

made at a resolution of 30 m available through the MapBiomas database was used (MapBiomas 2018).



**Figure 1** Land cover/use in the study area (~207,015 km<sup>2</sup>). The values in parentheses indicate the percentage of the study area occupied by each class.

### Habitat quality and connectivity models

We used habitat quality and connectivity pattern maps produced by Diniz et al. (detailed in Chapter 2). Multi-scale, multiple logistic regression models were used to predict the occurrence of the target species along the forest fragments with area equal or greater than 10ha (N = 29,900). We explored six variables describing forest patches and the landscape surrounding them as predictors of the species presence: patch area, patch climatic and topographic suitability, distance to urban infrastructure, matrix resistance,

immediate landscape cohesion and % of surrounding core area. Climatic and topographic suitability was modeled using species distribution models. As the last three variables are scale-dependent, they were obtained on spatial scale of species' response, which were identified at species level exploring the following scales: species daily movement distance and 25%, 50%, and 100% of the species' dispersal distance. The final map of habitat quality at forest fragment level was obtained by applying the best model explaining the presence of each species along the remaining patches of native vegetation in the study area.

Dispersal routes were predicted for each species separately through the approach implemented in the LandScape Corridors software (Ribeiro et al. 2017). This software was developed to simulate multiple-path functional ecological corridors and has as core the least-cost path algorithm (Ribeiro et al. 2017). At each simulation the algorithm selects different target and source points within the patches pair to be connected, thus representing different points of departure and arrival that individuals could use during movement routes. After simulating the possible routes, the software creates a density map showing how many simulated routes passed through each pixel. Likewise the most popular methodologies for connectivity analysis, the least-cost modeling is based on a layer known as resistance surface (Zeller et al. 2012). Resistance can be interpreted as the difficulty in terms of physiological demands, willingness of an organism to cross a particular environment and/or increase in mortality (Zeller et al. 2012). Resistance values related to land use/land cover classes were obtained through expert opinion. A framework based on the metapatch concept was used to determine the identity of the source-target patches from which dispersal paths were simulated (Zetterberg et al. 2010; Mimet et al. 2016). For all species, we configured the software LandScape Corridors to

simulate 30 dispersal events for each pair of target-source patches using MP method, which considers the information for each pixel separately, and the default value of the variability parameter (equal to 2).

### **Evaluation of umbrella performance**

We evaluated the potential umbrella of species (i.e., the ability of a species to encompass the spatial demands of other species through its own demands) separately for two conservation criteria: habitat quality and connectivity. We calculated the spatial overlap between habitat patches with occurrence predicted for one species in relation to the other ten (beneficiary species). We repeated the same procedure for the dispersal route maps. We used the average overlap and standard deviation as performance measures. High average and low standard deviations indicate that the species in question presented high spatial congruence in relation to the others and that this pattern was consistent among the beneficiary species. After defining the potential umbrella for all species, we selected the species that presented high performance for both conservation criteria and used its habitat network in the subsequent analyzes.

### **Definition and performance of the surrogate schemes**

We added the habitat quality and connectivity maps for the umbrella species identified in the previous step to build a habitat network based on the single-species surrogate strategy (umbrella scheme). We also formed networks considering species-specific groups (similarity-based schemes) delimited according to the following ecological characteristics: dispersal capacity, trophic level, and sensitivity to the anthropic matrix.

We identified the trophic level of the species (carnivores, herbivores, and omnivores) according to Paglia et al. (2012). We grouped herbivores, granivores, and frugivores in a single category and we called it “herbivores”. Species that had omnivorous diet plus any other diet (frugivorous or insectivorous diet) were grouped into a single category called “omnivores”. For the other two characteristics, the classification was made according to the following criteria. With regard to dispersal capacity, we considered as “short dispersers” all species with dispersal distance less than 1 km, “intermediate dispersers” those species with dispersal between 1 km and 10 km, and “wide dispersers” those species with dispersal greater than 10 km. To assign the level of sensitivity to the anthropic matrix, we added the resistance values of three land use classes: agriculture, pasture, and urban area. Then, we classified the species with “little sensitivity” to matrix when they presented values of resistance values of 200 resistance (or cost) units or less, “intermediate sensitivity” for species presenting resistance between 200 and 250 resistance (or cost) units, and “high sensitivity” for species with values higher than 250 resistance (or cost) units (Table 1).

