Combinando ecologia de paisagens e ecologia do movimento para entender conectividade e processos ecológicos

Combining landscape and movement ecology to understand connectivity and ecological processes

Bernardo Brandão Niebuhr dos Santos

Março 2018

BERNARDO BRANDÃO NIEBUHR DOS SANTOS

**Combinando ecologia de paisagens e ecologia do movimento para entender
conectividade e processos ecológicos**

**Combining landscape and movement ecology to understand connectivity and ecological
processes**

Tese apresentada ao Instituto de Biociências da
Universidade Estadual Paulista "Júlio de
Mesquita Filho", campus Rio Claro, como
requisito para obtenção do grau de Doutor em
Ecologia e Biodiversidade.

Orientador: Prof. Dr. Milton Cezar Ribeiro
Co-orientador: Profa. Dra. Laurence M. V.
Culot
Co-orientador: Prof. Dr. Otso Ovaskainen

Rio Claro-SP

Março de 2018

UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Rio Claro
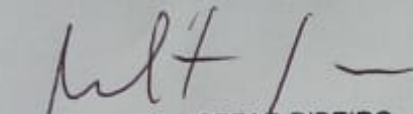
CERTIFICADO DE APROVAÇÃO

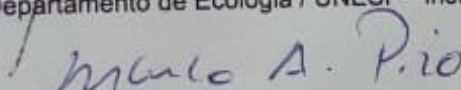TÍTULO DA TESE: Combining landscape and movement ecology to understand connectivity and ecological processes

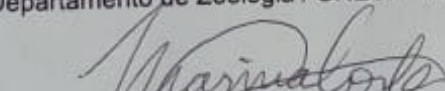AUTOR: BERNARDO BRANDÃO NIEBUHR DOS SANTOS
ORIENTADOR: MILTON CEZAR RIBEIRO
COORIENTADORA: LAURENCE MARIANNE VINCIANNE CULOT
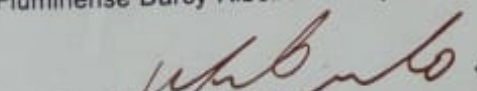
Aprovado como parte das exigências para obtenção do Título de Doutor em ECOLOGIA E BIODIVERSIDADE, área: BIODIVERSIDADE pela Comissão Examinadora:

Prof. Dr. MILTON CEZAR RIBEIRO
Departamento de Ecologia / UNESP - Instituto de Biociências de Rio Claro - SP

Prof. Dr. MARCO AURELIO PIZO FERREIRA
Departamento de Zoologia / UNESP - Instituto de Biociências de Rio Claro - SP

Profa. Dra. MARINA CORREA CORTES
Departamento de Ecologia / UNESP - Instituto de Biociências de Rio Claro - SP

Prof. Dr. CARLOS RAMÓN RUIZ MIRANDA
Centro de Biociências e Biotecnologia, Laboratório de Ciências Ambientais / Universidade Estadual do Norte Fluminense Darcy Ribeiro - Campos dos Goytacazes / RJ

Prof. Dr. DANILO BOSCOLO
Departamento de Biologia / Universidade de São Paulo, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto - SP

Rio Claro, 28 de março de 2018

DEDICATÓRIA

Dedico este trabalho às pequenas, Dani e Gal.

Com todo meu amor.

AGRADECIMENTOS

Aos membros da banca, pela generosidade de ler e discutir comigo essa tese, tanto em seu formato de projeto (Carlos Ruiz, Paulo Inácio Prado) como agora em sua forma final (Marco Pizo, Marina Côrtes, Carlos Ruiz, Danilo Boscolo – e, pelo apoio, a Sabrina Araújo, Ronaldo Morato, Mauro Galetti, Karl Mokross, Marcia Marques, Érica Hasui).

A todos os amigos, colegas e agregados do Laboratório de Ecologia Espacial e Conservação, o LEEC. Esse é um ambiente muito especial, e todos que passam por aqui contribuem pra isso. Agradeço a todos vocês por manterem esse espaço, as discussões, os LEEC Meetings, a energia e a alegria no dia a dia, por manterem um jeito divertido e colaborativo de fazer ciência. Em especial, agradeço a Milene, Natalia, Renata, Claudinha, Laurinha, Julia Oshima, Julia Assis, Maurício, Flavia, Felipe, Kauã, Camila, Teka, Andreia, Dani, Pati, Fernando-Miriam-Ian, John, Gambé, Juliana, Urucum, Giordano, Diego, Vinicius, Rodrigo, Thadeu, Pavel, André, pela amizade e pelas discussões, tão importantes nesse processo de doutorado. O ao Miltinho por orquestrar a dinâmica toda.

Aos outros colegas da pós, pela amizade e pela intensa troca de ideias, em especial Cléber, Barbara, Caro Bello, Carol Carvalho, Erison, Zé Wagner, Fernandinha, Bruno Leles.

Aos colegas que criaram e mantiveram as discussões do grupo estudo de Ecologia do Movimento, em especial, Milene, Claudinha, Julia, Karl, Miltinho, Dani, Laurinha, Ronaldo, Natalia, e tantos outros, e pela parceria na organização do I MEB.

Aos professores da pós, que tanto me inspiraram e ensinaram, em especial ao Miltinho, Danilo Boscolo, Mauro Galetti, Pedro Jordano, Tadeu Siqueira, Marco Pizo, Marina Côrtes, Karl Mokross e Marcio Araújo. Pedro e Mauro, vocês me introduziram ao incrível mundo da frugivoria e dispersão de sementes, sou muito grato por isso! Miltinho e DB, vocês foram grandes mestres do universo da ecologia de paisagens.

Ao prof. Juan Manuel Morales, por me incentivar no processo de aprendizado sobre movimento e sobre processos ecológicos, tanto em prosas como em seus trabalhos.

Ao prof. Marc Kéry, por compartilhar de forma tão didática um pouquinho do mundo da estatística Bayesiana, e ao Gonçalo Ferraz por propiciar esse espaço, no curso de Introdução à Estatística Bayesiana, na UFRGS.

Aos profs. Paulo Inácio e João Baptista, por criarem um espaço tão interessante de aprendizado de modelos estatísticos, no curso de máxima verossimilhança na USP.

Ao Paulo Inácio e ao Roberto Kraenkel, pelo aprendizado e parceria durante os cursos de verão de biologia matemática do IFT, durante vários anos.

Às professoras e amigas Sabrina Araújo e Isabela Varassin, e ao companheiro Ricardo Campos, pela parceria nas discussões sobre movimento e redes de interação, ainda que esse

de dados espaciais da Mata Atlântica e no desenvolvimento dos modelos de regeneração natural.

Ao Nica, Iça, Deny, Iza, Oscar, que foram nossa primeira família em Barão Geraldo, ainda que depois os caminhos tenham nos levado para lugares diferentes.

À Iça, por todos os momentos de companhia pra mim e pra Dani, durante todo esse tempo em Barão, por toda a amizade a carinho.

Aos vários amigos e amigas de Barão e Campinas, que tornaram esse um lugar tão especial para viver: Iça, Gabi, Alan Ricardo, Lucas, Marília, Renato, Sandra, Elis, Lara, Alan Carneiro, AnaLu, Fer, Lino e Lila, Ricardo, Debora e Ian.

À Nil e à sua linda família, por estar sempre de braços abertos cheios de amor para a minha família.

À Ivana e à equipe da Seção de Pós-Graduação do Instituto de Biociências da UNESP, que sempre me auxiliaram e seguraram as pontas quando eu perdia os prazos.

À Cris e ao time do Departamento de Ecologia da UNESP, pelo apoio logístico e organizacional, sempre.

À Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, processo 2013/50421-2) pelo financiamento e apoio em diversas partes desse processo de doutorado.

À CAPES pela bolsa, sem a qual nada disso teria sido materializado. O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001.

A Alexandra Elbakyan, por ter criado o sistema de compartilhamento de artigos *Sci-Hub*, que desafia o monopólio das grandes editoras e permite acesso livre à ciência de qualidade ao mundo todo, e a todos que têm contribuído para manter esse sistema.

E a tantas outras e outros que não cabem aqui, sou muito grato. Espero que os resultados do que aqui construí(mos) possa ser útil de alguma forma, e que eu possa retornar todo esse amor e apoio que tenho recebido.

RESUMO

A conectividade é uma propriedade das paisagens que influencia fortemente a abundância e a distribuição da biodiversidade e é chave para entender as interações entre organismos e os processos ecológicos resultantes de tais interações. Como a conectividade da paisagem é afetada tanto pela estrutura da paisagem como pelo comportamento e características dos organismos, tanto fatores intrínsecos quanto extrínsecos devem ser considerados em estudos ecológicos e práticas de conservação que utilizam uma abordagem de paisagens. Aqui nós combinamos elementos de ecologia de paisagens e ecologia do movimento para avaliar os efeitos de mudanças nas paisagens, como a perda e a fragmentação de habitat, sobre a persistência de populações, sobre a conectividade da paisagem, e sobre a dispersão de sementes e a regeneração natural. O foco não foi em um grupo ecológico ou ecossistema específico mas em como a interação entre o espaço e o movimento influenciam processos ecológicos em diferentes contextos. No primeiro capítulo, nós apresentamos uma ferramenta livre e de código aberto, chamada LandScape Metrics (LSMetrics), desenhada para calcular índices da paisagem calibrados ecologicamente, integrando a estrutura das paisagens às características comportamentais das espécies. Nós descrevemos a ferramenta e a aplicamos a dois contextos: a avaliação do status de fragmentação da Amazônia brasileira, que apesar de conter uma extensas áreas de floresta contínua, está sendo rapidamente fragmentada em suas margens mais ocupadas; e o desenho experimental de pesquisas ecológicas utilizando uma abordagem de paisagens, de maneira a aumentar a representatividade e minimizar a correlação entre variáveis da paisagem no planejamento de pesquisa. No segundo capítulo, nós focamos na conectividade da paisagem habitat por um primata ameaçado da Mata Atlântica, o mico lẽao dourado (*Leontopithecus rosalia*). Nós avaliamos os efeitos das estradas na diminuição da conectividade e encontramos um decréscimo no relacionamento genético entre indivíduos separados por estradas, independe do tipo de estrada. Nós também simulamos corredores ecológicos, levando em conta a estrutura da paisagem e a percepção da espécie, e indicamos locais para restauração de habitat e da conectividade entre populações. A conectividade simulada foi alta em locais onde os micos leões ocorrem e em trechos das estradas onde eles foram observados cruzando. Finalmente, no terceiro capítulo nós fomos para além da análise da paisagem e das populações animais e estendemos o conceito de conectividade de paisagens à restauração da conectividade, analisando o processo de dispersão de sementes por animais e a subsequente regeneração natural das florestas. Nós desenvolvemos a aplicamos modelos de simulação, baseados na estrutura da paisagem e na movimentação animal, para estimar a

dispersão de sementes pela paisagem. Nós verificamos uma relação entre a dispersão de sementes modelada e o potencial de regeneração natural de áreas de pastagem numa escala de paisagem, no Vale do Paraíba, na Mata Atlântica. Em todos os capítulos, nossa intenção foi de apresentar novos métodos e ferramentas, responder questões teóricas em ecologia de populações e comunidades, e aplicar essas ferramentas a situações reais que requerem diretrizes para conservação e restauração.

Palavras-chave: movimentação animal, conectividade de paisagens, conservação da biodiversidade, restauração florestal, ecologia aplicada

ABSTRACT

Landscape connectivity is a property of landscapes that greatly influences biodiversity abundance and distribution and is a key to understand interactions between organisms and the ecological processes provided by them. As landscape connectivity is affected by both landscape structure and the behavior and characteristics of organisms, both intrinsic and extrinsic factors must be considered in ecological studies and conservation planning. Here we combined landscape ecology and movement ecology frameworks to assess the effects of landscape changes such as habitat loss and fragmentation on the persistence of populations, on landscape connectivity, and on seed dispersal and natural regeneration. The focus was not on a specific group or ecosystem but on how the interplay between space and movement influences ecological processes in different contexts. In the first chapter, we presented a free and open source tool, called LandScape Metrics (LSMetrics), designed to calculate ecologically-scaled landscape indices by integrating landscape structure and behavioral characteristics of species. We described the tool and applied it to two contexts: the assessment of the fragmentation status of the Brazilian Amazon, that still present a large extent of continuous forest, but has being rapidly fragmented along its human occupied boundaries; and the design of sampling points for ecological research using a landscape approach, to maximize the representativeness and minimize the correlation between landscapes to be selected for research. In the second chapter, we focus on the landscape connectivity for an endangered primate of the Atlantic Forest, the golden lion tamarin (*Leontopithecus rosalia*). We assessed the effects of roads in disrupting connectivity and found a decrease in the pairwise genetic kinship between individuals separated by road, regardless of their type. We also simulated ecological corridors to indicate places for connectivity restoration. Simulated connectivity was shown to be high in sites where tamarins occur and in road sections where they were observed crossing. Finally, in the third chapter, in the last chapter we went beyond organismal populations and extended the concept of landscape connectivity to the restoration of forest connectivity by looking at the process of animal-mediated seed dispersal and the natural regeneration of forests. We developed and applied simulation models, based on landscape structure and animal movement, to estimate seed dispersal throughout the landscape. We then verified the relation between seed dispersal and the potential of natural regeneration of non forest areas at landscape level. In all chapters, we wished to present new methods and tools, address theoretical issues on population and community ecology, and made them applied to real world situations in need of conservation and restoration guidelines.

SUMÁRIO

Introdução

Uma das questões centrais da ecologia diz respeito às causas e consequências da distribuição e abundância dos organismos na natureza (Sutherland et al. 2013). Um método para abordar essa questão diretamente é olhar para as interações entre organismos, como animais e plantas, que se influenciam mutuamente em suas distribuições e abundâncias. Muitos grupos de animais dependem de plantas para se alimentar e de algum tipo de vegetação como habitat para viver. Dessa forma, a distribuição, abundância, e identidade das plantas afeta sua ocorrência, comportamento, atividade, e movimento. Por outro lado, animais agem como predadores e dispersores de muitas espécies de plantas, de maneira que seu comportamento e movimento afetam diretamente como as plantas se espalham e estabelecem no espaço, ao longo do tempo. Assim, avaliar quais fatores influenciam as interações entre espécies é um ponto chave para entender as dinâmicas populacionais desses dois grupos (Morales et al. 2010), assim como os processos ecológicos que daí decorrem, como a dinâmica entre predadores e presas, a dispersão de sementes, e a regeneração de habitats naturais (Morales et al. 2013; Carlo & Morales 2016).

Interações ocorrem somente quando há encontros biológicos. Dessa forma, elas precisam ser consideradas explicitamente no espaço e no tempo (Turchin 1998; Viswanathan et al. 2011), à luz do movimento dos organismos que propicia esses encontros. O movimento é o processo que conecta recursos, genes, e processos ecológicos entre locais diferentes (Jeltsch et al. 2013), torna possível a interação entre indivíduos e, em uma perspectiva mais ampla, provê conexões entre populações, comunidades e ecossistemas (Nathan et al. 2008).

Em um contexto de mudanças intensivas no uso e cobertura da terra em diversas regiões em todo o globo (Wade et al. 2003; Ribeiro et al. 2009; Taubert et al. 2018), é importante compreender como a estrutura da paisagem (mensurada em variáveis como a quantidade, a agregação, e a degradação de habitat) influenciam o movimento, as interações, e a dinâmica de populações. No nível individual, sabe-se que as modificações na paisagem influenciam, entre outras coisas, o uso de habitat e de recursos (p. ex, Boyle et al. 2012; Pozo-Montuy et al. 2013), a sobrevivência e as taxas de dispersão (p. ex., With & King 1999; Niebuhr et al. 2015). No nível populacional, são afetadas as taxas de crescimento, a abundância (Boyle & Smith 2010), a conectividade da paisagem e a variabilidade genética (Bascompte & Solé 1996; Keller & Largiadèr 2003; Mitrovski et al. 2008). Em nível de comunidade, a riqueza, a ocorrência, as taxas de extinção e *turnover* (p. ex., Andrén 1994; Martensen et al. 2012) e as propriedades de redes de interação são modificadas (Hagen et al.

2012), todos como consequência da interação entre múltiplos fatores (Fahrig 2003; Arroyo-Rodríguez & Dias 2010; Arroyo-Rodríguez et al. 2013). Ademais, alterações na quantidade e na configuração do habitat podem também alterar processos ecológicos: o fluxo de genes e indivíduos entre manchas de habitat (p. ex., Moraes et al. 2018) e o processo de dispersão de sementes, por exemplo, são influenciados pela estrutura da paisagem (p. ex., Kaplin & Lambert 2002; Galetti et al. 2006; Wosniack et al. 2013).

Se, por um lado, a perda e a fragmentação de habitat frequentemente têm efeitos negativos sobre a manutenção dos organismos em diferentes níveis (Fahrig 2003, mas veja 2017), por outro o movimento pode contrabalancear ou pelo menos reduzir essas consequências, dependendo de como os indivíduos se movem nas paisagens alteradas (Zollner & Lima 1999; Niebuhr et al. 2015). Os padrões da paisagem e a movimentação dos indivíduos interagem de tal forma que não podem ser pensados separadamente para avaliar como as plantas e animais interagem e como a dinâmica de suas populações muda ao longo do tempo.

Um conceito chave que, por definição, combina as abordagens de paisagens e de movimento é a conectividade das paisagens. A conectividade é definida como a característica da paisagem que facilita (ou impede) a movimentação de genes, propágulos (pólen e sementes), indivíduos e populações entre suas diferentes partes (Taylor et al. 1993; Rudnick et al. 2012). Ela possui duas componente, a estrutural e a funcional. A conectividade estrutural descreve as características físicas da paisagem, como elas podem facilitar ou dificultar a movimentação de organismos, e depende exclusivamente da estrutura e da composição da paisagem (Rudnick et al. 2012). Já a conectividade funcional, para além de ser influenciada pela estrutura da paisagem, está relacionada a como os organismos percebem e interagem com a paisagem, como se comportam em relação aos diferentes tipos de habitat, em fim, como se movimentam e dispersam (Taylor et al. 2006). Dessa maneira, a conectividade funcional só pode ser pensada e aplicada pela integração de medidas da estrutura da paisagem com componentes da ecologia do movimento (Bélisle 2005). Além disso, a conectividade das paisagens tem sido mostrada como uma das variáveis espaciais mais importantes em explicar a ocorrência de espécies e diferentes processos ecológicos (p. ex., Uezu et al. 2005; Martensen et al. 2008, 2012; Baguette et al. 2013).

Nesse contexto, na presente tese partimos do pressuposto de que elementos de ecologia de paisagens e de ecologia do movimento precisam ser integrados se queremos de fato entender as causas e consequências dos processos ecológicos. O objetivo foi unir ferramentas e conceitos das duas disciplinas afim de propor métodos de análise, entender como se estrutura a conectividade de paisagens e quais suas consequências ecológicas, e

utilizar isso para propor medidas de conservação e restauração. O foco não foi em um tipo de organismo ou ecossistema específico, mas nos processos ecológicos em si, em diferentes contextos. A ideia de conectividade foi utilizada em aplicações em três localidades distintas, nas florestas Amazônica e Atlântica, que situam-se entre as florestas tropicais mais extensas e ricas em biodiversidade (Morellato & Haddad 2000; Ribeiro et al. 2009; Laurance et al. 2011). Além disso, o estudo mobilizou uma complexidade de dados de diferentes naturezas, modelos estatísticos e de simulação. As análises daí decorrentes foram organizadas em três capítulos.

O primeiro capítulo buscou responder: como podemos integrar a percepção das espécies à estrutura da paisagem para criar métricas de paisagem que tenham significado ecológico? Como essas métricas podem auxiliar a compreensão do processo de fragmentação de habitat e o planejamento de pesquisas em ecologia de paisagens, contextos reais que envolvem problemas ambientais? Para isso desenvolvemos uma ferramenta livre e de código aberto, denominada LandScape Metrics (LSMetrics), na qual desenhamos e implementamos o cálculo de diferentes índices da paisagem, entre métricas de conectividade estrutural e funcional, de heterogeneidade espacial, e métricas relacionadas à presença de bordas. Aplicamos então essa ferramenta para avaliar o processo e status de fragmentação da Amazônia brasileira e ao desenho experimental em ecologia de paisagens em uma região fragmentada da Mata Atlântica brasileira que foi sujeita à uma recente crise hídrica, o sistema Cantareira. Por seu foco metodológico mas também aplicado, esse capítulo foi desenhado para ser submetido à *Ecological Modelling & Software*.

O segundo capítulo tem como foco a avaliação da conectividade da paisagem habitada por um primata ameaçado da Mata Atlântica, o mico leão dourado (*Leontopithecus rosalia*). Buscamos responder como a presença de diferentes tipos de estrada afeta a conectividade entre populações, e como as características da paisagem e da espécie podem ser utilizadas para propor locais para re-conectar fragmentos de habitat e restaurar a conectividade. Para isso, estimamos como diferentes tipos de estradas interferem na conectividade e usamos o conhecimento de especialistas sobre a percepção da espécie, a respeito dos tipos de uso da terra na paisagem, para propor corredores e conexões entre as manchas florestais ocupadas pelos micos leões. Esse capítulo foi desenhado para ser submetido à revista *Conservation Biology*.

Por fim, no terceiro capítulo vamos além do efeito das paisagens e da conectividade sobre as espécies e buscamos olhar pormenorizadamente para o processo de manutenção e aumento da conectividade, provido pela fauna no processo de dispersão de sementes.

Especificamente, buscamos responder: Como podemos identificar, em paisagens fragmentadas, locais mais propícios a receber chuva de sementes e a regenerar naturalmente, de forma a restaurar a conectividade entre fragmentos? Como a estrutura da paisagem e o movimento da fauna frugívora interagem para determinar padrões de dispersão de sementes e propiciar a regeneração natural? Desenvolvemos modelos de simulação, integrando a estrutura da paisagem e a movimentação da fauna frugívora, para estimar padrões de dispersão de sementes e relacionar esses padrões com o potencial de regeneração natural de áreas sem vegetação natural. Esses modelos foram aplicados à região do Vale do Paraíba, na Mata Atlântica paulista, e comparados aos dados de regeneração natural das florestas dessa região ao longo de 20 anos. A identificação de áreas com maior potencial de dispersão de sementes e de regeneração natural é um passo importante para priorizar esforços e desenhar políticas de incentivo de restauração florestal, que visem o aumento da área e da conectividade das florestas. Por seu foco aplicado, esse capítulo está desenhado para ser submetido ao *Journal of Applied Ecology*.

A integração de elementos da ecologia de paisagens e do movimento vem sendo estudada há pelos menos duas décadas (Lima & Zollner 1996; Nathan 2008; Baguette et al. 2013; Jeltsch et al. 2013). Essa tese vem a contribuir com essa discussão oferecendo ferramentas e olhando especificamente para dinâmicas ecológicas em ambientes fragmentados nas florestas tropicais dos Neotrópicos. Ao longo de toda a tese tivemos a intenção de apresentar novos métodos e ferramentas, responder questões teóricas em ecologia de populações e comunidades, e aplicar essas ferramentas a situações reais que requerem diretrizes para conservação e restauração.

Referências

Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71**:355–366.

Arroyo-Rodríguez V, Dias PAD. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology **72**:1–16.

Arroyo-Rodríguez V, Moral EC, Mandujano S, Chapman CA, Reyna-Hurtado R, Fahrig L. 2013. Assessing habitat fragmentation effects on primates: the importance of evaluating questions at the correct scale. Pages 13–28in L. K. Marsh and C. A. Chapman, editors.Primates in Fragments: Complexity and Resilience. Springer, New York.

Baguette M, Blanchet S, Legrand D, Stevens VM, Turlure C. 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews **88**:310–326.

Bascompte J, Solé R V. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. Journal of Animal Ecology **65**:465–473.

Bélisle M. 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology. Ecology **86**:1988–1995.

Boyle SA, Smith AT. 2010. Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? Biological Conservation **143**:1134–1143.

Boyle SA, Zartman CE, Spironello WR, Smith AT. 2012. Implications of habitat fragmentation on the diet of bearded saki monkeys in central Amazonian forest. Journal of Mammalogy **93**:959–976.

Carlo TA, Morales JM. 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rarebiased seed dispersal. Ecology **97**:1819–1831.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics **34**:487–515.

Fahrig L. 2017. Ecological Responses to Habitat Fragmentation per se. Annual Review of Ecology and Systematics **48**.

Galetti M, Donatti CI, Pires AS, Guimarães Jr. PR, Jordano P. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: The combined effects of defaunation and forest fragmentation. Botanical Journal of the Linnean Society **151**:141–149.

Hagen M et al. 2012. Biodiversity, Species Interactions and Ecological Networks in a Fragmented World. Advances in Ecological Research **46**:89–120. Elsevier Ltd.

Jeltsch F et al. 2013. Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. Movement Ecology **1**:6. Available from http://www.movementecologyjournal.com/content/1/1/6 (accessed April

28, 2014).

Kaplin BA, Lambert JE. 2002. Effectiveness of seed dispersal by Cercopithecus monkeys: implications for seed input into degraded areas. Page (Levey DJ, Silva WR, Galetti M, editors). CABI Publishing, Oxon.

Keller I, Largiadèr CR. 2003. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society B **270**:417–423.

Laurance WF et al. 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation **144**:56–67. Elsevier Ltd. Available from http://dx.doi.org/10.1016/j.biocon.2010.09.021.

Lima SL, Zollner PA. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology & Evolution **11**:131–135.

Martensen AC, Pimentel RG, Metzger JP. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation. Biological Conservation **141**:2184–2192.

Martensen AC, Ribeiro MC, Banks-Leite C, Prado PI, Metzger JP. 2012. Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. Conservation Biology **26**:1100–1111.

Mitrovski P, Hoffmann AA, Heinze DA, Weeks AR. 2008. Rapid loss of genetic variation in an endangered possum. Biology Letters **4**:134–138.

Moraes AM, Ruiz-Miranda CR, Galleti-Jr. PM, Niebuhr BBS, Alexandre BR, Grativol AD, Muylaert R de L, Ribeiro JW, Ribeiro MC. 2018. Landscape resistance influences dispersal and gene flow of endangered golden lion tamarins (Leontopithecus rosalia) within the Atlantic Forest. In review in Biological Conservation.

Morales JM, García D, Martínez D, Rodriguez-Pérez J, Herrera JM. 2013. Frugivore behavioural details matter for seed dispersal: a multi-species model for cantabrian thrushes and trees. PLoS ONE **8**:e65216.

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B **365**:2289–2301.

Morellato LPC, Haddad CFB. 2000. Introduction: The Brazilian Atlantic Forest. Biotropica **32**:786–792.

Nathan R. 2008. An emerging movement ecology paradigm. Proceedings of the National Academy of Sciences of the United States of America **105**:19050–19051.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America **105**:19052–19059.

Niebuhr BBS, Wosniack ME, Santos MC, Raposo EP, Viswanathan GM, Da Luz MGE, Pie MR. 2015. Survival in patchy landscapes: the interplay between dispersal, habitat loss and fragmentation. Scientific Reports **5**:11898. Nature Publishing Group. Available from http://dx.doi.org/10.1038/srep11898.

Pozo-Montuy G, Serio-Silva JC, Chapman C a., Bonilla-Sánchez YM. 2013. Resource Use in a Landscape Matrix by an Arboreal Primate: Evidence of Supplementation in Black howlers (Alouatta pigra). International Journal of Primatology **34**:714–731. Available from http://link.springer.com/10.1007/s10764-013-9691-y (accessed December 19, 2013).

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation **142**:1141–1153.

Rudnick DA et al. 2012. The Role of Landscape Connectivity in Planning and Implementating Conservation and Restoration Priorities. Issue in Ecology **16**:1–20.

Sutherland WJ et al. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology **101**:58–67.

Taubert F, Fischer R, Groeneveld J, Lehmann S, Müller MS, Rödig E, Wiegand T, Huth A. 2018. Global patterns of tropical forest fragmentation. Nature **554**.

Taylor PD, Fahrig L, Henein K, Merriam G. 1993. Connectivity Is a Vital Element of Landscape Structure. Oikos **68**:571. Available from http://www.jstor.org/stable/3544927?origin=crossref.

Taylor PD, Fahrig L, With KA. 2006. Landscape connectivity: a return to the basics. Pages 29–43in K. R. Crooks and M. Sanjayan, editors.Connectivity Conservation. Cambridge University Press, Cambridge.

Turchin P. 1998. Quantitative analysis of movement. Sinauer Associates, Inc. Publishers, Sunderland.

Uezu A, Metzger JP, Vielliard JME. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation **123**:507–519.

Viswanathan GM, da Luz MGE, Raposo EP, Stanley HE. 2011. The Physics of Foraging: an Introduction to Random Searches and Biological Encounters. Cambridge University Press, Cambridge.

Wade TG, Riitters KH, Wickham JD, Jones KB. 2003. Distribution and causes of global forest fragmentation. Conservation Ecology **7**:7.

With KA, King AW. 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecology **14**:73–82.

Wosniack ME, Santos MC, Pie MR, Marques MCM, Raposo EP, Viswanathan GM, da Luz MGE. 2013. Unveiling a mechanism for species decline in fragmented habitats: fragmentation induced reduction in encounter rates. Journal of the Royal Society Interface **11**:20130887.

Zollner PA, Lima SL. 1999. Search strategies for landscape-level interpatch movements. Ecology **80**:1019–1030.

1 Landscape Metrics (LSMetrics): a spatially explicit tool for calculating connectivity and other ecologically-scaled landscape metrics

Bernardo Brandão S. Niebuhr[a,b,1,*], Felipe Martello[a,c,1], John Wesley Ribeiro[a], Mauricio Humberto Vancine[a,b], Renata de Lara Muylaert[a,b], Vanessa Ellen Wendt Campos[a,b], Juliana Silveira dos Santos[a,d,e], Vinicius Rodrigues Tonetti[a,b], and Milton Cezar Ribeiro[a,b]

[a] Laboratório de Ecologia Espacial e Conservação, Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, SP, Brazil

[b] Universidade Estadual Paulista (UNESP), Instituto de Biociências, Campus Rio Claro, 13506-900 Rio Claro, SP, Brazil

[c] Departamento de Ciências Ambientais, Universidade Federal de São Carlos (UFSCar), 13565-905, São Carlos, SP, Brazil

[d] International Institute for Sustainability, Estrada Dona Castorina 124, 22460-320, Rio de Janeiro, Brazil

[e] Rio Conservation and Sustainability Science Centre, Department of Geography and the Environment, Pontifícia Universidade Católica, 22453900, Rio de Janeiro, Brazil

*Corresponding author. Universidade Estadual Paulista (UNESP), Instituto de Biociências, Campus Rio Claro, 13506-900 Rio Claro, SP, Brazil. Tel. +55 19 9 9150-0970.
E-mail addresses: **bernardo_brandaum@yahoo.com.br** (B.B.S. Niebuhr),
felipemartello@gmail.com (F. Martello), **jw.ribeiro.rc@gmail.com** (J.W. Ribeiro),
mauricio.vancine@gmail.com (M.H. Vancince), **renatamuy@gmail.com** (R.L. Muylaert),
vanessaellen@hotmail.com (V.E.W. Campos), **juliana.silveiradossantos@gmail.com** (J.S. dos Santos), **vrtonetti@gmail.com** (V.R. Tonetti), **miltinho.astronauta@gmail.com**,
mcr@rc.unesp.br (M.C. Ribeiro).

[1] Authors contributed equally to this work.

Abstract

Fauna movement capacity within a landscape influences population and community dynamics and ecological processes, and is strongly affected by landscape structure. Still, calculating functional connectivity and other relevant ecologically-scaled landscape indices considering species perception and gap-crossing capability is tricky, especially for large and fine scale maps. We present Landscape Metrics (LSMetrics), a free and open source Python- and GRASS GIS-based package for calculating indices of structural and functional connectivity, landscape diversity, and edge related metrics. Output maps are spatially explicit, so that each landscape cell present an index value, and metrics may be summarized at local, patch, and landscape level. Besides, each landscape cell may be classified into one of six landscape categories: core, edge, stepping stone, corridor, branch or matrix, that may connect landscape elements and ecological processes and contribute to a functional view of landscapes. Here we present the package description, its details and usage, and exemplify its application in two study cases. In the first the package is used to describe the fragmentation status of the Brazilian Amazon, one of the most biodiverse ecosystems in the world. The Amazon was shown to be much less fragmented than other threatened ecosystems, such as the Atlantic Forest, but is already highly fragmented in the Southeastern and Southern part, where the vectors of intense human occupation are located. The second application aims at showing a method to design sampling points for ecological research using a landscape approach, in a highly fragmented region of the Atlantic Forest of Southeastern Brazil. Landscape metrics were used to guarantee variation and independence in the spatial variables for an appropriate planning of a landscape ecology research. The performance and accessibility of LSMetrics, as well as its integration with other GRASS GIS tools, makes it a valuable tool for embedding maps with the ecological meaning to be used in biodiversity research and in the management of current environmental issues.

Software and data availability

LSMetrics package is free and open source, under the GNU GPL version 2 license, and may be obtained at the GitHub repository: https://github.com/LEEClab/LS_METRICS, with all R scripts used here for the applications. It is written in Python and runs within a GRASS GIS environment, a free GIS software available at http://grass.osgeo.org/. It runs in all Operating Systems where GRASS GIS 7.0.0 or newer runs: MS-Windows XP or newer, MacOS X 10.4.10 or newer, recent GNU/Linux or a Unix variant. All the spatial data used in the case studies were produced by MapBiomas, an inter institutional initiative to generate Brazil's annual land use and land cover time series and make it available for free. Maps are available at their website: http://mapbiomas.org/#.

1.1 Introduction

The conversion of natural habitats into human mediated land uses causes fragmentation and habitat loss, which are currently a major threat to biodiversity and the ecological processes it provides (Fahrig 2003, Haddad et al. 2015). In these fragmented landscapes, both the structure and the composition of landscapes may be important in determining the presence of organisms, their interactions, and the functions the biota perform over the space (Fahrig 2003, Driscoll et al. 2013). The comprehension of how space affects biodiversity – an ultimate question of landscape ecology – is essential not only within the research agenda but also for environmental management and conservation planning (Correa Ayram et al. 2016). For instance, the identification of conservation and restoration priority areas is one of the most used strategies for conserving biodiversity. Landscapes patterns comprise a central point in identifying such areas (e.g., Tambosi et al. 2014), since measures at landscape level such as patch size, connectivity, and habitat availability are between the criteria most used in the selection of priority areas (Correa Ayram et al. 2016).

As landscape patterns are strongly related to biodiversity, landscape metrics may be good proxies for biodiversity indices, ecosystem functions, and how they are spatially distributed. Here we take the term "landscape metric" as a quantitative measurement of landscape patterns (Vos et al. 2001), so they may differentiate and quantify variation in habitat loss and fragmentation (Fahrig 2003), landscape configuration (Martensen et al. 2012), and spatial heterogeneity, for

instance. Technological developments have led to the availability of free and updated remote sensing data as well as the popularization of geographic information systems that greatly contributed to the increase in the use of landscape metrics (Correa Ayram et al. 2016). However, there are still many difficulties in adapting these tools to understand new and urgent ecological questions (Sutherland et al. 2013) and apply them to conservation issues at multiple scales, from local species loss to regional urban growth and the intensification of land use exploration at global scale (Foley et al. 2005, Lapola et al. 2014). Addressing these questions require, at least: (i) the analysis of series of maps from different ecosystems at multiple scales; (ii) making landscape metrics spatially explicit, so that metrics can be assessed at specific locations and also summarized at the patch and landscape levels; (iii) the computational processing of large spatial data sets; and (iv) the inclusion of information on species' characteristics such as landscape perception and gap-crossing capability, so that landscape metrics can be functionally and ecologically relevant (Vos et al. 2001).

Landscape connectivity, for instance, is a spatial variable measured in different ways in environmental studies (Tischendorf and Fahrig 2000, Bélisle 2005) and is often quantified by the presence of physical connections between patches, such as strip-shaped corridors (see Martensen et al. 2012 for an example). This structural connectivity is informative in many situations (Tischendorf and Fahrig, 2000), but it fails to capture important aspects of landscape function, leading to inappropriate land management strategies (Taylor et al. 2006). An alternative is to calculate metrics of functional connectivity, which demand biological knowledge on the species or functional group of interest, such as gap crossing capability (Bélisle 2005, Awade and Metzger 2008) and matrix permeability (Rayfield et al. 2010). Functional landscape connectivity is defined as the degree to which a landscape facilitates or impedes movement of organisms and materials among resource patches (Taylor et al. 1993) and is a faithful measure to describe the interaction between landscape structure and an species' perspective. Conservation actions that focus only on conserving a certain natural area without guaranteeing gene flow, migration and recolonization of organisms may be inefficient (Rudnick et al. 2012).

Some of the most used software packages that calculates landscape metrics (*e.g.* Fragstats, Path Analyst, V-Late) do not allow the users to visualize the spatial distribution of the variables. Rather than having a value of a specific landscape metric in determined localities

(usually sampling points), making landscapes patterns spatially explicit allows users to identify how such values change across space. This visualization may help landscape ecologists in experimental design, facilitating the selection of a set of landscapes considering a gradient of specific metrics (e.g. percentage of habitat or heterogeneity). Such visualization can also facilitate environmental managers in strategic conservation decision-making, since it can help identifying priority regions for restoration and conservation and areas to be connected by corridors.

To calculate spatially explicit landscapes metrics that account for species movement attributes, we developed a free and open-source package called LandScape Metrics (LSMetrics). LSMetrics allows one to classify each landscape cell into landscapes categories that represent functions of landscape elements in space (such as edge, interior, stepping stone, and corridor), calculates structural and functional connectivity measures considering attributes of different species of interest, and estimate the amount of habitat, edge and core areas, considering multiple scales. Here we presented the package and showed environmental applications using it. In section 2 we described the package, its usage and workflow, and detailed the definition and implementation of each metric. In section 3, we showed two applications of LSMetrics, one assessing the fragmentation status of a large and biodiverse forest ecosystem, the Brazilian Amazon, and the other exemplifying the use of landscape metrics to sampling design in landscape ecology research. Finally, we discussed potential uses of the package, as well as its main advantages and limitations.

1.2 The LSMetrics package

LSMetrics is a free package developed in Python that works within the environment of the free geographic information system GRASS - Geographic Resources Analysis Support System (Neteler *et a*l. 2012). The software uses a user-friendly graphical user interface (GUI) but may also be run through command line as Python scripts. The workflow of LSMetrics is shown in Fig. 1. The installation files, upgrades, demonstration maps, and an online tutorial are available at GitHub (https://github.com/LEEClab/LS_METRICS). The package is open-source and is intended to be always open to the implementation of new metrics or new ways of calculating the ones already implemented.

The installation is very simple and having GRASS GIS version 7.x is the only requirement for running the package. The current version operates through the GUI in Ubuntu Linux and Windows Vista, 7, 8 and 10 operational systems, but versions for MacOS will also be made available in the near future. The script version also runs in MacOS. To ensure free copying, distribution, and modifications of the package and its source code, LSMetrics is distributed under the terms of the GNU General Public License, version 2 (GPLv2; see http://www.gnu.org/licenses/).

1.2.1 Input data and output files in LSMetrics

The package uses input raster maps with integer values only, in which each cell represents an area considered to be homogeneous, like a land use or vegetation type. Maps can be either binary (0 = matrix and 1 = habitat; Fig. 1) or multi-class (e.g. land use and land cover maps). The majority of landscape metrics are calculated using binary raster maps, except for the landscape diversity indices, which only make sense for multi-class raster maps. LSMetrics may also transform multiple class maps into binary ones before the calculation of metrics.

Once a GRASS project is created and raster maps are imported into it, using r.import or r.in.gdal (or other r.in.*) modules, for instance, LSMetrics may be run in two ways (Fig. 1). The first is calling the Python application and opening the GUI; the second is building a Python script (or opening a Python shell inside GRASS GIS prompt) and calling each landscape metric as a Python function. Both methods allow the users to run multiple metrics with various parameters and scales, for multiple maps, in a single run. The most appropriate method depend on the aim of the calculation and the familiarity the user has with Python programming.

LSMetrics output is a raster map for each combination of metric and parameters chosen. The user selects, from the package interface, which output raster maps will be exported (by default, in ".tiff" format). The other metrics selected are not exported but kept within the GRASS project. As several of the metrics use parameters measured in meters, such as edge depth, gap crossing capability, and the scale of analysis around the cells, and the areas are reported in hectares, the package was developed to analyze data sets using metric projections. We encourage users to use projections such as UTM, Polyconic, Lambert and Albers and avoid using geographic projections. In addition to maintaining the data within the GRASS GIS database and

exporting raster maps, LSMetrics also exports lists of values (e.g. fragment size, patch size, habitat, core, edge, and matrix amount) in text format that may be edited and interpreted in any statistical software or worksheet preferred by the user.
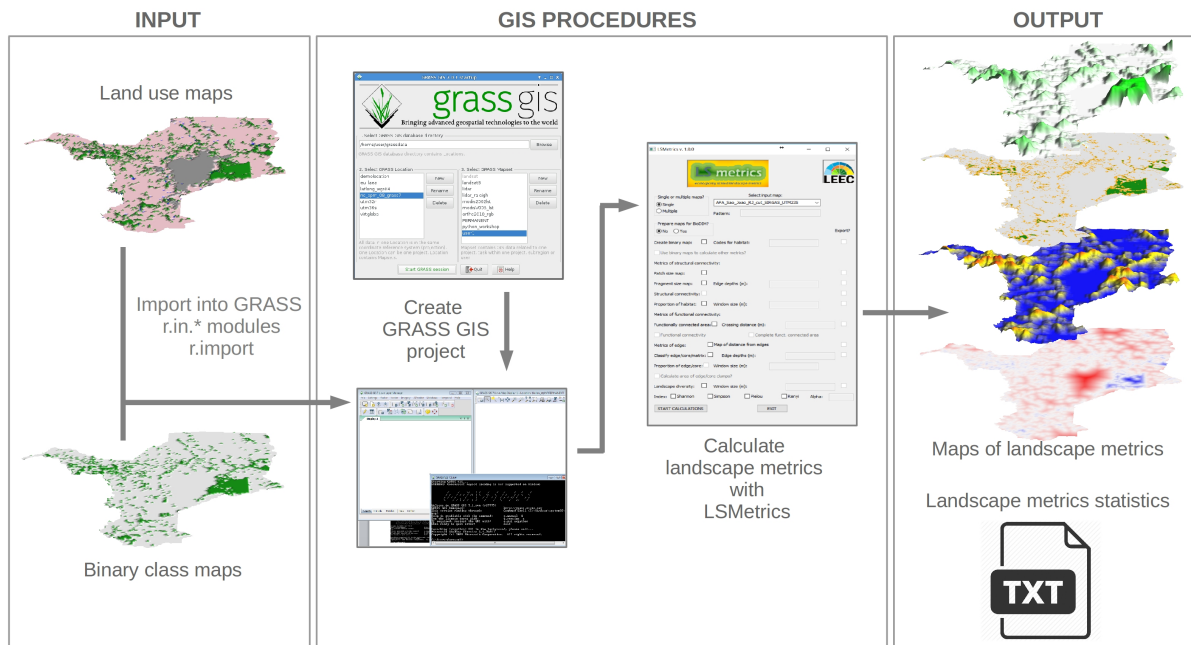
Figure 1. Flowchart showing the usage of LSMetrics. Land use or binary class input maps are prepared outside LSMetrics with GIS software. A GRASS GIS location is opened and maps must be imported. Then LSMetrics calculates metrics for each input raster map. The output consists of a series of metrics maps and text files with metrics statistics.