We constructed similarity-based networks by adding the habitat quality and connectivity maps of all species within each of the three categories for a given ecological characteristic, totaling nine similarity-based networks. For each ecological characteristic, we also formed networks in order to maximize the diversity of categories using the fewest possible species to represent them (three species). We built all possible networks from the combination of three species each belonging to a different category within a given ecological characteristic, thus totaling 48 networks for each characteristic.

To compare the efficiency of the networks formed from the different schemes (umbrella, similarity, and diversity), we measured the spatial agreement between the final surrogate networks and the single-species-optimized scenarios, the latter being formed from the sum of habitat maps and connectivity of each species individually. We adopted the average and standard deviation of the correlation coefficients in relation to optimized scenarios for all species and for the species within each ecological grouping as performance measures. A network with high average and low standard deviation indicates that its final structure is able to efficiently cover the individual demands and does so in a similar way throughout the species. We standardized all networks to range from 0 to 1 before correlation tests. We used the “all-species-combined network” as a reference to compare the performance of the different surrogate schemes.

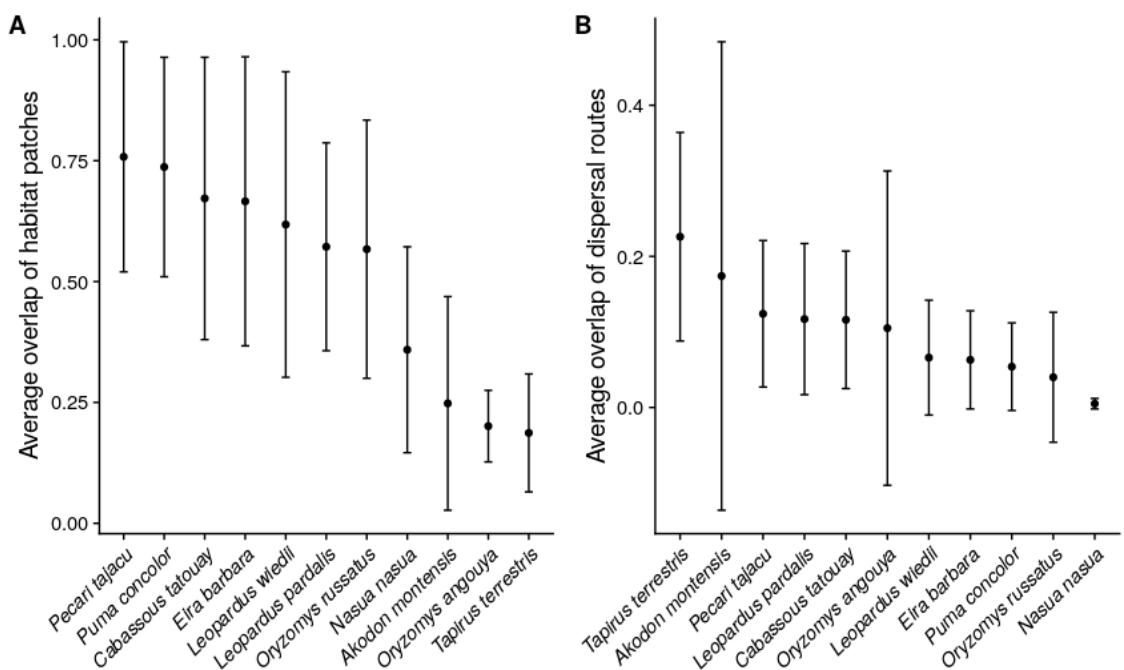
**Table 1** Classification of 11 species of mammals according to dispersal capacity, trophic level, and sensitivity to the anthropic matrix.