1.2.2 Description of the landscape metrics

Before describing the landscape metrics calculated by LSMetrics, it is important to define some concepts as they are adopted here. First, the most basic elements of analysis within landscapes are patches. A *patch* is defined as a clump of contiguous cells of the same class (value = 1 in the binary maps; it generally corresponds to habitat for a set of organisms, but may also represent other land use types or vegetation physiognomies). Both the 8- (default) and the 4-neighborhood rule may be considered when defining which cells are contiguous and are part of the same patch (Fortin and Dale 2005). We also distinguish between a patch and a *fragment* – a

clump of cells of the same class, structurally isolated from others by removing narrow landscape elements that are part of patches, such as corridors and branches (see description below). For instance, a single habitat patch may be formed by two or more fragments connected by habitat corridors.

To completely understand the landscape elements used here, we consider that not all parts of habitat patches are equivalent. The boundaries – or *edges* – are subject to different environmental conditions and generally present a distinct biota, compared to the interior of patches (Murcia 1995). As the region of the patch that suffer edge influence is ecosystem and context dependent (Murcia 1995, Harper and Macdonald 2011), edge depth is a parameter defined by the user. Based on a given edge depth, the first functionality of LSMetrics is to classify the cells into elements according to its potential functions in the landscape, similarly to GUIDOS package (Vogt and Riitters 2017). The elements are: (i) *core area*, interior cells of patches, not subject to edge influence; (ii) *edge area*, all patch cells closer than the edge depth to boundaries between patch and non-patch environments; (iii) *stepping stones*, isolated patches composed solely by edge (without core area), that may be used as stops and connections in the dispersal of organisms between patches (Saura et al. 2014); (iv) structural *corridors*, narrow strip-shaped elements, defined by clumps of cells with a width smaller than twice the edge depth, that structurally connect fragments; (v) *branches*, elements as narrow as corridors but linked to only one fragment (not connecting fragments); and (vi) *matrix*, areas that do not correspond to habitat or to the land use class of interest (value = 0 in binary class maps).

Given these definitions, below we described the landscape metrics calculated by LSMetrics. Although we referred here to the class of interest (value 1 in the binary maps) as habitat, it may represent any other land use class represented in a binary class map. The following metrics are calculated for binary class maps:

Metrics of structural connectivity:
- *Patch size*. It is the summed area (in hectares) of all cells in a habitat patch. Two maps are created for each landscape: a patch identity (PID) map, which sets a distinct integer number to each habitat patch, and a patch size map, which sets the area of the patch to all

cells that belong to it; matrix cells are set to NULL in both. Statistics text files created contain the ID and the area of each patch in the landscape.

- *Fragment size* (sensu Martensen et al. 2008). It is the summed area (in hectares) of all cells in a habitat fragment. The only parameter to define fragment size is the edge depth, used to classify corridors (with width smaller or equals twice the edge depth) and separate fragments that pertain to the same habitat patch. If there are no fragments connected to a focal fragment, patch size and fragment size are equivalent. In all other cases, as a patch may be composed of several fragments and corridors linking them, fragment size is always smaller than the size of the patch that contains it. Two maps are created for each landscape, equivalent to patch size output maps: a fragment ID (FID) and a fragment size map. Statistics text files created contain the ID and the area of each fragment in the landscape.
- *Structural connectivity* (sensu Martensen et al. 2008). Represents the area of habitat that is structurally connected to a given fragment – corridors, branches, and other fragments. In practice, it is calculated as the difference (in hectares) between patch size and fragment size; therefore, it also depends on the edge depth parameter, used to define corridors and fragments. When a patch has only one fragment, its structural connectivity is zero. Also, only cells of fragments are given structural connectivity values; cells of corridors and other landscape elements are set to NULL. Statistics text files created contain the ID of the fragments and their structural connectivity value.
- *Proportion of habitat*. It is the percentage of habitat (0 to 100%) within an area around each cell of the landscape. In practice, it is calculated as the mean of the binary class map values contained within a moving window, whose side size is chosen by the user. The user can also determine the window shape as a square (default) or a circle (in this case the window size correspond to the diameter of the circle).

Metrics of functional connectivity:
- *Functionally connected area* (sensu Ribeiro et al. 2009). It is the sum of the area (in hectares) of the local patch and of all patches accessible to the organism, given this organism is able to cross a gap distance in the matrix to reach other patches. This is calculated by generating a buffer of size equal to half of the gap crossing capacity of the

organism, around all patches, grouping all habitat patches close enough in the same clusters of patches, and summing up the area of all the grouped patches. The gap crossing capacity, in meters, is a parameter defined by the user according to the organism or process of interest. Two maps are created for each landscape: a functional patch ID (fPID) map, which sets a distinct integer number to each cluster of habitat patches, and a functional patch area map, which sets the functionally connected area to all cells that belong to a given cluster of functionally connected patches; matrix cells are set to NULL in both. Statistics text files created contain the ID and the area of each functional patch in the landscape.

- *Functional connectivity* (sensu Martensen et al. 2008). It is the sum of the habitat area (in hectares) available to an organism that is able to cross a given distance between patches, without considering the area of the local patch. It is calculated as the difference between functionally connected area and patch size. All matrix cells are set to NULL. Statistics text files created contains the ID of each structural patch and its functional connectivity.
- *Complete functionally connected area*. It is equivalent to the functionally connected area, but the value of functionally connected area is also set to the buffer cells around each functional patch, even if they are originally matrix.

Edge metrics:
- *Classification of landscape cells in landscape structural elements*. Given an edge depth defined by the user, the cells of a landscape may be classified into edge, core, and matrix, in which case binary maps of edge/non-edge areas and core/non-core areas are also created. Alternatively, landscapes may be classified in more elements (core/edge/stepping stone/corridor/branch/matrix), as described above. Statistics text files created contain the a number that identifies each landscape structural element and the summed area of each element in the landscape.
- *Proportion of edge and core areas*. Given an edge depth and a scale, defined by the user, maps showing the proportion of edge and core areas around each cell in the determined scale (window size) are calculated. The calculation is equivalent to the proportion of habitat and uses the binary maps of edge/non-edge and core/non-core as input.

- *Distance to edges*. Given the boundaries between habitat patches and non-habitat matrix, in this map each cell is set a value corresponding to its distance to the nearest habitat edge cell, in meters. Positive values correspond to cells in the matrix and negative values to locations inside patches.
- *Size of edge and core clumps*. Given edge and core areas were identified, contiguous cells are clumped into edge and core clumps (i.e., cells of edge and core that pertain to the same patch), and their areas are calculated (in hectares). Two maps are created for each one (edge/core) for each landscape: an edge (core) clump ID (edge or core PID) map, which sets a distinct integer number to each clump of edge (core) cells, and a clump area map, which sets the the area of those clumps; non-edge (non-core) cells are set to NULL in both.

The following metrics may be calculated for land use maps (and may make sense only for maps with more than two classes):

- *Landscape diversity*. Diversity indices may be calculated for a given window size around each cell, taking into account the number of different land use classes and their relative proportion. To calculate that, the GRASS addon *r.diversity* is used (Rocchini et al. 2013). Therefore, four indices of landscape diversity may be calculated, based on the information theory and the entropy concept: Shannon, Simpson, Pielou, and Renyi. See Rocchini et al. (2013) for more information on the indexes.

To make it easier, LSMetrics allows users to enter lists of parameters, such as edge depths, gap crossing capacities, and window sizes, so that landscape metrics can be calculated for multiple scales, for different contexts and for species with different behavioural responses to landscape structure. Details on usage and on the metrics may be found in the LSMetrics manual (Appendix C).

1.3 Environmental applications

To exemplify the usage of LSMetrics we performed two real world case studies. In the first application we assessed the fragmentation status of the Brazilian Amazon, a great part of the widest and richest most biodiverse ecosystem in the world, which is currently subject to high

deforestation rates (Andersen et al. 2002). We analyzed how metrics vary throughout the biome for organisms that respond to landscape structure differently. In the second case study, we used landscape metrics to draw the sampling design of an ecological research agenda with a landscape approach. To that extent, we focused on the Cantareira-Mantiqueira corridor, in the Atlantic Forest of Southeastern Brazil, a fragmented forest region that supplies water to the largest urban center in South America and was recently subject to large crisis in water supply (Coutinho et al. 2015). The data and technical details of both case studies are shown in Appendices A and B.

1.3.1 Fragmentation status of the Brazilian Amazon

Understanding landscape patters of an ecosystem – how natural habitat areas are spatially spread and where the greatest focus of environmental change occur – is an important step to plan where to focus conservation ans restoration efforts (see, e.g., Ribeiro et al. 2009, Rodrigues et al. 2009). The Amazon forest, the most biodiverse ecosystem in the World, covers an area of about 5,3 million km^2, which represents 40% of global tropical forest area, and it is threatened by habitat loss, degradation and fragmentation (Laurance et al. 2011). In Brazil, this biome has been facing an increase in deforestation rates over the years, in a process of intensification of agriculture and livestock, and its original forest area has been reduced by at least 15% (Laurance et al. 2011, Aragão et al. 2014). Here we assessed the fragmentation status of the Brazilian Amazon forest by calculating the distribution of patch sizes, the amount of forest at different distances from edges, and how landscape connectivity changes for organisms with different dispersal capabilities.

The Brazilian Amazon is formed mainly by medium sized forest patches, with between 1,000 and 25,000 ha (Fig. 2A). This is very contrasting if we compare it with the Brazilian Atlantic Forest, in which more than 80% of the patches have less than 50 ha in size (Ribeiro et al. 2009). Still, the distribution of patch sizes is very asymmetric: more than 80% of Amazon patches are below 50,000 ha, but summed they account for less than 0.5% of the total forest area. Almost 98% of the Amazon forest is located in only a few forest fragments with between 10 and 90 million hectares in size (Fig. 2A, A1). This asymmetry is patch size makes it comparable to the Atlantic Forest (Ribeiro et al. 2009) and to other tropical forest around the world (Taubert et al. 2018). Expected forest cluster size is high compared to the the extinction thresholds and the

minimum area needed for most species to occur (see, e.g., Magioli et al. 2015, Regolin et al. 2017), and increases rapidly with the gap crossing capacity of the organism (Fig. 2B). This may be observed in detail in Fig. A1. Species that can cross only 200 m of matrix between forest patches can potentially access large areas (Fig. A1-E), even in the most fragmented parts of the Amazon (Fig. A1-F).

As forest patches are large, the proportion of forest area that correspond to edge is relatively low, compared to more fragmented ecosystems (Ribeiro et al. 2009): about 10% of the forest is within 100 m from the edges, and more than 50% of the forest is further than 1 km from the edges (Fig. 2C). This value seem to have decreased in the last 15 years (when 50% of the forest area was further than 1700 m from edges; Broadbent et al. 2008), indicating the shrinkage of patches and increase of the overall fragmentation. On the other hand, given the extent of forest in the Amazon, this corresponds to an enormous amount of forest under edge effects, what may have several environmental consequences (Broadbent et al. 2008), such as the decrease in carbon storage in the forest (Pütz et al. 2014) and a change in animal abundances and distribution (Lenz et al. 2014).

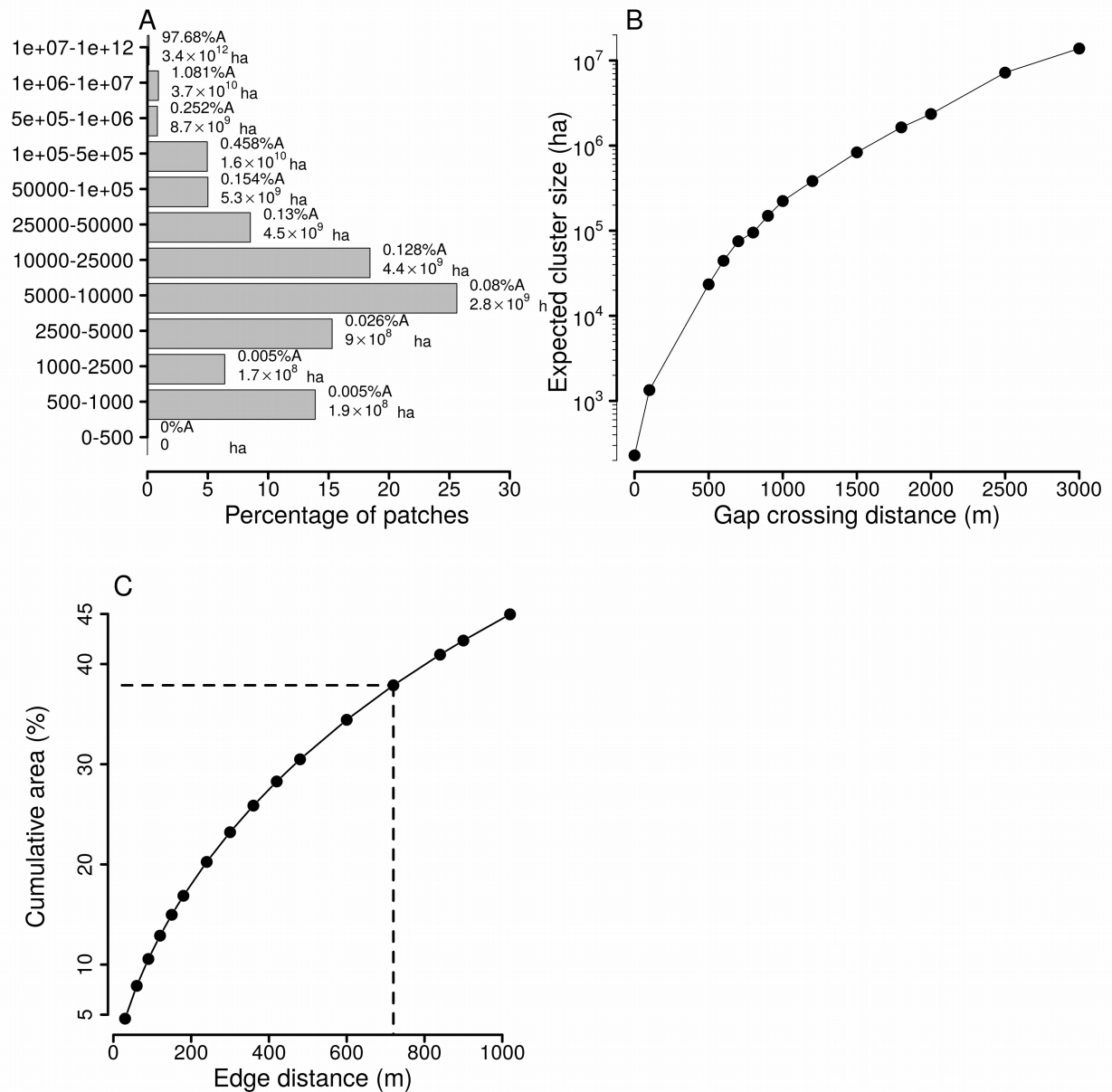Figure 2. Description of the landscape structure of the Brazilian Amazon. (A) Percentage of forest patches according to patch size classes. The percentage of total forest area (%A) and the total area, in hectares, is shown besides each bar. (B) Average functionally connected patch for organisms that can cross different gap distances between patches. (C) Forest area located at different distances from patch edges.

Overall, the Amazon is less fragmented than most tropical forest ecosystems in the World and still present large areas of continuous forest (Brinck et al. 2017). The most fragmented regions are found at the South and East of the biome, where the larger urban areas are located and where there is an expanding vector of deforestation for extensive agriculture and livestock (Fig. A1). Although the area of forest is still very large in the Amazon, it is necessary to understand how much forest there is and how it is distributed to face the current and future challenges in terms of deforestation and land use change (Davidson et al. 2012). As we showed, LSMetrics is a tool that gives a step in this direction and may help the management and planning of land use in the Amazon and other ecosystems worldwide.

1.3.2 Experimental design using a landscape approach

Landscape ecology research is of utmost importance to understand how biodiversity and ecological processes are influenced by space and how they change in a world where habitat loss and fragmentation are widespread. Knowledge on the relation between landscape patterns and processes, the occurrence and persistence of species, and the maintenance of ecosystem services is also very important to determine conservation and restoration policies. On the other hand, good research practices on landscape ecology are very challenging: it is often hard to draw spatial replicates (Hurlbert 1984), considering variation and independence on the spatial variables of interest (Wang et al. 2014), and taking into account multiple scales at which these variables matter (Jackson and Fahrig 2015). The challenge already starts when deciding what sites to be sampled. A poor sampling design may incur in limitations or even an impossibility of performing appropriate analysis of the ecological data.

Suppose one wants to perform a community ecology study in heterogeneous landscapes. The question may be to understand how different spatial processes affect the patterns of composition, diversity, or to infer about assembling rules of communities. Different taxa may be affected by different variables at different scales, such as the local or regional amount of habitat, the heterogeneity, and the structural or functional connectivity of landscapes. A sampling design to answer such questions needs a set of sampling landscapes in which there is a gradient in the variation of spatial variables and independence between them (Wang et al. 2014).

Here we used a landscape approach to define sampling points considering spatial variables generated by LSMetrics package for the Cantareira water system, in the Atlantic Forest of Southeastern Brazil. For illustration purposes, we calculated only patch size and Shannon landscape diversity metrics, the last using a 5 km extent. We then sampled twenty landscapes guaranteeing that a gradient in both these variables was represented and minimizing the correlation between them (Fig. 3). This usage of landscape metrics can be extended to a large set of landscape metrics, so that an ecological research agenda may be planned by considering different spatial variables and planning multi-scale studies with different taxa. Also, other optimization methods may be used, in order to maximize some measures (such as the variation in the lansdcape metrics) and minimize other variables (e.g. spatial autocorrelation), while avoinding some places where sampling is restricted (as area of war or environmental conflict and properties where the owners do not accept the entrance of researchers). This is a very important and currently neglected step to produce meaningful landscape ecology, useful for the application to current environmental issues, where LSMetrics is useful.
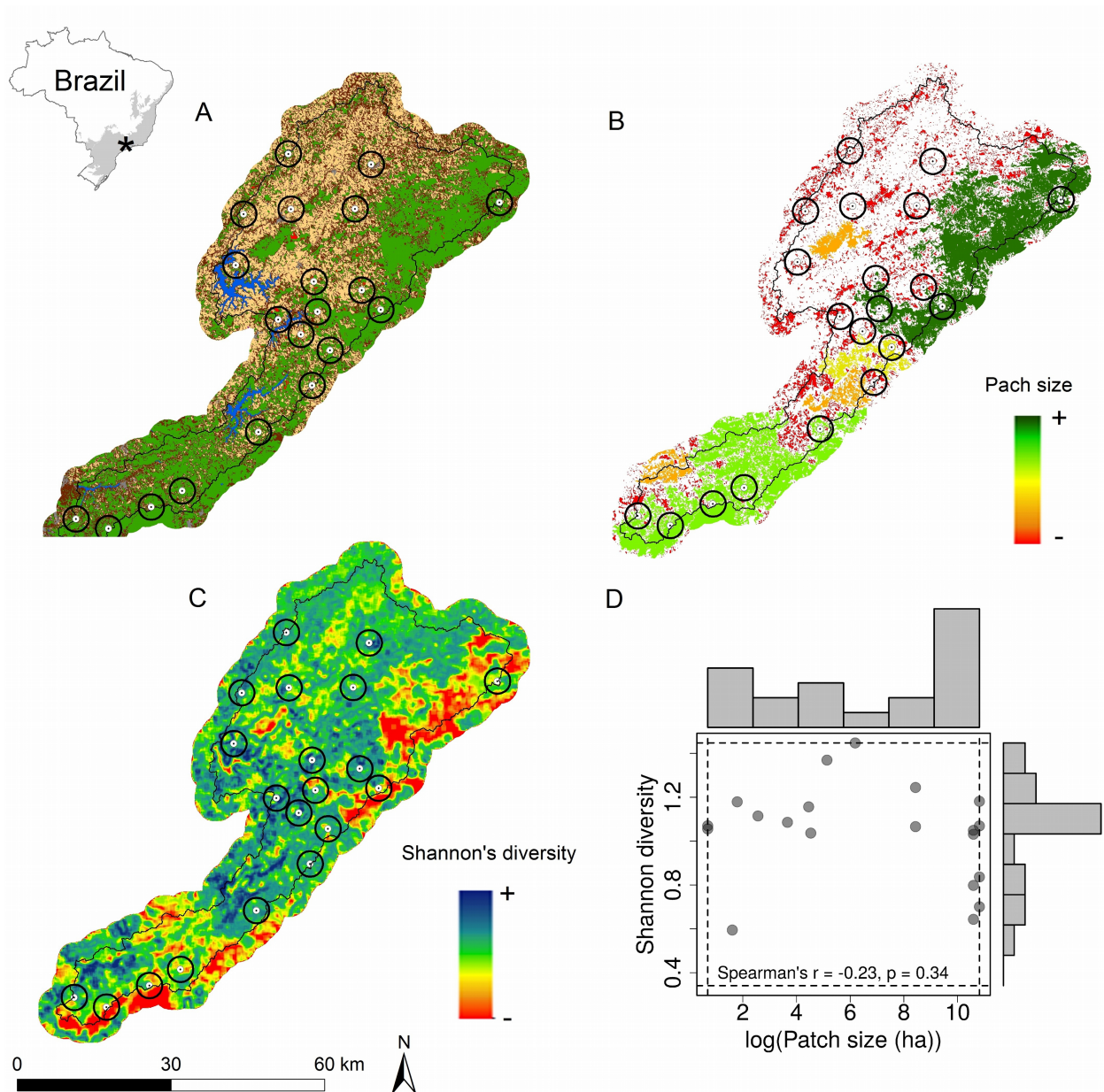
Figure 3. Illustration of a sampling design for ecological research at the Cantareira system, at the Southeastern Atlantic Forest, in Brazil. Land use (top left), patch size (top right), and landscape diversity at a 5 km extent (bottom left) maps are shown with a set of 20 landscape samples. These samples were chosen in order to guarantee variation in both landscape metrics and to minimize their correlation (bottom right panel).

1.4 Discussion

Here we described and showed environmental applications of the LSMetrics package, designed to facilitate the calculation of connectivity and other ecologically-scaled landscape metrics. Landscape metrics may be of great use in face of current environmental issues. Beyond the assessment of landscape patterns (Broadbent et al. 2008, Ribeiro et al. 2009, Taubert et al. 2018, present study), landscape metrics have been used to identify causes and search for focii of increased disease transmissivity (Rudnick et al. 2012), understand animal dispersal routes, gene flow (Moraes et al. 2018), and plan ecological corridors (McRae et al. 2008, Rudnick et al. 2012, Chapter 2), assess the importance and representativeness of individual habitat patches in a fragmented landscape (Rubio and Saura 2012), and prioritize sites for habitat conservation and restoration (Rudnick et al. 2012, Correa Ayram et al. 2016 Chapter 3), just to mention some examples. Ecological research also benefits from the use of landscape metrics, from the design (present study, Fahrig 2013) to the analysis of biodiversity data (Fahrig 2003, 2017). LSMetrics sums to the existing tools by calculating simple and straightforward metrics, as a free software, that may be easily integrated with a myriad of GIS tools available through GRASS GIS (GRASS Development Team 2017).

In addition to the easy-to-use GUI, we highlight three advantages of LSMetrics compared with the existing alternatives: a) the user can simultaneously analyze a large amount of independent landscapes and consider many parameter values (extent, edge depth, gap crossing capabilities), facilitating the performance of repetitive analyses; b) many of the results are provided not only as summary tables or text files: all landscape metrics is stored in each landscape cell, which makes the visualization and modeling simpler as the user does not need to combine *rasters*, *shapefiles* and summary tables to visualize the metrics – that allows one to easily cross this information with the sampling locations for statistical analyses; and c) LSMetrics use the power of GRASS GIS to manage raster maps and handle large-sized datasets. Although other software and/or packages have similar advantages for some of these aspects, to our knowledge LSMetrics is the first software that combines these three advantages.

As the source code for LSMetrics is freely available at GitHub, the scientific community can easily make changes or include any other ecologically relevant landscape metrics to the package. Finally, as both GRASS GIS and Python language are free, anyone can have access to

LSMetrics and perform landscape analyses at no cost. This is particularly important for developing countries as well as for NGOs or municipalities with low income. One just needs to install the GRASS GIS, connect to GitHub, download LSMetrics, select a land use or land cover map, calculate the metrics and start landscape management planning for environmental conservation and human wellbeing in a couple of hours if the landscape is small.

Acknowledgments

1.5 References

Andersen, L. E., C. W. J. Granger, E. J. Reis, D. Weinhold, and S. Wunder. 2002. The Dynamics of Deforestation and Economic Growth in the Brazilian Amazon. Cambridge University Press, Cambridge.

Aragão, L. E. O. C., B. Poulter, J. B. Barlow, L. O. Anderson, Y. Malhi, S. Saatchi, O. L. Phillips, and E. Gloor. 2014. Environmental change and the carbon balance of Amazonian forests. Biological Reviews 89:913–931.

Awade, M., and J. P. Metzger. 2008. Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. Austral Ecology 33:863–871.

Bélisle, M. 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology. Ecology 86:1988–1995.

Brinck, K., R. Fischer, J. Groeneveld, S. Lehmann, M. Dantas De Paula, S. Pütz, J. O. Sexton, D. Song, and A. Huth. 2017. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. Nature Communications 8:14855.

Broadbent, E. N., G. P. Asner, M. Keller, D. E. Knapp, P. J. C. Oliveira, and J. N. Silva. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141:1745–1757.

Correa Ayram, C. A., M. E. Mendoza, A. Etter, and D. R. P. Salicrup. 2016. Habitat connectivity in biodiversity conservation. Progress in Physical Geography 40:7–37.

Coutinho, R. M., R. A. Kraenkel, and P. I. Prado. 2015. Catastrophic regime shift in water reservoirs and são paulo water supply crisis. PLoS ONE 10:1–14.

Davidson, E. A., A. C. De Araújo, P. Artaxo, J. K. Balch, I. F. Brown, M. M. Mercedes, M. T. Coe, R. S. Defries, M. Keller, M. Longo, J. W. Munger, W. Schroeder, B. S. Soares-Filho, C. M. Souza, and S. C. Wofsy. 2012. The Amazon basin in transition. Nature 481:321–328.

Driscoll, D. A., S. C. Banks, P. S. Barton, D. B. Lindenmayer, and A. L. Smith. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in Ecology and Evolution 28:605–613.

Fahrig, L. 2003. Efects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fahrig, L. 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. Journal of Biogeography 40:1649–1663.

Fahrig, L. 2017. Ecological Responses to Habitat Fragmentation per se. Annual Review of Ecology and Systematics 48.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science 309:570–574.

Fortin, M.-J., and M. R. T. Dale. 2005. Spatial Analysis: A guide for ecologist. Cambridge University Press, Cambridge.

GRASS Development Team. 2017. Geographic Resources Analysis Support System (GRASS) Software, Version 7.2. Open Source Geospatial Foundation. Electronic document: http://grass.osgeo.org.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052.

Harper, K. A., and S. E. Macdonald. 2011. Quantifying distance of edge influence: a comparison of methods and a new randomization method. Ecosphere 2:art94.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–212.

Jackson, H. B., and L. Fahrig. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24:52–63.

Lapola, D. M., L. A. Martinelli, C. A. Peres, J. P. H. B. Ometto, M. E. Ferreira, C. A. Nobre, A. P. D. Aguiar, M. M. C. Bustamante, M. F. Cardoso, M. H. Costa, C. A. Joly, C. C. Leite, P. Moutinho, G. Sampaio, B. B. N. Strassburg, and I. C. G. Vieira. 2014. Pervasive transition of the Brazilian land-use system. Nature Climate Change 4:27–35.

Laurance, W. F., J. L. C. Camargo, R. C. C. Luizão, S. G. Laurance, S. L. Pimm, E. M. Bruna, P. C. Stouffer, G. Bruce Williamson, J. Benítez-Malvido, H. L. Vasconcelos, K. S. Van Houtan, C. E. Zartman, S. A. Boyle, R. K. Didham, A. Andrade, and T. E. Lovejoy. 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation 144:56–67.

Lenz, B. B., K. M. Jack, and W. R. Spironello. 2014. Edge effects in the primate community of the biological dynamics of forest fragments project, Amazonas, Brazil. American Journal of Physical Anthropology 155:436–446.

Magioli, M., M. C. Ribeiro, K. M. P. M. B. Ferraz, and M. G. Rodrigues. 2015. Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest. Animal Conservation 18:499–511.

Martensen, A. C., R. G. Pimentel, and J. P. Metzger. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation. Biological Conservation 141:2184–2192.

Martensen, A. C., M. C. Ribeiro, C. Banks-Leite, P. I. Prado, and J. P. Metzger. 2012. Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. Conservation Biology 26:1100–1111.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

Moraes, A. M., C. R. Ruiz-Miranda, P. M. Galleti-Jr., B. B. S. Niebuhr, B. R. Alexandre, A. D. Grativol, R. de L. Muylaert, J. W. Ribeiro, and M. C. Ribeiro. 2018. Landscape resistance influences dispersal and gene flow of endangered golden lion tamarins (Leontopithecus rosalia) within the Atlantic Forest. In review in Biological Conservation.

Murcia, C. 1995. Edge effects in fragmented forests: Implications for conservation.

Pütz, S., J. Groeneveld, K. Henle, C. Knogge, A. C. Martensen, M. Metz, J. P. Metzger, M. C. Ribeiro, M. D. De Paula, and A. Huth. 2014. Long-term carbon loss in fragmented Neotropical forests. Nature Communications 5:1–8.

Rayfield, B., M.-J. Fortin, and A. Fall. 2010. The sensitivity of least-cost habitat graphs to relative cost surface values. Landscape Ecology 25:519–532.

Regolin, A. L., J. J. Cherem, M. E. Graipel, J. A. Bogoni, J. W. Ribeiro, M. H. Vancine, M. A. Tortato, L. G. Oliveira-Santos, F. M. Fantacini, M. R. Luiz, P. V. De Castilho, M. C. Ribeiro, and N. C. Cáceres. 2017. Forest cover influences occurrence of mammalian carnivores within Brazilian Atlantic Forest. Journal of Mammalogy 98:1721–1731.

Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni, and M. M. Hirota. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141–1153.

Rocchini, D., L. Delucchi, G. Bacaro, P. Cavallini, H. Feilhauer, G. M. Foody, K. S. He, H. Nagendra, C. Porta, C. Ricotta, S. Schmidtlein, L. D. Spano, M. Wegmann, and M. Neteler. 2013. Calculating landscape diversity with information-theory based indices: A GRASS GIS solution. Ecological Informatics 17:82–93.

Rodrigues, R. R., P. H. S. Brancalion, and I. Isenhagen, editors. 2009. Pacto pela restauração da Mata Atlântica: Referencial dos conceitos e ações de restauração florestal. LERF/ESALQ/Instituto BioAtlântica, São Paulo.

Rubio, L., and S. Saura. 2012. Assessing the importance of individual habitat patches as irreplaceable connecting elements: An analysis of simulated and real landscape data. Ecological Complexity 11:28–37.

Rudnick, D. A., S. J. Ryan, P. Beier, S. A. Cushman, F. Dieffenbach, C. W. Epps, L. R. Gerber, J. Hartter, J. S. Jenness, J. Kintsch, A. M. Merenlender, R. M. Perkl, D. V. Preziosi, and S. C. Trombulak. 2012. The Role of Landscape Connectivity in Planning and Implementating Conservation and Restoration Priorities. Issue in Ecology 16:1–20.

Saura, S., Ö. Bodin, and M.-J. Fortin. 2014. Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. Journal of Applied Ecology 51:171–182.

Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D. D. Cameron, Y. Carmel, D. A. Coomes, T. Coulson, M. C. Emmerson, R. S. Hails, G. C. Hays, D. J. Hodgson, M. J. Hutchings, D. Johnson, J. P. G. Jones, M. J. Keeling, H. Kokko, W. E. Kunin, X. Lambin, O. T. Lewis, Y. Malhi, N. Mieszkowska, E. J. Milner-Gulland, K. Norris, A. B. Phillimore, D. W. Purves, J. M. Reid, D. C. Reuman, K. Thompson, J. M. J. Travis, L. A. Turnbull, D. A. Wardle, and T. Wiegand. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology 101:58–67.

Tambosi, L. R., A. C. Martensen, M. C. Ribeiro, and J. P. Metzger. 2014. A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. Restoration Ecology 22:169–177.

Taubert, F., R. Fischer, J. Groeneveld, S. Lehmann, M. S. Müller, E. Rödig, T. Wiegand, and A. Huth. 2018. Global patterns of tropical forest fragmentation. Nature 554.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity Is a Vital Element of Landscape Structure. Oikos 68:571.

Taylor, P. D., L. Fahrig, and K. A. With. 2006. Landscape connectivity: a return to the basics. Pages 29–43 *in* K. R. Crooks and M. Sanjayan, editors.Connectivity Conservation. Cambridge University Press, Cambridge.

Tischendorf, L., and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. Oikos2 90:7–19.

Vogt, P., and K. Riitters. 2017. GuidosToolbox: universal digital image object analysis. European Journal of Remote Sensing 50:352–361.

Vos, C. C., J. Verboom, P. F. M. Opdam, and C. J. F. Ter Braak. 2001. Toward ecologically scaled landscape indices. American Naturalist 183:24–41.

Wang, X., F. G. Blanchet, and N. Koper. 2014. Measuring habitat fragmentation: An evaluation of landscape pattern metrics. Methods in Ecology and Evolution 5:634–646.

Appendix A – The fragmentation status of the Brazilian Amazon

A1) Introduction

The tropical forests have become one of the main targets of human actions in recent decades (Myers et al. 2000). The rapid population growth and agricultural development have shrunk continuous forest areas into smaller patches surrounded by different types of matrix (Lewis et al. 2015). According to Fao (2010), these forests have been losing almost 13 million hectares per year due to land use change, in a process of intensification of agriculture and livestock.

The Amazon forest, the most biodiverse ecosystem in the World, covers an area of about 5,3 million km^2, which represents 40% of global tropical forest area, and it is threatened by habitat loss, degradation and fragmentation (Laurance et al. 2011). In Brazil, this biome has been facing an increase in deforestation rates over the years and its original forest area has been reduced by 15% (Laurance et al. 2011; Aragão et al. 2014). Besides an overall area reduction, the forest fragmentation process also produces small patches, with different shapes, unevenly distributed in the landscape, which could increase the isolation between patches (Fahrig 2003; Broadbent et al. 2008; Arroyo-Rodríguez & Dias 2010). Other factors could negatively affect this new landscape, such as edge effects, an increase of tree mortality, changes in the composition of plant and animal communities, a decrease in species richness, a modified resource availability and a consequent alteration in the Amazon ecosystem functioning (Hooper et al. 2005; Kupfer et al. 2006; Laurance et al. 2011, 2017).

Habitat reduction and fragmentation tend to decrease the richness and abundance of native species in the forest patches. The increase in the isolation between patches introduce barriers to animals movements, thus decreasing the chances of patch recolonization after local extinction (Haddad et al. 2015). Given the importance of tropical forests in harboring more than half of the global biodiversity, including known and undescribed species (Dirzo & Raven 2003), as well as their role in the global carbon cycle and climate system (Davidson et al. 2012; Pütz et al. 2014), it is a major question to understand how the Amazon forest is affected by the fragmentation process and which will be the impacts on ecosystem functions. Therefore, here we assessed the

fragmentation status of the Brazilian Amazon forest by calculating the distribution of patch sizes, the amount of forest at different distances from edges, and how landscape connectivity changes for organisms with different dispersal capabilities.

A2) Spatial data and landscape metrics

Our study area was the Amazon biome located in Brazil, which encompass a wide range of forest types. The effect of fragmentation on the Amazon forest was analyzed through these landscape metrics: patch size (ha), functional connectivity (ha), and classification of edge, core area and matrix.

We obtained the Amazon land cover map available for download on the Mapbiomas website (www.mapbiomas.org) with 30 m resolution. Before the landscape analysis, we generated an Amazon Forest map, selecting only categories considered for us as forest (primary forest, secondary forest, degraded forest, flooded forest, mangrove forest, open forest and forestry, codes 3 to 9 according to Mapbiomas metadata) and then we converted it into a binary forest map (1 = forest habitat and 0 = matrix). Afterwards, using the LSMetrics package and GRASS 7.2.2 (GRASS Development Team 2017) we generated the other maps to extract the remaining landscape metrics:

- patch size;

- functional connectivity, considering organisms with a gap crossing capacity varying from 100 m to 1,000 m (with steps of 100 m), and 1,200 m, 1,500 m, 1,800 m, 2,000 m, 2,500 m and 3,000 m;

- classification of the landscape in matrix, core, and edge areas, considering edge depth values from 30 m to 1,000 m.

A3) Results

Here we show the maps of functionally connected area for organisms with different crossing capabilities (other results are described in the main text). Although for the whole Amazon fragmentation levels are low and large forest patches corresponds basically to hydrographic watersheds, separated by large rivers (Fig. A1-A), a closer look at some locations

show an elevated status of fragmentation and a dominance of small forest patches (Fig. A1-B). These areas are located mainly at the Southern and Eastern parts of the Brazilian Amazon. The organisms shown are understory mixed-species flocks, that generally do not cross open areas (Develey & Stouffer 2001), the reddish hermit (*Phaethornis ruber*), that can cross 100 m gaps, and the cheastnut eared aracari (*Pteroglossus castanotis*), that can cross up to 200 m between forest patches (Lees & Peres 2009). As the gap crossing capability increases, the area available to the organisms also increases. This does not mean all this area will be occupied – most species are restrained by many other behavioral, ecological, and environmental factors. Still, this landscape metric represents the potential area to be used or occupied by these species, and may have important consequences for understanding species ranges and distribution.
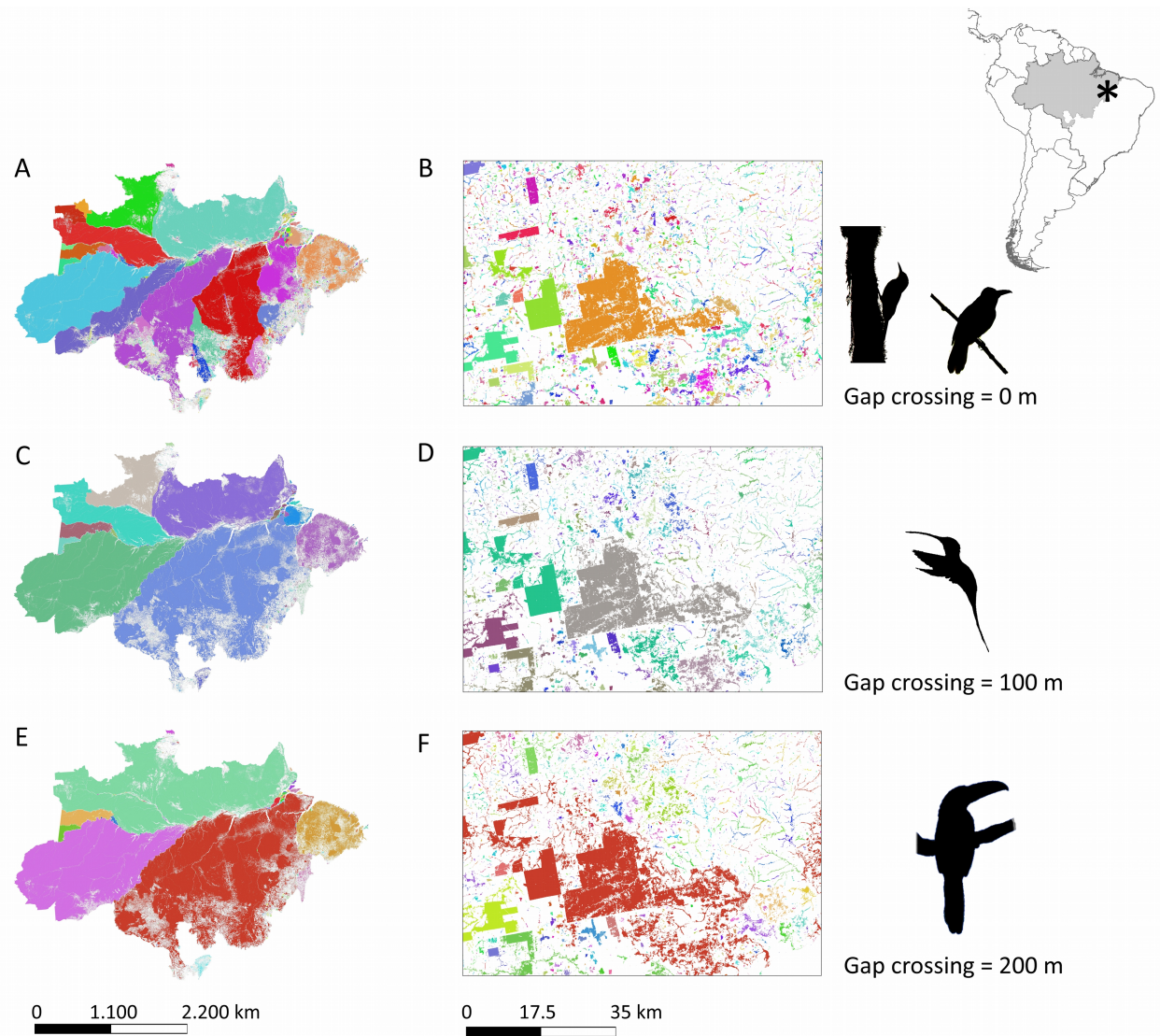
Figure A1. Illustration of the functionally connected forest area for the Brazilian Amazon for three species with different gap crossing capabilities. Figs. A, C, and E show the whole Brazilian Amazon region, and B, D, and E show a zoom to an area in its Eastern part (area location shown by an asterisk in the inset at the top right). Clumps of functionally connected forest patches are shown in the same color. A and B correspond to species that hardly cross gaps between patches (e.g., understory mixed-species flocks), C and D correspond to species with 100 m gap crossing (e.g., the reddish hermi) and E and F to species with 200 m gap crossing capability (such as cheastnut eared aracari).