Species	Dispersal <sub>km</sub>	Dispersal capacity	Diet	Sensitivity to matrix
<i>Akodon montensis</i>	0.22	short	omnivore	low
<i>Cabassous tatouay</i>	15.35	wide	carnivore	low
<i>Eira barbara</i>	3.03	intermediate	omnivore	intermediate
<i>Leopardus pardalis</i>	31.26	wide	carnivore	intermediate
<i>Leopardus wiedii</i>	9.82	intermediate	carnivore	high
<i>Nasua nasua</i>	2.98	intermediate	omnivore	low
<i>Oryzomys angouya</i>	0.46	short	herbivore	high
<i>Oryzomys russatus</i>	0.32	short	herbivore	high
<i>Pecari tajacu</i>	7.56	intermediate	herbivore	intermediate
<i>Puma concolor</i>	60.00	wide	carnivore	low
<i>Tapirus terrestris</i>	25.85	wide	herbivore	intermediate

## RESULTS

There was greater average overlap between the primary habitat patches of the species than among their dispersal routes (Figure 2). There was no significant relationship

between dispersal capacity and umbrella performance of the target species for neither primary habitat ( $N = 11$ ,  $R^2 = 0.10$ ,  $F = 1.01$ ,  $p = 0.339$ ) nor connectivity ( $N = 11$ ,  $R^2 = 0.005$ ,  $F = 0.05$ ,  $p = 0.827$ ). Surprisingly, the species that presented the greatest agreement in the habitat patches distribution in relation to other species, *Tapirus terrestris*, was also the species that showed the greatest capacity to cover the dispersal paths of the others through its pattern of movement (Figure 2). Although the species *Akodon montensis* showed an average congruence close to that of *Tapirus terrestris* in relation to the dispersal routes, its spatial overlap variation was approximately three times greater in comparison to *Tapirus terrestris* (coefficient of variation of 1.78 and 0.61, respectively). Among all species, *Pecari tajacu* showed a higher average overlap and lower standard deviation for both habitat patches and dispersal routes and, therefore, we selected this species as the umbrella species for the other analyzes.