Appendix B – A landscape approach on the sampling design of ecological research

B1) Introduction

Landscape ecology research is of utmost importance to understand how biodiversity and ecological processes are influenced by space and how they change in a world where habitat loss and fragmentation are widespread (Taubert et al. 2018). Knowledge on the relation between landscape patterns and processes, the occurrence and persistence of species, and the maintenance of ecosystem services is also very important to determine conservation and restoration policies (Rudnick et al. 2012; Correa Ayram et al. 2016). On the other hand, performing good research on landscape ecology is very challenging: it is often hard to draw spatial replicates (Hurlbert 1984), considering variation and independence on the spatial variables of interest (Wang et al. 2014), and taking into account multiple scales at which these variables matter (Jackson & Fahrig 2015). The challenge already starts when deciding what sites to be sampled. A poor sampling design may incur in limitations or even an impossibility of performing appropriate analysis of the ecological data.

Suppose one wants to perform a community ecology study in a heterogeneous landscapes. The question may be to understand how different spatial processes affect the patterns of composition, diversity, or to infer about assembling rules of communities. Different taxa may be affected by distinct spatial variables at different scales, such as the local or regional amount of habitat, the heterogeneity, and the structural or functional connectivity of landscapes. A sampling design to answer such questions needs a set of sampled landscapes in which there is a gradient in the variation of spatial variables and independence between them. Here we describe a method to use a landscape approach to define sampling points considering spatial variables generated by LSMetrics package.

To do so, we use as a study model the Cantareira water system, in the Atlantic Forest of Southeastern Brazil, a fragmented forest region that was recently subject to large crisis in the water supply and is close to the largest urban centers of the country (Coutinho et al. 2015).

B2) Spatial data and landscape metrics

To exemplify the use of LSMetrics in studies of landscape ecology, we compiled data from the Cantareira water system. This is one of the largest water systems in the world and it is composed by five reservoirs. Its rivers supply millions of people that inhabit the largest urban area of South America (Pontes et al. 2016). Cantareira system's forest patches form a corridor that connect two large blocks of forests: Serra da Mantiqueira in the northern portion and Serra da Cantareira in the south. In addition to provide an important ecosystem service, water supply, the Cantareira-Mantiqueira corridor is located in the Atlantic Forest, one of the richest and most threatened biodiversity *hotspots* in the world (Morellato & Haddad 2000; Ribeiro et al. 2009), being considered a priority area for environmental conservation by the Brazilian government (Ordinance MMA n. 9, 01/23/2007). Land use in this region comprises anthropogenic areas of low yield pastures (46%), water reservoirs (3%), Atlantic forest remnants (40%) and the remaining 11% represents agriculture and urban areas (Uezu et al. 2017).

Data of Cantareira – Mantiqueira corridor were compiled from MapBiomas data base (mapbiomas.org; MapBiomas 2017; Souza-Jr & Azevedo 2017). MapBiomas is a Brazilian initiative formed by a collaborative network composed by non-governmental organizations, universities and technology companies interested in understanding the dynamic of land use in Brazil. A temporal series of land cover and land use maps from the year of 1985 to 2017 was developed for the Brazilian Biomes. Each Biome has a group of several specialists of land use and remote sensing that uses satellite image to compose the mappings. We used data from collection 2.3, released in 2017 (http://mapbiomas.org/pages/announcement_note_collection2_3#). This collection employ Landsat 8 images obtained in 2016 and processed by several algorithms and an image processing workflow to generate the land use and land cover maps (see algorithms and workflow in detail in (Souza-Jr & Azevedo 2017). The available raster (30 m of resolution) classify land cover in a clear way on a pixel by pixel format.

To consider the Cantareira-Mantiqueira corridor we employed the Cantareira water system polygon. Because some metrics are calculated pixel by pixel based on a window size, we established a buffer of 3 km around our study area in a way that pixels located near the limits of the polygon could be correctly analyzed. We calculated patch size and Shannon landscape diversity index based on a window size of 5,000 m using LSMetrics. Patch size was calculated

considering only forest remnants and landscape diversity the different land use classes. The classes considered in the MapBiomas raster for our study areas were: natural forest, forestry, natural wet areas, pastures, agriculture, agriculture or pasture (not specified each), urban areas and water bodies.

B3) Selection of landscapes

We aimed to select 20 circular landscape samples with diameter equals 5 km. First we generated thousands of points within habitat patches in the Cantareira system and randomly kept only those at least 5 km far apart from each other, to guarantee minimum spatial autocorrelation and avoid pseudo-replicates (Hurlbert 1984). Second we extracted the values of the two landscape metrics, using the output raster maps from LSMetrics, at these pre-selected points. We then drew 100 samples of 20 landscapes and calculated the correlation between the landscape metrics and the variance of the difference between values of each metric, for each sample. The samples were then ordered so that the first ones minimized the correlation between metrics and maximized variance for each metric (i.e., the representativeness of the whole range of each metric values). The landscapes shown in Fig. 3 of the main text are the first set of samples in this list. We can observe that, even after this process, the distribution of values of the metrics for these landscape is far from a uniform distribution, which may be related to constraints and characteristics of the study area, as well as to the size of the landscapes sampled. The R script for such analysis may be found in the LSMetrics GitHub repository (scripts folder).

Literature cited

Aragão LEOC, Poulter B, Barlow JB, Anderson LO, Malhi Y, Saatchi S, Phillips OL, Gloor E. 2014. Environmental change and the carbon balance of Amazonian forests. Biological Reviews **89**:913–931. Available from http://doi.wiley.com/10.1111/brv.12088.

Arroyo-Rodríguez V, Dias PAD. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology **72**:1–16.

Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, Silva JN. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation **141**:1745–1757. Available from http://linkinghub.elsevier.com/retrieve/pii/S0006320708001377 (accessed July 16, 2012).

Correa Ayram CA, Mendoza ME, Etter A, Salicrup DRP. 2016. Habitat connectivity in biodiversity conservation. Progress in Physical Geography **40**:7–37. Available from http://journals.sagepub.com/doi/10.1177/0309133315598713.

Coutinho RM, Kraenkel RA, Prado PI. 2015. Catastrophic regime shift in water reservoirs and são paulo water supply crisis. PLoS ONE **10**:1–14.

Davidson EA et al. 2012. The Amazon basin in transition. Nature **481**:321–328.

Develey PF, Stouffer PC. 2001. Effects of roads on movements by understory birds in mixed-species flocks in Central Amazonian Brazil. Conservation Biology **15**:1416–1422.

Dirzo R, Raven PH. 2003. Global State of Biodiversity and Loss. Annual Review of Environment and Resources **28**:137–167. Available from http://www.annualreviews.org/doi/10.1146/annurev.energy.28.050302.105532.

Fahrig L. 2003. Efects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics **34**:487–515.

FAO. 2010. Global Forest Resources Assessment 2010. FAO Forestry Paper **163**.

GRASS Development Team. 2017. Geographic Resources Analysis Support System (GRASS) Software, Version 7.2. Open Source Geospatial Foundation. Electronic document: http://grass.osgeo.org. Available from http://grass.osgeo.org.

Haddad NM et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances **1**:e1500052.

Hooper DU et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75**:3–35.

Hurlbert SH. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187–212.

Jackson HB, Fahrig L. 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography **24**:52–63.

Kupfer JA, Malanson GP, Franklin SB. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography **15**:8–20.

Laurance WF et al. 2011. The fate of Amazonian forest fragments: A 32-year investigation. Biological Conservation **144**:56–67. Elsevier Ltd. Available from http://dx.doi.org/10.1016/j.biocon.2010.09.021.

Laurance WF, Camargo JLC, Fearnside PM, Lovejoy TE, Williamson GB, Mesquita RCG, Meyer CFJ, Bobrowiec PED, Laurance SGW. 2017. An Amazonian rainforest and its fragments as a laboratory of global change. Biological Reviews **93**:223–247.

Lees AC, Peres CA. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. Oikos **118**:280–290.

Lenz BB, Jack KM, Spironello WR. 2014. Edge effects in the primate community of the biological dynamics of forest fragments project, Amazonas, Brazil. American Journal of Physical Anthropology **155**:436–446.

Lewis SL, Edwards DP, Galbraith D. 2015. Increasing human dominancee of tropical forests. Science **349**:827–832.

MapBiomas. 2017. Project MapBiomas - Collection 2.3 of Brazilian Land Cover & Use Map Series, accessed on Feb. 2018 through the link: http://mapbiomas.org/#.

Morellato LPC, Haddad CFB. 2000. Introduction: The Brazilian Atlantic Forest. Biotropica **32**:786–792.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853–858.

Pontes LM, Viola MR, Silva MLN, Bispo DFA, Curi N. 2016. Hydrological modeling of tributaries of Cantareira system, Southeast Brazil, with the swat model. Engenharia Agrícola **4430**:1037–1049. Available from http://dx.doi.org/10.1590/1809-4430-Eng.Agric.v36n6p1037-1049/2016.

Pütz S, Groeneveld J, Henle K, Knogge C, Martensen AC, Metz M, Metzger JP, Ribeiro MC, De Paula MD, Huth A. 2014. Long-term carbon loss in fragmented Neotropical forests. Nature Communications **5**:1–8.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation **142**:1141–1153.

Rudnick DA et al. 2012. The Role of Landscape Connectivity in Planning and Implementating Conservation and Restoration Priorities. Issue in Ecology **16**:1–20.

Souza-Jr C, Azevedo T. 2017. MapBiomas General "Handbook": algorithm theoretical base document & results.

Taubert F, Fischer R, Groeneveld J, Lehmann S, Müller MS, Rödig E, Wiegand T, Huth A. 2018. Global patterns of tropical forest fragmentation. Nature **554**.

Uezu A, Sarcinelli O, Chiodi R, Jenkins CN, Martins CS. 2017. Atlas dos serviços ambientais do sistema Cantareira.

Wang X, Blanchet FG, Koper N. 2014. Measuring habitat fragmentation: An evaluation of landscape pattern metrics. Methods in Ecology and Evolution **5**:634–646.

Appendix C - Manual for LSMetrics v. 1.0.0

Bernardo Niebuhr, Renata Muylaert, Felipe Martello

Contents

Welcome to the LSMetrics wiki manual!

LandScape Metrics (LSMetrics) is a free and open-source package that calculates landscape connectivity and other ecologically-scaled landscape metrics. It is intended to be used as a tool for environmental research as well as for landscape management, conservation, and restoration. It uses land use or binary class (e.g., habitat/non-habitat) maps to calculate metrics of structural and functional connectivity, edge-based landscape metrics, and landscape diversity indices. It incorporates edge depth and the capacity of organisms on crossing gaps between habitat patches to re-classify and calculate metrics considering the landscape at the perspective of different species and functional groups. Besides, metrics are spatially explicit and may be assessed at multiple scales.

LS Metrics was developed in Python 2.7 and runs within a GRASS GIS environment (currently, GRASS 7.0.x or newer). Here you will find a brief description of the program functionalities so you can quickly use it. We wish to make sure you can easily install GRASS, import your input maps, run LSMetrics and export or use its output in various ways.

If you have suggestions on how to improve this tutorial, feel free to contact us or open an issue.

Authors and contributors

Authors:

- Bernardo B. S. Niebuhr <bernardo_brandaum@yahoo.com.br>
- Felipe Martello <felipemartello@gmail.com>
- John Wesley Ribeiro <jw.ribeiro.rc@gmail.com>
- Mauricio Humberto Vancine <mauricio.vancine@gmail.com>
- Milton Cezar Ribeiro <mcr@rc.unesp.br>

Contributors:

- Juliana Silveira dos Santos <juliana.silveiradossantos@gmail.com>
- Vinicius Rodrigues Tonetti <vrtonetti@gmail.com>
- Renata L. Muylaert <renatamuy@gmail.com>
- Vanessa Ellen Weidt Campos <vanessaellen@hotmail.com>

Citation

Please cite LSMetrics when using the package in your work:

Niebuhr, B. B. S.; Martello, F.; Ribeiro, J. W.; Vancine, M. H.; Muylaert, R. L.; Campos, V. E. W.; Santos, J. S.; Tonetti, V. R.; Ribeiro, M. C. Landscape Metrics (LSMetrics): a spatially explicit tool for calculating connectivity and other ecologically-scaled landscape metrics. *In preparation.*

LSMetrics Copyright and License Information

LandScape Metrics (LSMetrics) is Copyright, 2013-2018 by Bernardo B. S. Niebuhr, Milton C. Ribeiro, John W. Ribeiro, and Mauricio H. Vancine, under terms of the GNU General Public License (GPLv2). This includes all software, documentation, and associated materials.

LSMetrics is free and open source software, you can redistribute it and/or modify it under the terms of the GNU General Public License as published by the Free Software Foundation, either version 2 of the license, or (at your discretion) any later version.

This program is distributed in the hope that it will be useful, but WITHOUT ANY WARRANTY; without even the implied warranty of MERCHANTABILITY or FITNESS FOR A PARTICULAR PURPOSE. See the GNU General Public License for more details here.

If you want to know more about free and open source software, look this and that.

Brief description

The package

LandScape metrics (LSMetrics) is a free and open source package developed calculates multiple landscape metrics for raster data.

The package uses input raster maps with integer values only, in which each cell represents an area considered to be homogeneous, such as a land use or vegetation type. The maps can be either binary (1 = habitat, 0 = non-habitat) or multi-class (e.g. land use and land cover maps). The majority of landscape metrics are calculated using binary class raster maps, except for the landscape diversity indices, which only make sense for multi-class raster maps. LSMetrics may also transform multiple class maps into binary ones before the calculation of metrics.

Once a GRASS project is created and raster maps are imported into it, using r.import or r.in.gdal (or other r.in.*) modules, for instance, LSMetrics may be run in two ways (see the Figure below). The first is calling a python application and opening the GUI; the second is building a Python script (or opening a Python shell inside GRASS GIS prompt) and calling each landscape metric as a Python function. Both methods allow the users to run multiple metrics with various parameters and scales, for multiple maps, in a single run.

The output maps consist in raster maps for each chosen landscape metric, as well as text files with statistics of some of the metrics at the patch or class level, to be analyzed with any statistical software.
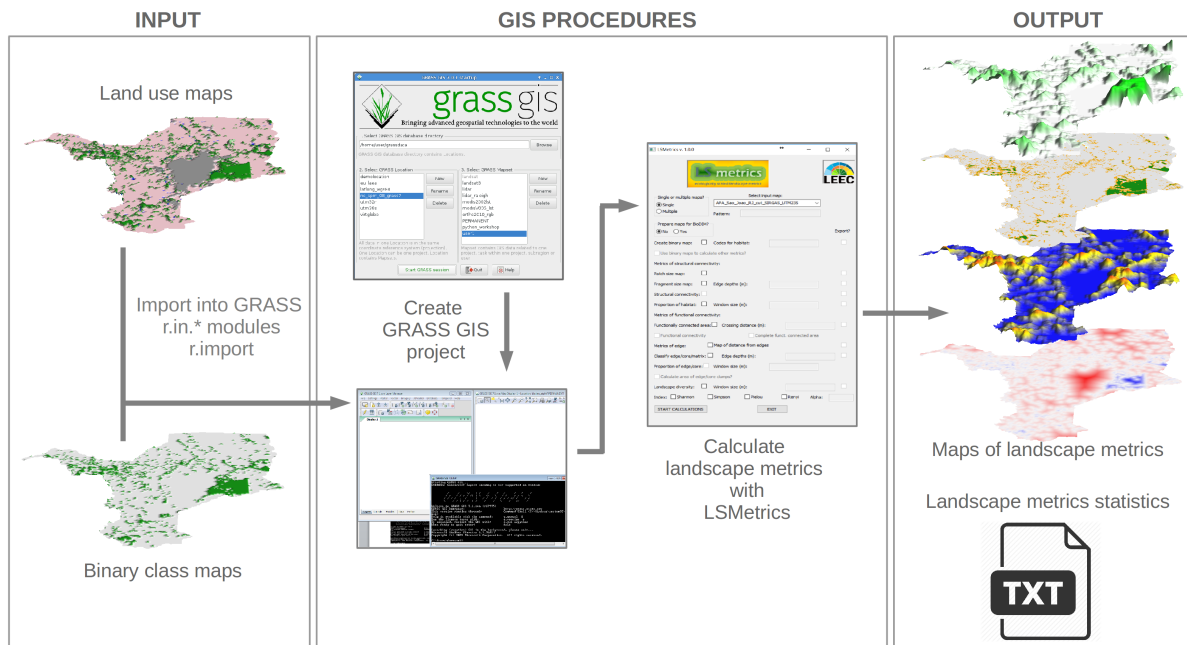
Metrics

LSMetrics currently perform the following calculations:

Preparation of inputs:

- Transformation of land use maps in binary class maps

Metrics of *structural connectivity*:

- Patch size

- Fragment size

- Structural connectivity

- Proportion of habitat

Metrics of *functional connectivity*:

- Functionally connected area

- Functional connectivity

- Complete functionally connected area

Edge-based metrics:

- Classification in core/edge/matrix

- Classification in landscape elements: edge/core/stepping stones/corridors/branches/matrix

- Binary maps: edge/non-edge

- Binary maps: core/non-core

- Proportion of edge area

- Proportion of core area

- Area of clumps of edge and core areas

Landscape diversity (through the r.diversity GRASS addon):

- Shannon

- Simpson

- Pielou

- Rényi

For more information on the metrics calculated and details on implementation, look at the publication:

Niebuhr, B. B. S.; Martello, F.; Ribeiro, J. W.; Vancine, M. H.; Muylaert, R. L.; Campos, V. E. W.; Santos, J. S.; Tonetti, V. R.; Ribeiro, M. C. Landscape Metrics (LSMetrics): a spatially explicit tool for calculating connectivity and other ecologically-scaled landscape metrics. *In preparation.*

The repository

The LSMetrics repository is organized in 7 folders:

- `_LSMetrics_v1_0_0`: Here the main pieces of the LSMetrics code are located:
    1. `LSMetrics_v1_0_0.py`: main script.

2. `test_LSMetrics.py`: a Python script with the list of functions of LSMetrics and their usage as Python functions (outside GUI).
3. `r_diversity.py`: The r.diversity GRASS addon as python code, used to calculate landscape diversity indices in LSMetrics.

- `previous_versions`: Old versions of the code.
- `grassdb_test`: raster maps for testing. This includes:

1. `APA_Sao_Joao_RJ_cut_SIRGAS_UTM23S.tif`: A land use map in Rio de Janeiro state, Brazil, inside the Golden Lion Tamarin occurrence region. The map was classified based on LANDSAT 7 satellite images.
2. `SP_RioClaro_use_raster.tif`: A land use raster of the municipality of Rio Claro, State of São Paulo, Brazil.

Using LSMetrics

Here we describe how to install and use LSMetrics step-by-step. If you have questions or suggestions to make it more didatic, please contact us!

1. Downloading LSMetrics

First download the .zip package or clone it into your local enviroment using GitHub Desktop or `git`:

```
# Choose the directory where to clone LSMetrics
cd path/to/LSMetrics_dir

# Clone it
git clone "https://github.com/LEEClab/LS_METRICS.git"
```

2. Have GRASS GIS installed

LSMetrics runs within GRASS GIS and uses many of its modules and functionalities, so you first need to have GRASS installed in your computer. We recommend you install GRASS version 7.2.2. Follow the instructions.

Installing GRASS GIS

LSMetrics was developed and runs inside GRASS GIS environment, version 7.2.x. Thus, we strongly recommend the use of one of these GRASS versions. It is possible to download this software at the GRASS GIS website.
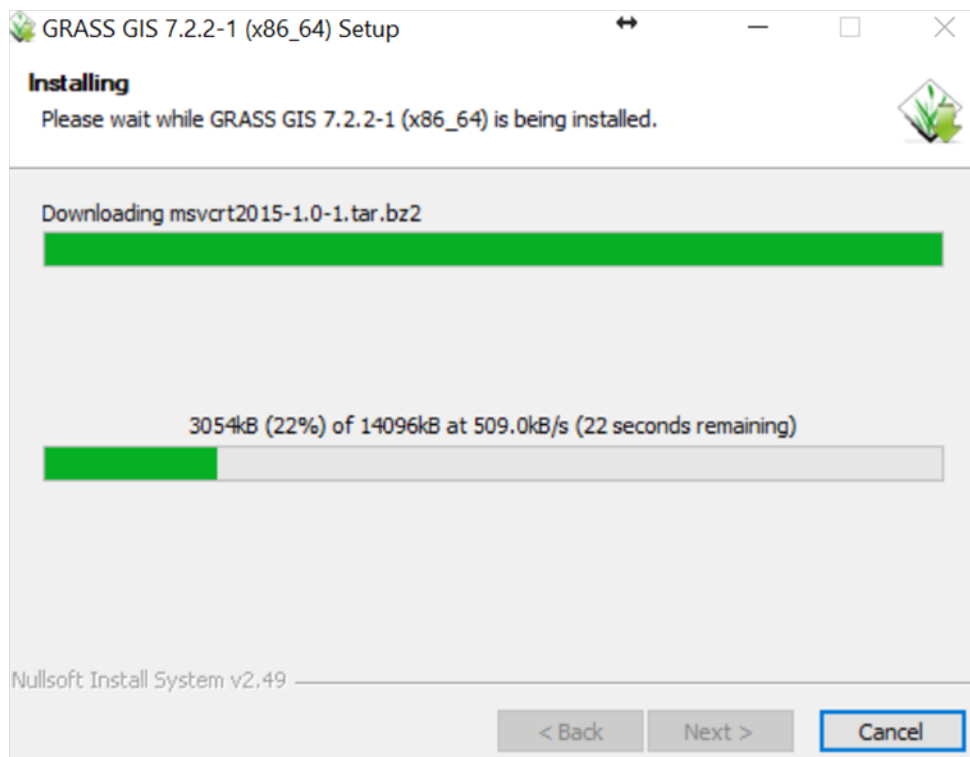
MS Windows

GRASS GIS is available for different versions of Windows. Download the `.exe` file and install it in your computer. Alternativelly, you may download the OSGeo4W package, which includes QGIS, GDAL, GRASS and other GIS tools. More information on GRASS installation on Windows can be found here.

Ubuntu Linux

The installation of GRASS GIS in Ubuntu is simple. In the terminal, it is necessary to enter all following lines:

```
sudo add-apt-repository ppa:ubuntugis/ubuntugis-unstable
sudo apt-get update
sudo apt-get install grass
```

For more information or previous versions of GRASS, click here.

GRASS GIS is also available for other Linux distributions, but we have not tested LSMetrics on them. If you wish to test it, please informs us either by e-mail or by an issue, so that we can include information about it here (and thanks in advance!).

MacOS

For information on GRASS GIS installation on MacOS, take a look here.

LSMetrics was not tested through the Graphical User Interface (GUI) in MacOS yet. If you want to do it, please tell us so that we can adapt the GUI slightly to it. However, LSMetrics package is expected to run in any MacOS platform through Python command line.

3. Preparation of inputs

Prepare your input maps outside GRASS GIS

LSMetrics input maps can be binary maps or non-binary land use maps. Binary maps contain "1" and "0" values; "1" represent a kind of habitat or land use of interest, while "0" represents all other land use classes. Non-binary maps can include different land use classes, such as different types of forests and matrices (pasture, plantations, highways). Each class is then assigned a integer code. For example, in the map shown below forest pixels have code "6", pastures are "12", water equals "8", and roads equals "3". The user must to define the codes of each class of the land use map using GRASS GIS or any other GIS software, so that they can select the codes of their interest in LSMetrics.

See in the figure below a land use raster representation with several classes, using as example a location in Rio de Janeiro, near the Poço das Antas Biological Reserve.
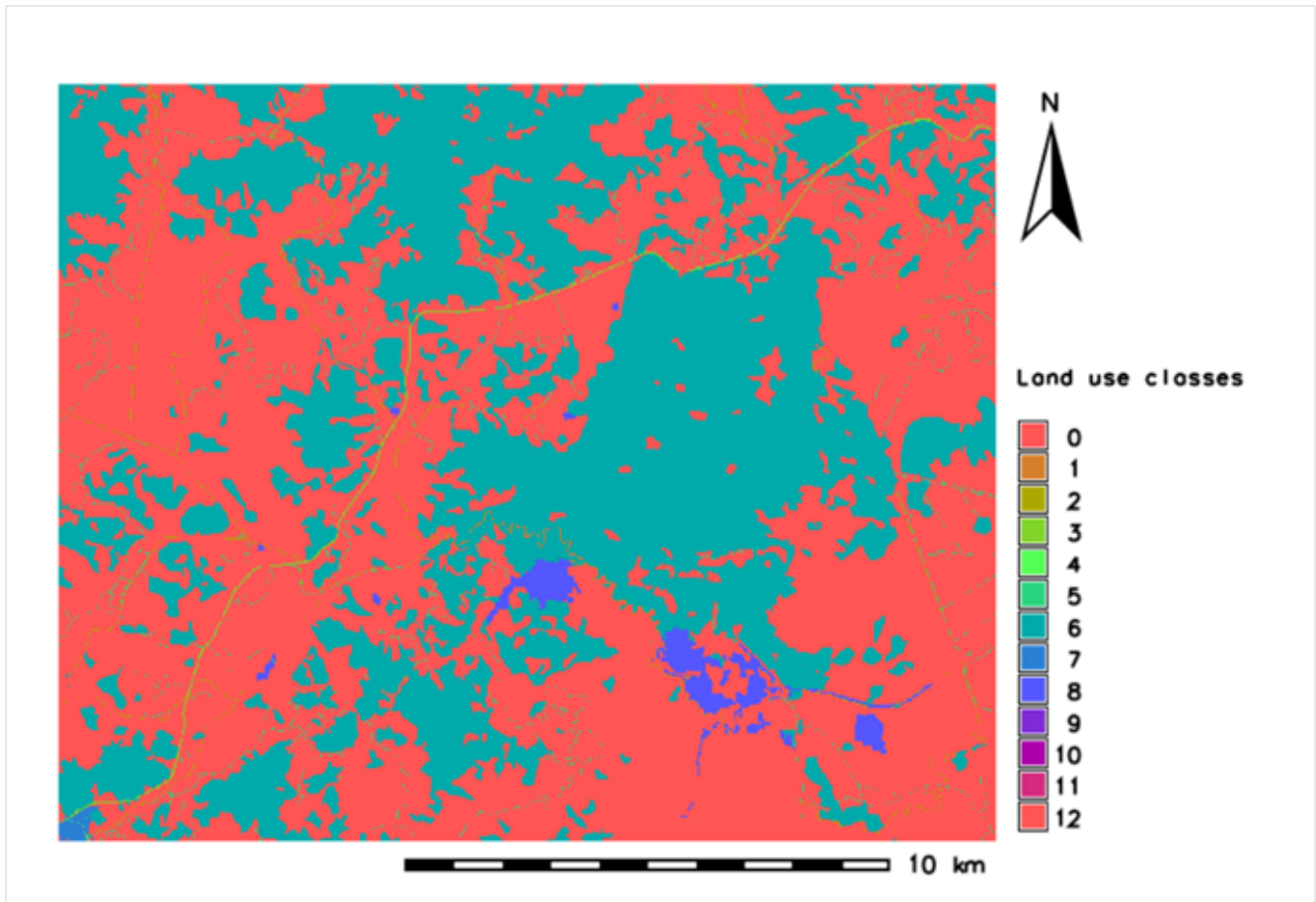
Note that the codes are showed as integers. See the main codes meaning below, in comparison with a satellite image for the same area:
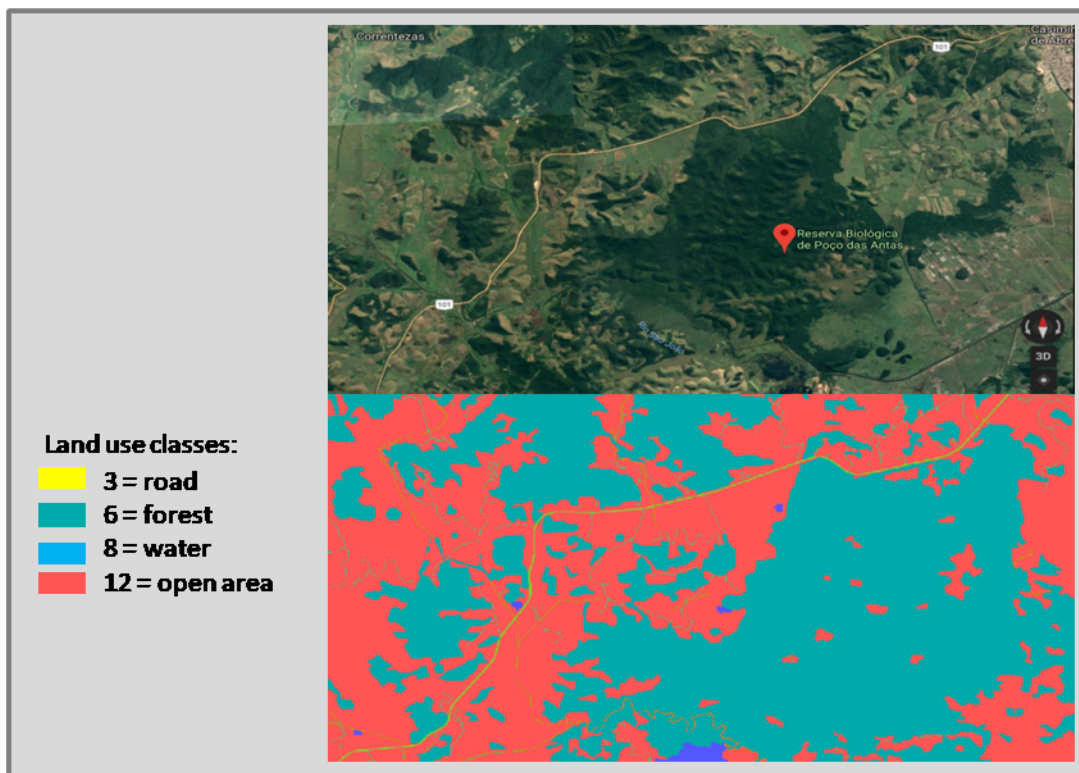
The LS metrics repository also contains a map with land use classes in the municipality of Rio Claro, for testing purposes. We used the Rio Claro map to run the examples of metrics in the Output links.

Satellite images can be classified by image interpretation or automatic classification algorithms (supervised or unsupervised). If you still need to map your study area, consider the following auxiliary readings and video:

- QGIS tutorial by LEEC team

- Supervised and unsupervised classification

- Tutorial 1: Your First Land Cover Classification

There are many alternatives of land use maps and binary maps for different geographic regions. Take a look at some examples:

- MapBiomas

- Global Forest Watch

- Land use and land cover in Brazil

Reference system

As LSMetrics uses meters and hectares the default units for calculating distances and areas, raster input maps must be exported in a metric coordinate reference system (CRS), such as Albers or UTM coordinate systems. Please, check the next sessions on creating a GRASS Location and be sure about your working EPSG code.

4. Starting

To start calculating metrics, first you need to create or open a GRASS GIS project (called location) and then open the LSMetrics GUI through command line.

Open or load a GRASS project
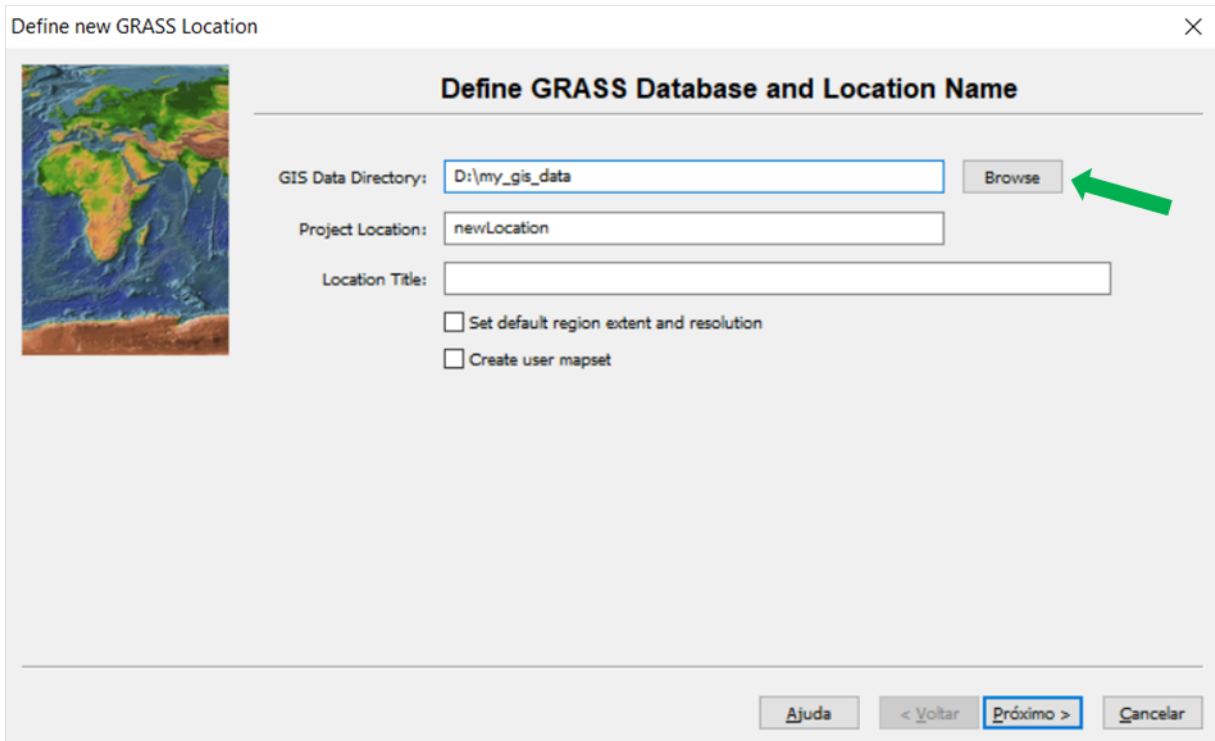
Open GRASS GIS and load or create your project location. If you do not know how to configure a project in GRASS, take a look here. Here we show one way of creating a GRASS location.

A GRASS location is a project that keeps all maps and spatial data cohesive under the same Datum and Projection. To work with your own GIS data, you must create a location with an **EPSG** (a code that represent a combination of datum and projection) that is similar to your data's. For example, if your rasters are in UTM 23 South projection with a SIRGAS 2000 datum, your GRASS location should be exactly on this projection. Follow the next steps to create a projection and import a raster map, so you can run LSMetrics with your own data.

Click on New Location wizard as follows:
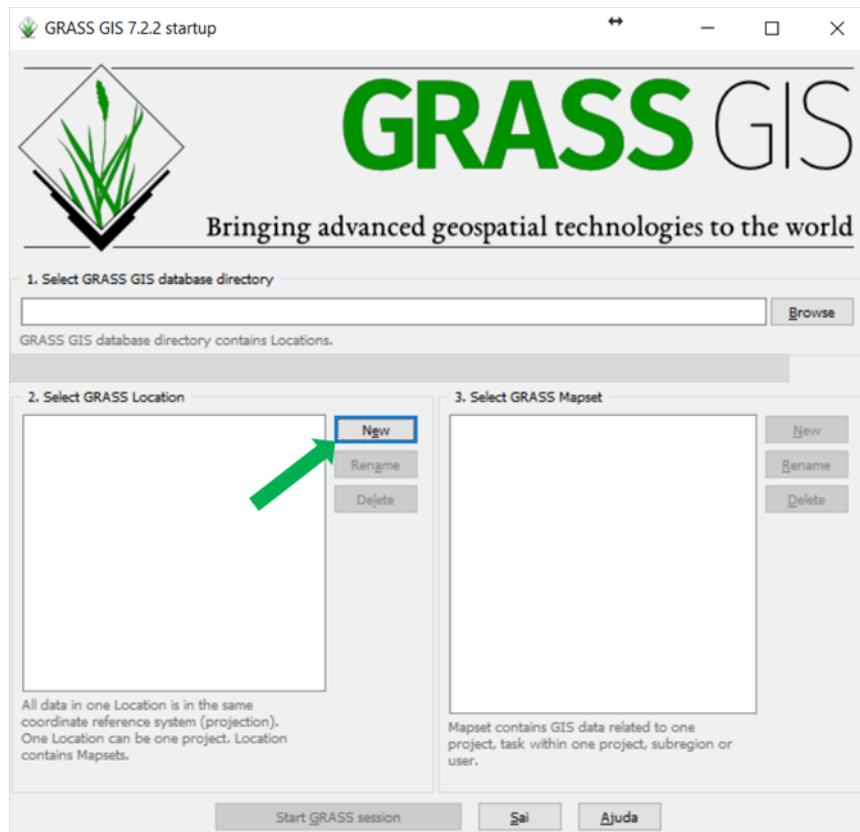
Browse the file containing the rasters of interest:
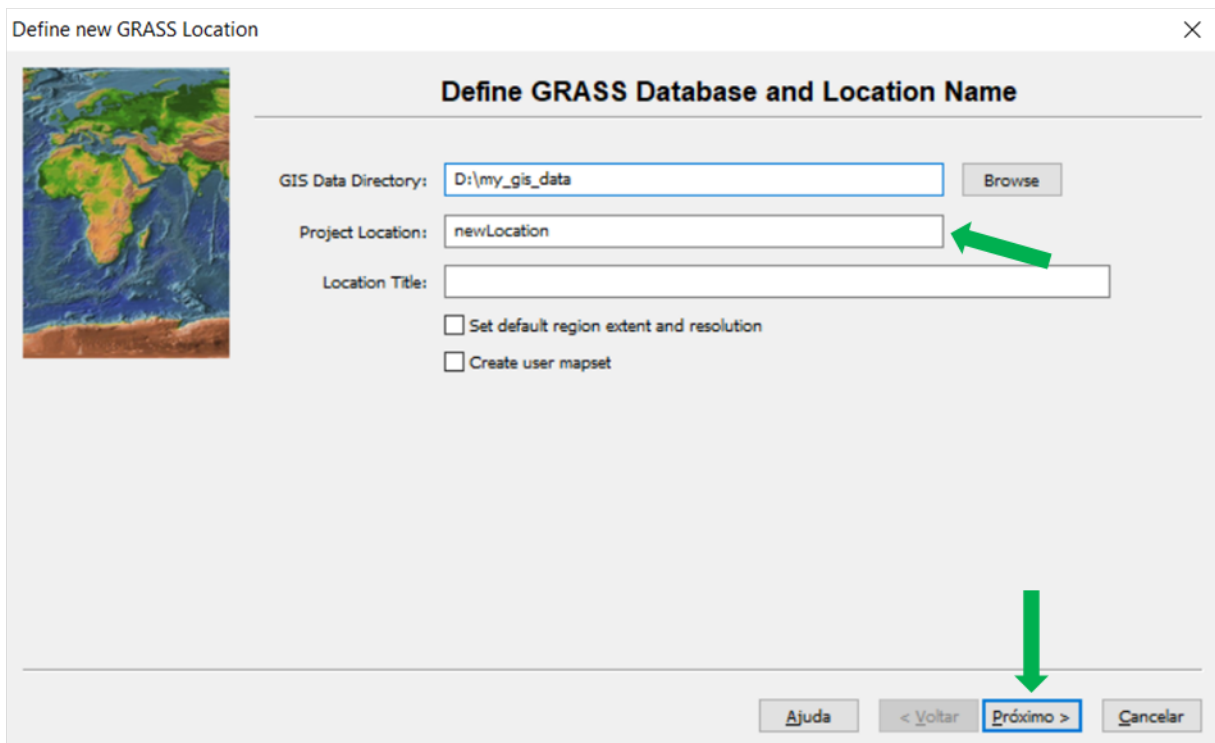
Choose a simple name for your Location (Here we keep as the default **newLocation**):
(Please avoid using spaces and special characters on the name of the location!!!)
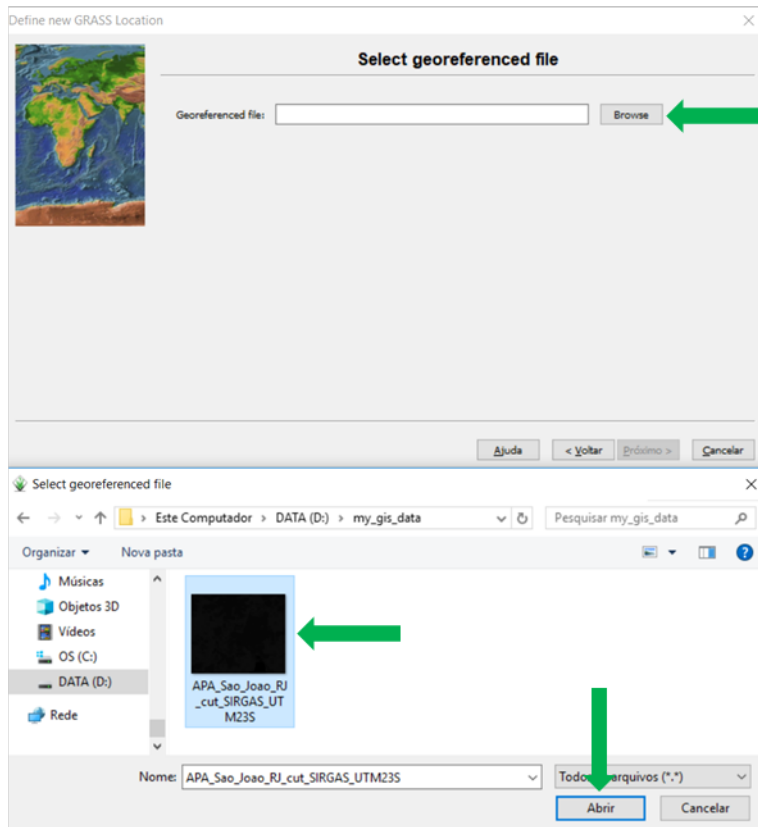