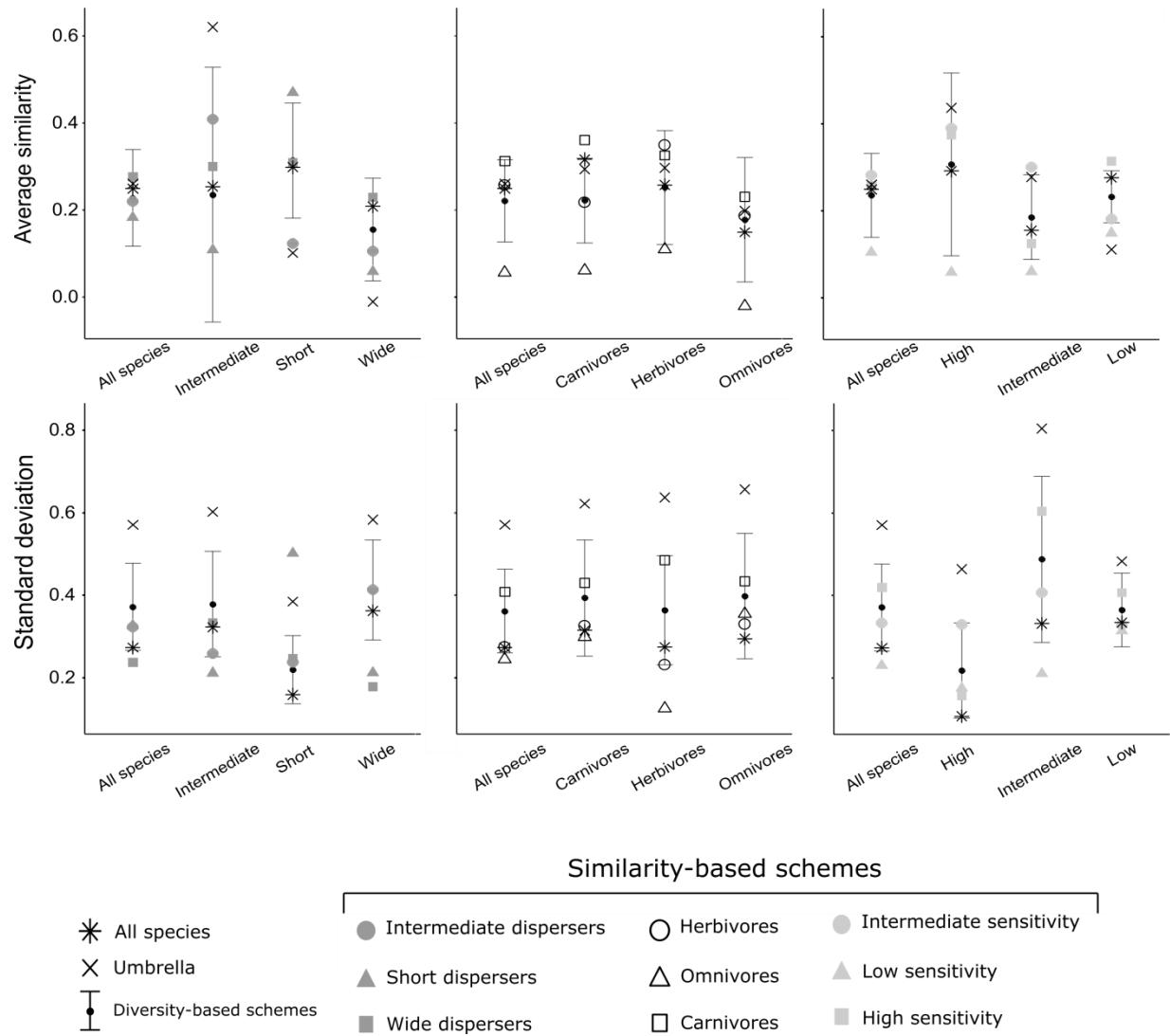


**Figure 2** The potential of the 11 target species as habitat (A) and connectivity (B) umbrella species measured by the average spatial congruence among the predicted habitat patches and the dispersal routes, respectively, for each of the target species in

relation to the ten other species. The central value represents the mean and the bars represent the standard deviation.

The umbrella scheme presented an average performance similar to multispecies schemes, but also had the highest values of standard deviation (Figure 3). Thus conservation of areas based on the requirements of a single species would retain the individual conservation criteria for the other species in a widely variable way, being efficient for some species, but underrepresenting others. Specifically, the umbrella scheme performed poorly in indicating important areas for conservation of short and wide dispersers as well as for species with low sensitivity to the matrix (Figure 3). The network based on the demands of *Pecari tajacu* was more efficient than the others scheme only in representing the needs of species with dispersal capacity similar to its own capacity (intermediate).

Similarity-based schemes had superior performance in representing their component species only when three grouping categories were used: carnivores, species with intermediate sensitivity to matrix and short dispersal species (Figure 3). The omnivore network had the worst performance in representing groups of species for any category of trophic level, even for the omnivorous species. A similar result was obtained for the network formed exclusively by species with low sensitivity to matrix. In general, diversity-based networks had average performances and standard deviations comparable to the all-species scheme, regardless of the ecological feature considered.



**Figure 3** Efficiency of different surrogate schemes to represent the spatial demands of all species and species groups (e.g., only carnivores, only short dispersal species) determined according to three ecological characteristics: dispersal capacity, trophic level, and matrix sensitivity. The average similarity was calculated using the Spearman rank correlation coefficient between the networks derived from the different schemes and the species-specific networks. The average and standard deviations of the diversity-based schemes were calculated from 48 networks, representing all possible combinations of three species, each of which representing one of the three categories within each ecological characteristic.

## DISCUSSION

Systems of protected area must adequately represent and ensure the long-term maintenance of biodiversity (Margules and Pressey 2000). However, species-based surrogates are often used because incorporating all species of a region in conservation planning is not a feasible task, regardless of its size. Here, we evaluated the performance of conservation scenarios generated from different surrogate schemes based on one and multiple species. We compared the efficacy of multispecies scenarios relative to a conservation solution provided by the use of an umbrella species identified systematically. We further explored the potential trade-off between the diversity of ecological characteristics represented in multispecies networks and their performance in addressing the individual demands of the component species.