Now it is time to select your working EPSG, which is basically the spatial reference system of your data. If you don't know which one is it, figure it out here.
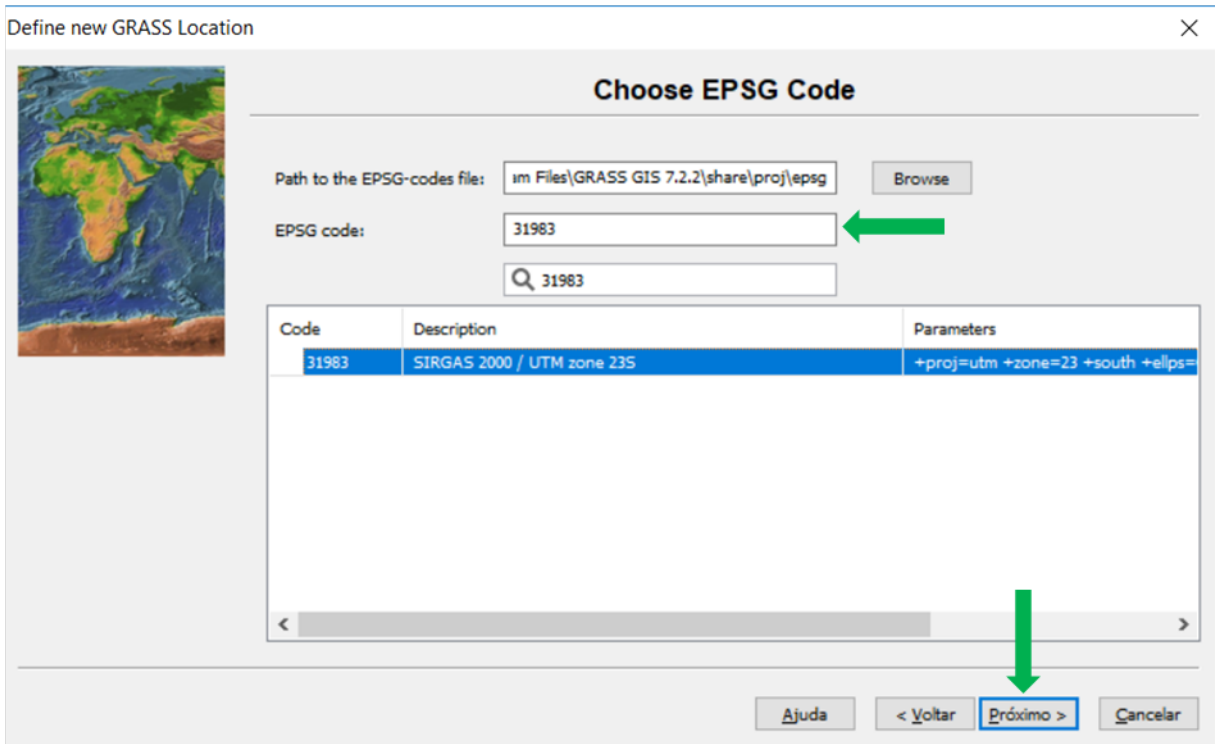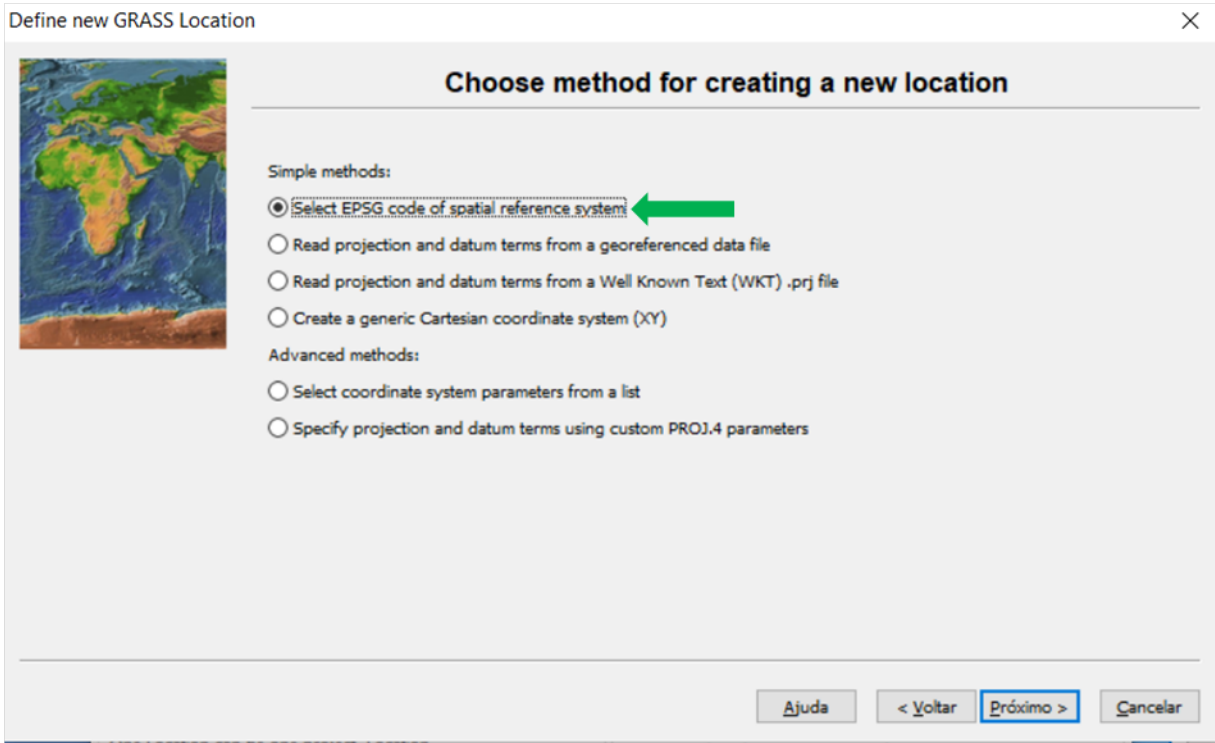
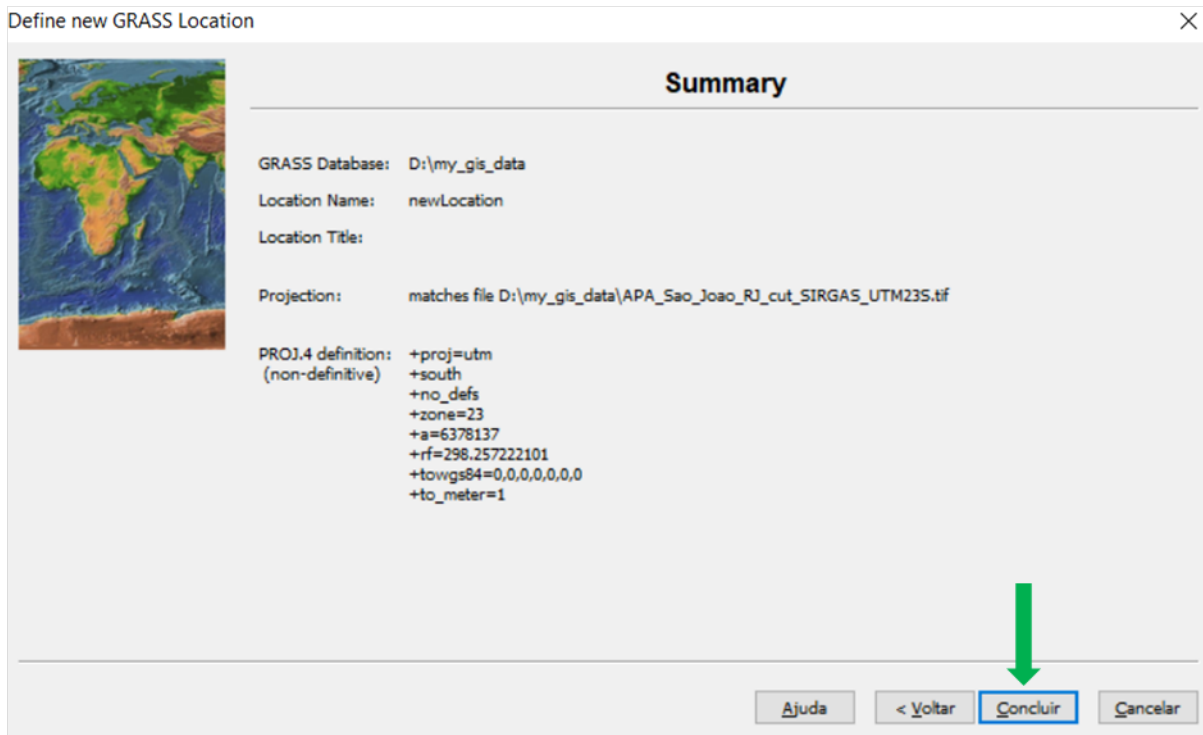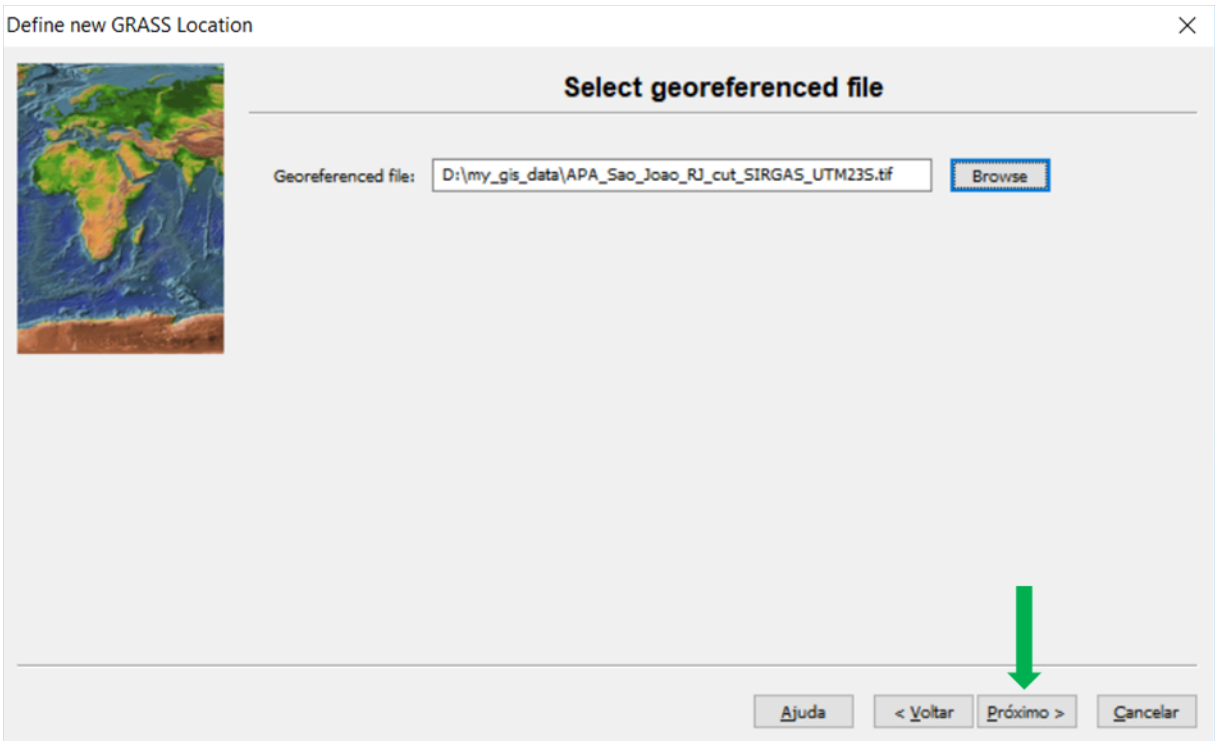You also can easily read the right spatial references system from a georeferenced file.
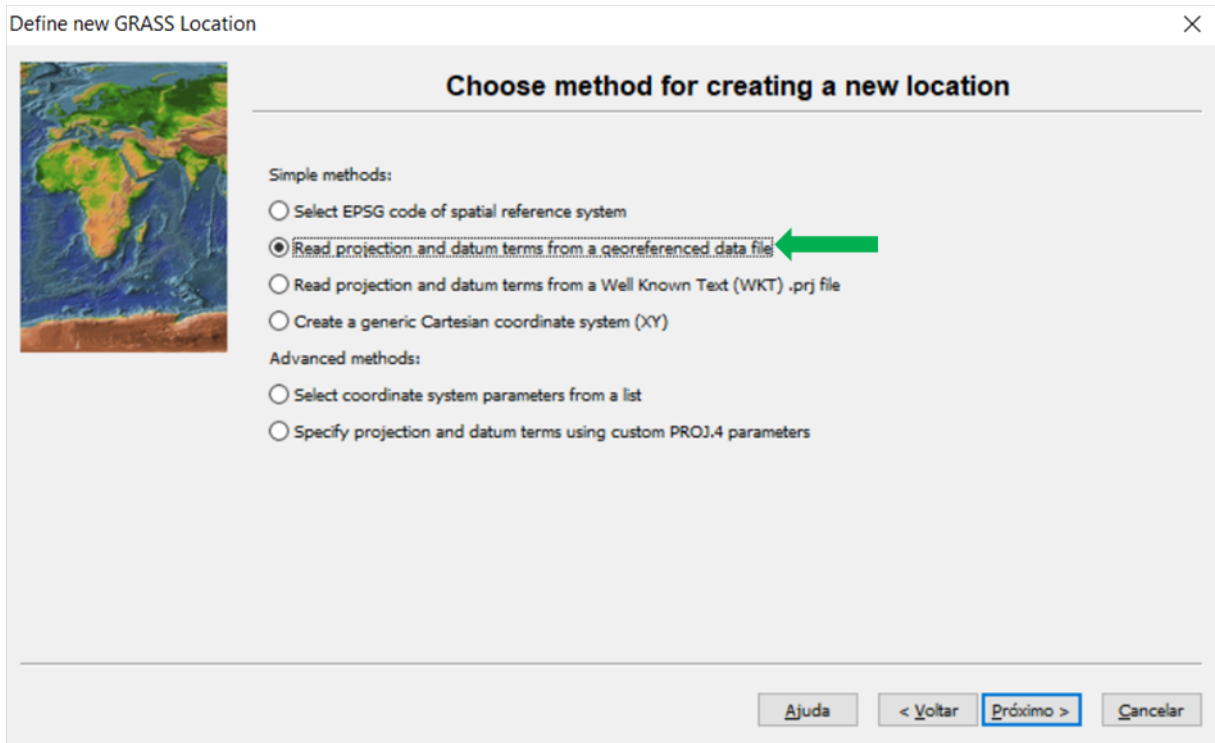
Just find the file in you computer and GRASS will get the EPSG code from it. Follow the steps:

Done! Now you created a GRASS GIS location!

## Import your maps into GRASS (your own SIG data)

Import maps right after creating the location

After creating a GRASS project, you can readily import the raster used for selecting the EPSG to GRASS environment. If you click "No", then you can also import your rasters easily - see below.
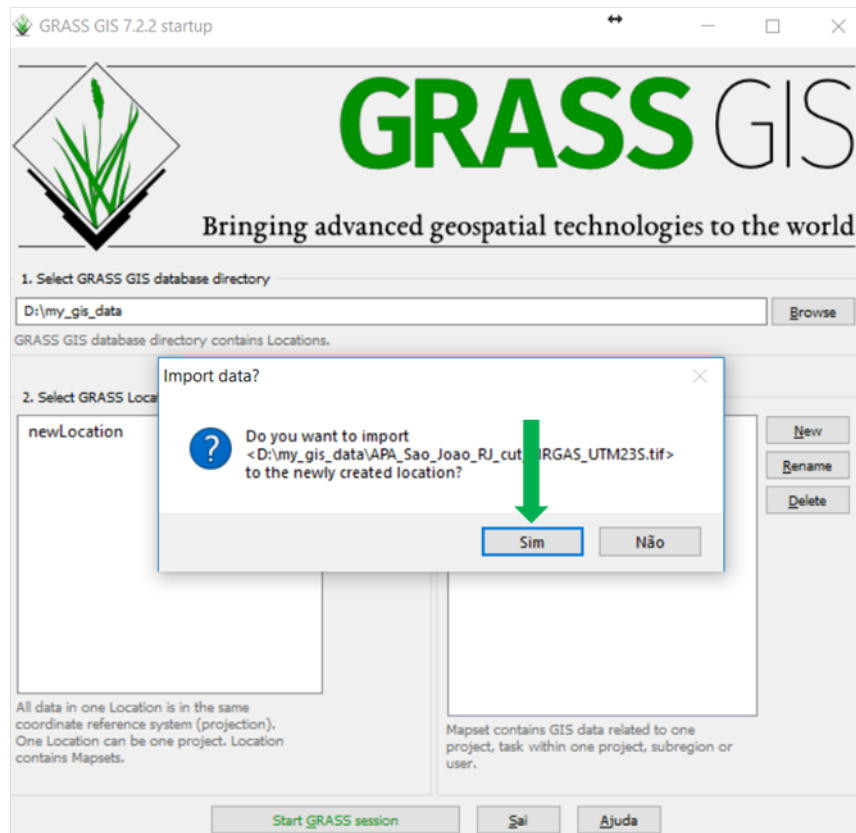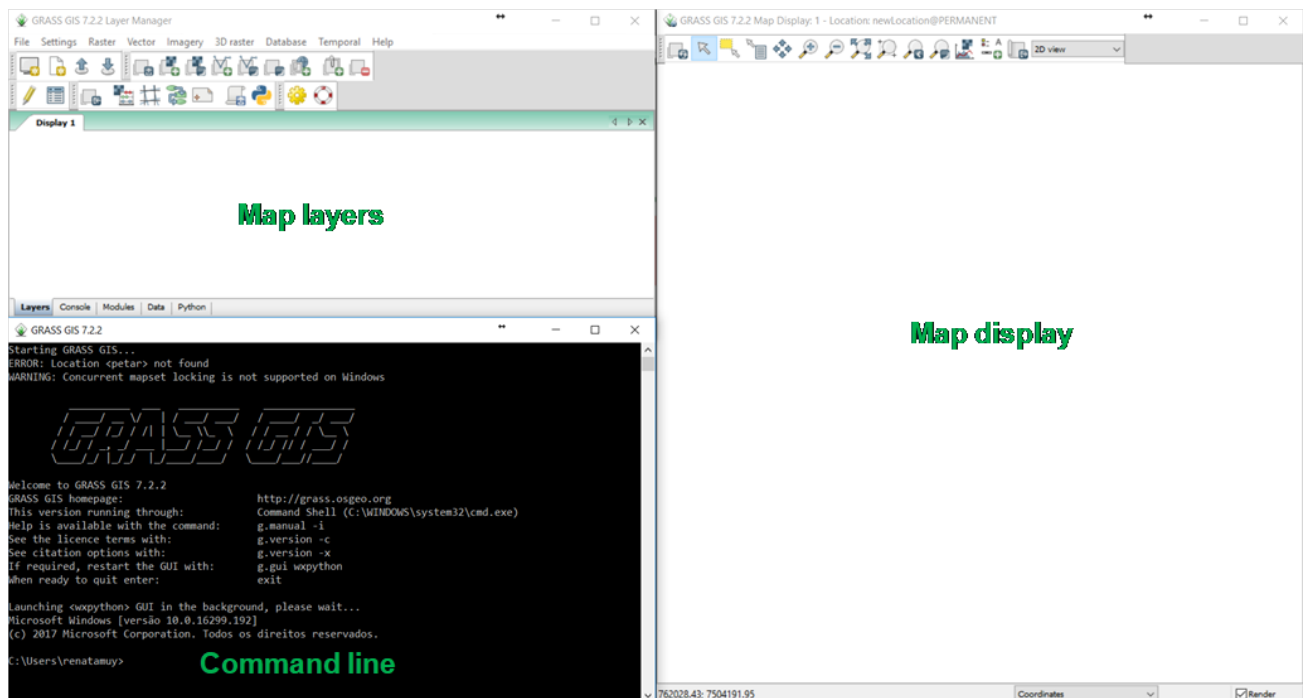