The overlap of spatial requirements among species showed that they, generally, share a greater similarity in the distribution of primary habitats than in dispersal habitats. This is not surprising since the universe of forest fragments from which the occurrence of the species was assessed was known, whereas the potential pathways of dispersal were not. Therefore, a greater disagreement of the landscape areas used for dispersal among species was already expected due to three main factors: the particularities of species movement ecology, the unique sets of patches with predicted occurrence from which the dispersal was simulated, and the random components of the connectivity model. Separate assessment of the species potential as umbrella for primary habitat and connectivity conservation revealed that the umbrella species identified for one conservation goal cannot always be extrapolated to the other. If the species identified here as the best connective umbrella (*Tapirus terrestris*) was used for prioritization of

habitat quality, the primary habitat representation for most other species would be strongly compromised. Species that use different breeding and foraging habitats may disperse along similar routes or, conversely, some species may exhibit considerable overlapping of primary habitats, but disperse in unique ways across the same landscape (Breckheimer et al. 2014). Thus, we suggest that the identification of umbrella species be made by explicitly taking into account the specific conservation objectives as well as the composition and spatial configuration of the study area (Diniz et al. 2018).

Our results showed that the single-species network with the highest capacity to indicate habitat and connectivity for the other species (selected to compose the umbrella scheme) had a general performance similar to the other multispecies scenarios. However, the umbrella scheme was the least comprehensive, showing a widely varying representation among species. This suggests that if this surrogate scheme were adopted to establish conservation priorities in the study area, some species would be inefficiently protected, such as those with extreme dispersal capacities and less sensitive to the matrix the most impaired. High standard deviations for criteria retention among species were also fund by Meurant et al. (2018) when species with broad home ranges, considered by the authors as potential umbrella species, were used as a surrogate scheme to prioritize multispecies habitat networks. This study also found that the use of the umbrella scheme also led to under-representation of the needs of small body mass species. Therefore, as many previous studies have found, our results suggest that designing protected areas or wildlife linkages considering only the requirements of umbrella species may consist of an inefficient conservation strategy (e.g., Beier et al. 2009; Brodie et al. 2015; Meurant et al. 2018; Wang et al. 2018). Conservation planning

should include species with high potential to meet the demands of other species, but should not be developed only around one or another species with this characteristic.

Contrary to our expectations, similarity-based schemes had limited and inconsistent performance through the categories of the ecological characteristics. For example, our analysis indicated that the carnivore network provided the best conservation scenarios for carnivores, as found by Brodie et al. (2015), but this result was not repeated for the other two trophic levels. Considering all three ecological characteristics, similarity-based schemes were more efficient than the other schemes in representing their component species only when three of the nine categories of grouping were used. For the other six categories, producing networks according to the ecological similarity of the species had comparable or inferior efficiency to the diversity schemes that, in turn, had practically the same performance as the all-species scenario. A similar result was also found by Meurant et al. (2018) who revealed that only half of the species present in a broader pool of forest species when systematically selected to represent the diversity of habitat and/or movement requirements of the whole group provide efficient multispecies network. The similar performances between the schemes based on similarity and diversity independently of the ecological feature used shows that the categories of groupings used, except for three, were not able to capture the similarities in habitat and connectivity patterns between species. Therefore, we suggest that future studies investigate the potential of other factors such as sensitivity to fragmentation or barriers to dispersal as well as minimum habitat requirements as criteria of grouping, since they can be determinant in the spatial agreement of important areas for connectivity between species (Diniz et al. 2018).

In an ideal world for biodiversity conservation, if all remaining natural landscape could be protected, or at least maintained without additional anthropogenic changes, the use of ecological surrogates would not be necessary. However, given the budget constraints for conservation and the continuous human-induced environmental changes, both scenarios are utopian. Thus, the use of manageable components of biodiversity, such as species and landscapes, in conservation planning becomes indispensable. Therefore, it is crucial to define which surrogate strategies will be able to provide reliable conservation solutions. Our results offer four main insights into the use of surrogate species to determine conservation priorities. First, the identification of umbrella species must be made explicitly in accordance with conservation objectives; extrapolations of the umbrella property of a species from other analyzes with divergent objectives should be avoided. Second, multispecies networks are more comprehensive than networks based on a single species and, therefore, habitat prioritization should include species with great potential to indicate the requirements of other species, but should not be done exclusively for a single-species surrogate. Third, group-based networks of ecologically similar species do not always offer more efficient solutions. Fourth, the selection of a small subset of species representing the diversity of ecological features present in the species pool can be as efficient as directly considering the demands of all species.

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## **CONCLUSÕES**

O desenvolvimento desta tese contribuiu para uma maior compreensão de como a seleção de espécies substitutas e a escolha de estratégias metodológicas podem afetar as soluções de conservação. Os resultados obtidos fornecem pelo menos cinco lições valiosas que podem ajudar a orientar a identificação de prioridades de conservação para múltiplas espécies em escala regional:

**(1) Diferentes modelos de conectividade têm diferentes perspectivas do processo de dispersão.** Como os modelos de conectividade têm seus próprios fundamentos e arcabouços matemáticos, ao escolhermos um modelo específico, estamos assumindo diferenças importantes sobre a ecologia de dispersão das espécies. Portanto, se quisermos encontrar áreas importantes para manter o fluxo de indivíduos ao longo das paisagens, devemos selecionar o(s) modelo(s) de conectividade de acordo com as características de movimento das espécies-alvo, para além da disponibilidade de dados e dos objetivos do estudo.

**(2) A escolha da abordagem metodológica para a projeção de redes de habitat pode ser decisiva para a conservação das espécies-alvo.** Nós demonstramos que o uso das ferramentas analíticas mais populares para projetar redes de habitats não é intercambiável. As prioridades de conservação e a eficiência na representação individual das espécies-alvo podem variar amplamente entre redes projetadas a partir de diferentes modelos de conectividade e algoritmos de priorização. Portanto, a estratégia metodológica para delinear redes de habitat deve ser escolhida de uma maneira que esteja fortemente alinhada com os objetivos de conservação, ao invés de ser arbitrariamente selecionada, assumindo equivalência entre as diferentes abordagens disponíveis.

**(3) A seleção de espécies guarda-chuva deve basear-se tanto nas características das espécies quanto nas características das paisagens.** Nós demonstramos que a composição e configuração da paisagem, adicionalmente às características das espécies relacionadas à dispersão e ao uso do habitat, são determinantes para o desempenho de

uma espécie como guarda-chuva para conectividade. Portanto, sugerimos que a identificação de espécies guarda-chuva seja feita explicitamente em projetos focados na conservação da conectividade, evitando a transferência dessas entre paisagens ou regiões com diferentes padrões espaciais.

**(4) *Redes de habitat projetadas para múltiplas espécies são mais eficientes do que redes construídas considerando apenas as demandas de uma única espécie substituta.***

Nossos resultados indicaram que nem sempre uma boa espécie guarda-chuva para conectividade também será eficiente para a conservação de habitats primários, e vice-versa. Além disso, mesmo que uma espécie apresente um bom desempenho como guarda-chuva tanto para a conectividade quanto para a conservação de habitats primários, redes baseadas em espécies substitutas únicas podem ter um desempenho muito variável na representação das outras espécies. Portanto, redes projetadas a partir das necessidades de múltiplas espécies têm maior capacidade de atenderem similarmente às demandas espaciais das espécies-alvo do que redes construídas em torno das exigências de uma única espécie guarda-chuva, mesmo que essa tenha sido sistematicamente identificada.

**(5) *Poucas espécies substitutas representando a diversidade de características presentes no conjunto total de espécies podem ser suficientes.*** Nós mostramos que as redes de habitat construídas a partir do agrupamento de espécies ecologicamente semelhantes geralmente não são mais eficazes do que aquelas geradas usando o menor número de espécies capazes de maximizar a diversidade de características representadas. Nós constatamos também que esses cenários baseados na diversidade tiveram uma eficiência semelhante ao cenário construído considerando todas as espécies-alvo.