Importing data within a GRASS session

First you can start your GRASS session by pressing the START GRASS button.
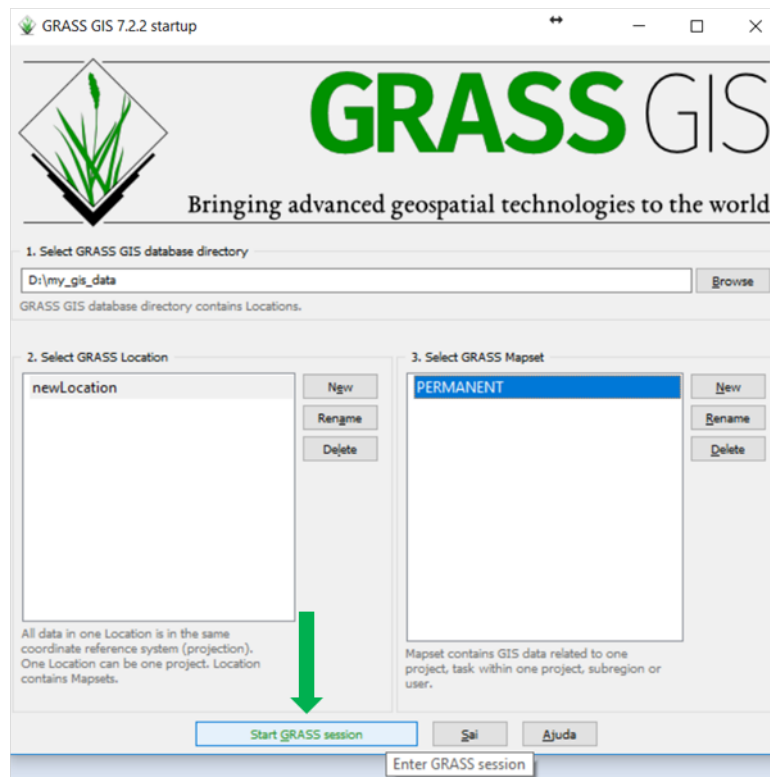
Now that you opened a grass session, see how GRASS-GIS looks like. Basically you have thee windows - a shell terminal, in which you can run GRASS procedures through command line; and two Graphical User Interface windows:
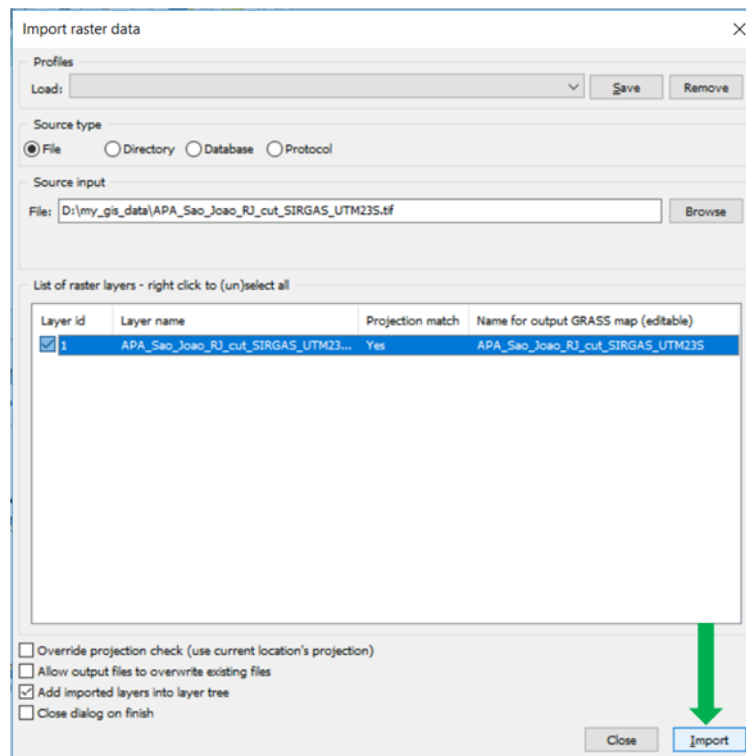

Let´s import your raster data using the function r.in.gdal, but clicking:
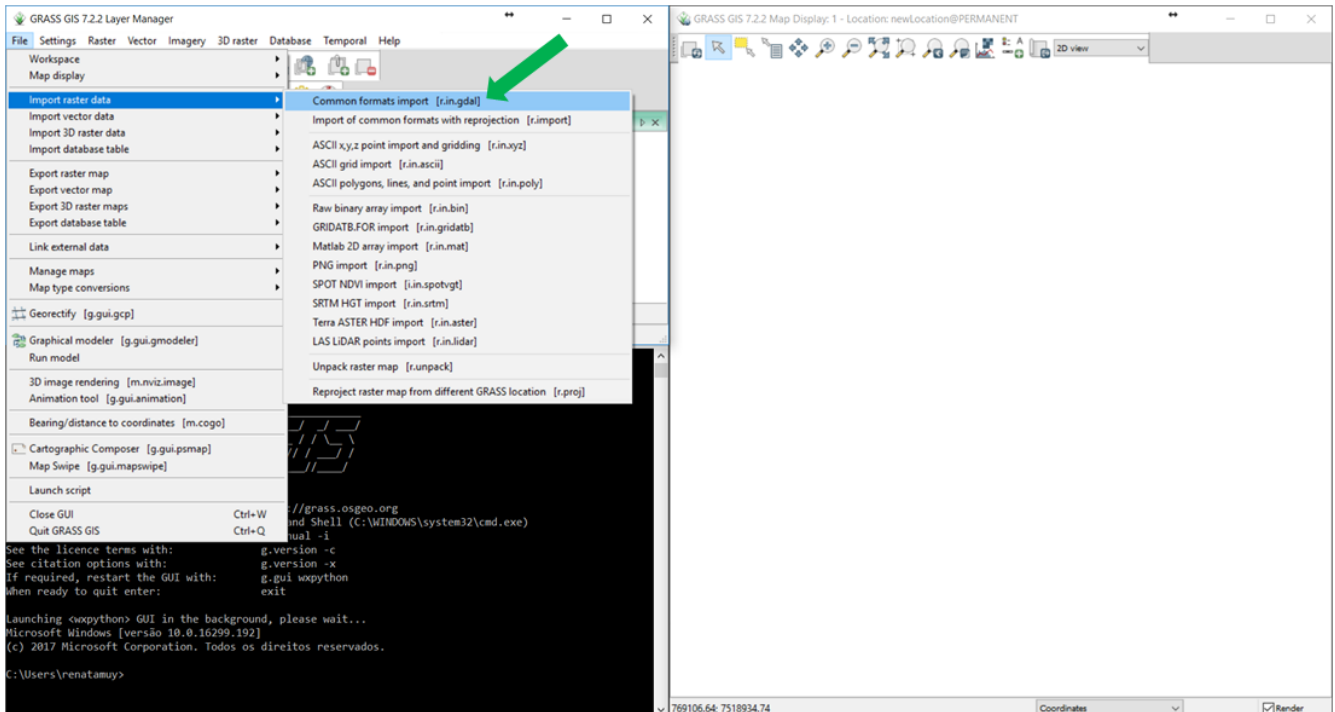
Where is your raster data? Browse to import:
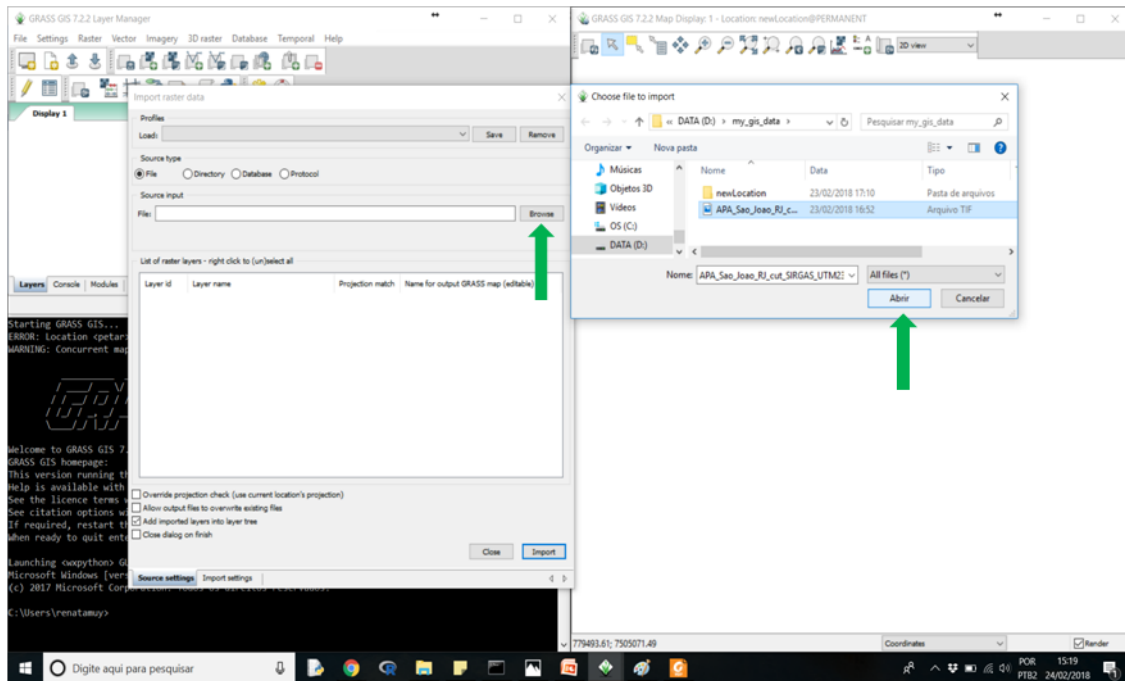
And finally, click on "Import":

Follow the next session to visualize your imported map(s) in GRASS display with our example data.

If you want more information on importing maps into GRASS, have a look at this and this.

**Observation: Make sure that your imported maps are in a projected coordinate reference system (CRS), in which distances are measured in meters, so that areas and distances are calculated in a meaningful way by LSMetrics.**

GRASS database for testing

To make your life easier, we make available a GRASS database with two raster images, for testing. Select the file grassdb_test and **Start GRASS session** as follows:

Note that you can display the maps either by coding or by clicking. If you choose clicking, then follow the steps to visualize out both example data:
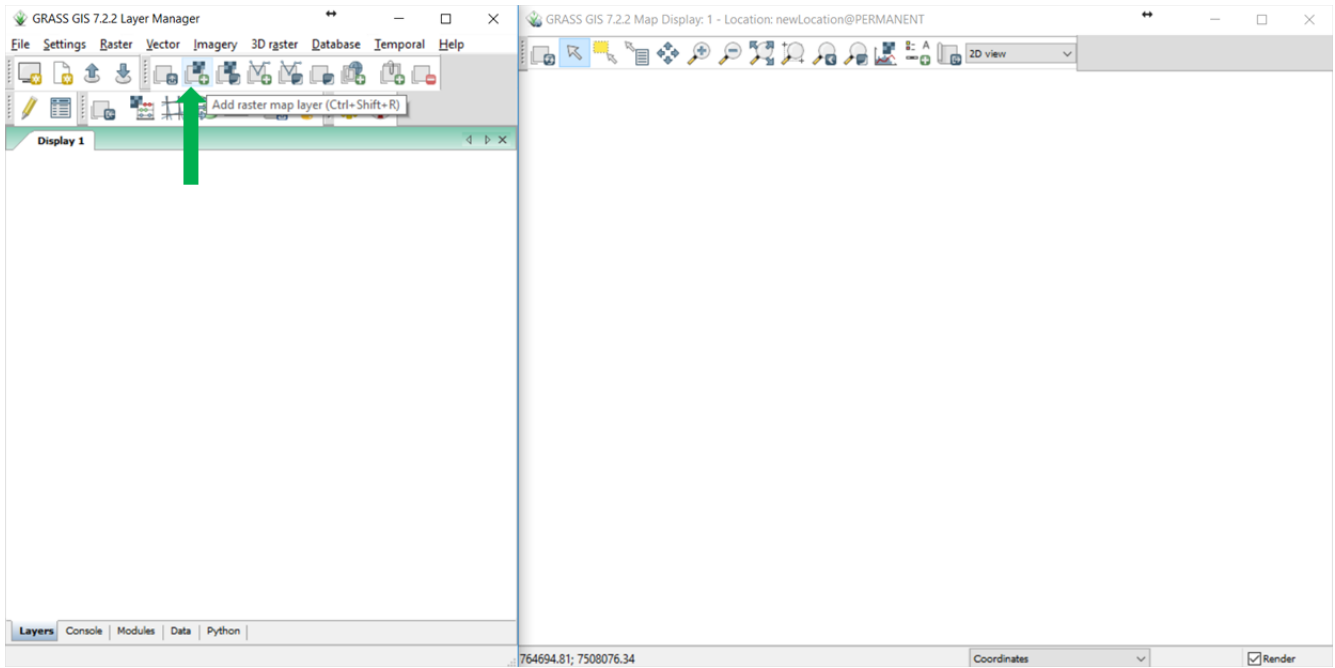
Choose the São João raster map:
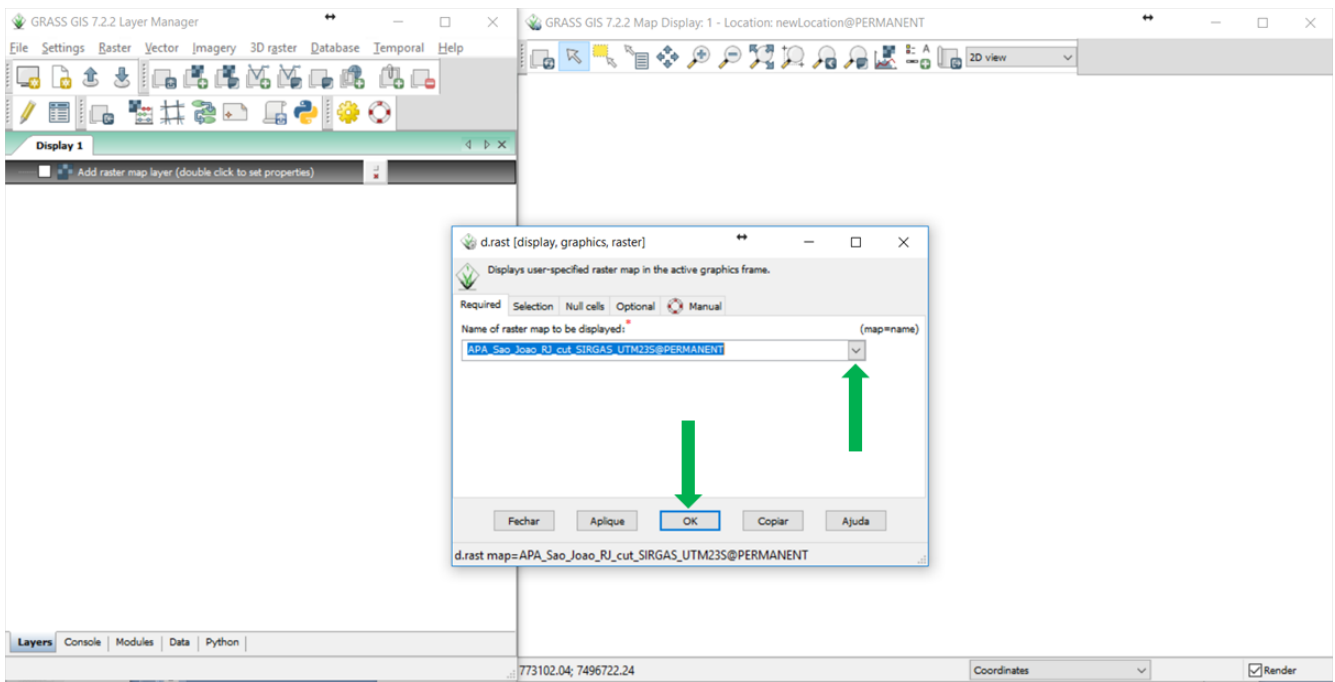
Choose the Rio Claro raster map:
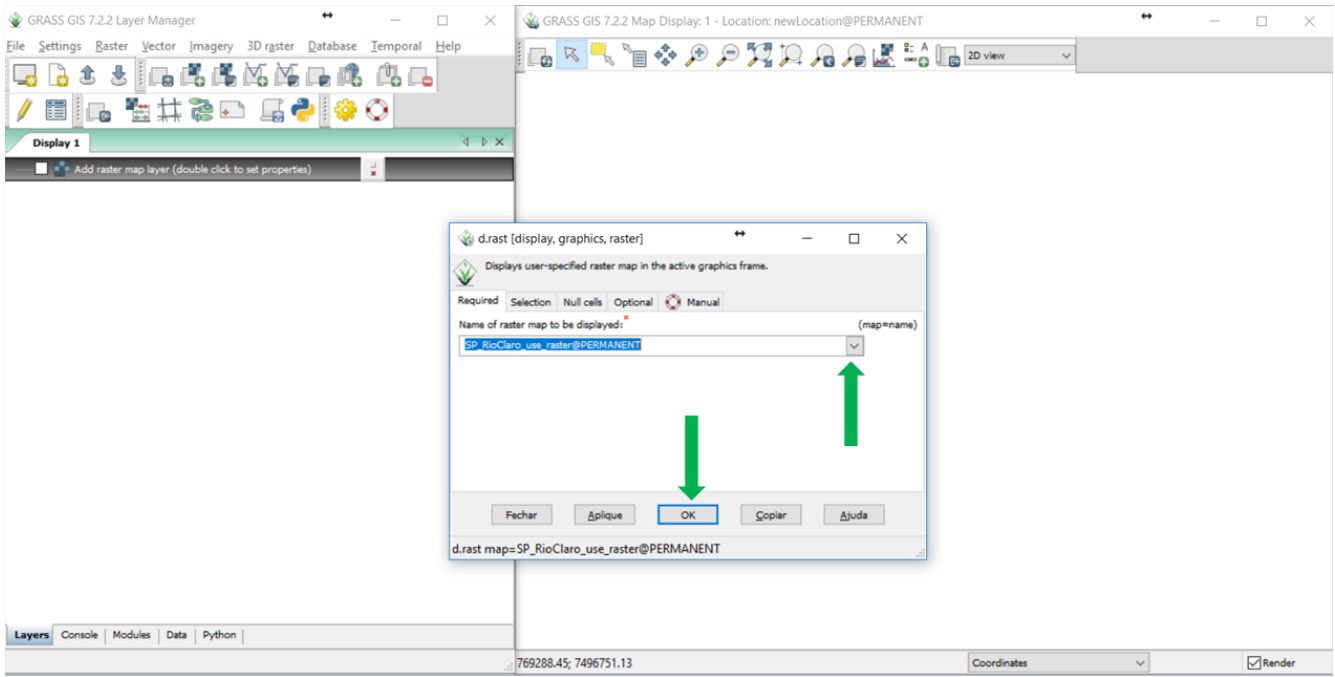
Now see below how the example maps will appear in GRASS display:

São João, State of Rio de Janeiro:
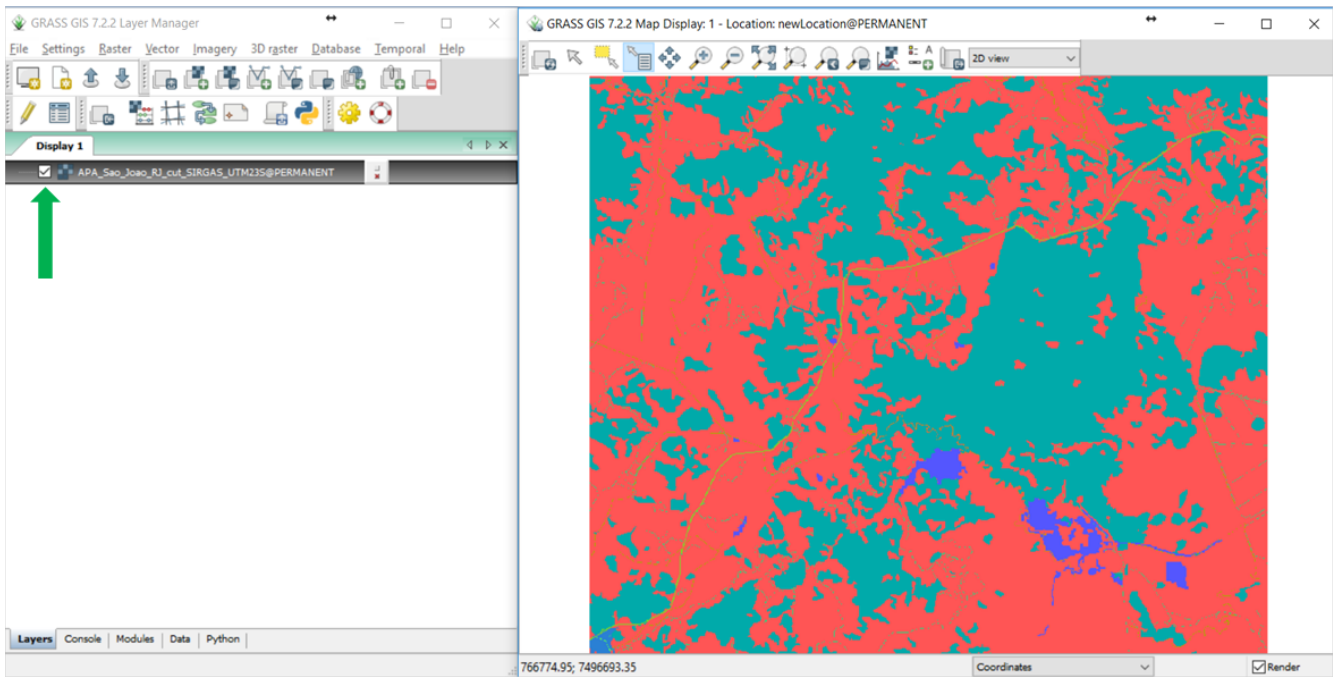
Rio Claro land use map, State of São Paulo:

On GRASS GIS display, you can evaluate the pixel values using the `Query results` tool. Se below:

Now see the code for showing the already existent example data:

```
d.rast map=APA_Sao_Joao_RJ_cut_SIRGAS_UTM23S@PERMANENT
```

```
d.rast map=SP_RioClaro_use_raster@PERMANENT
```

Run LSMetrics

Now it is finally time to use the package itself. Use the GRASS terminal (the black screen) to start LSMetrics. First change to LSMetrics directory and run it using python:
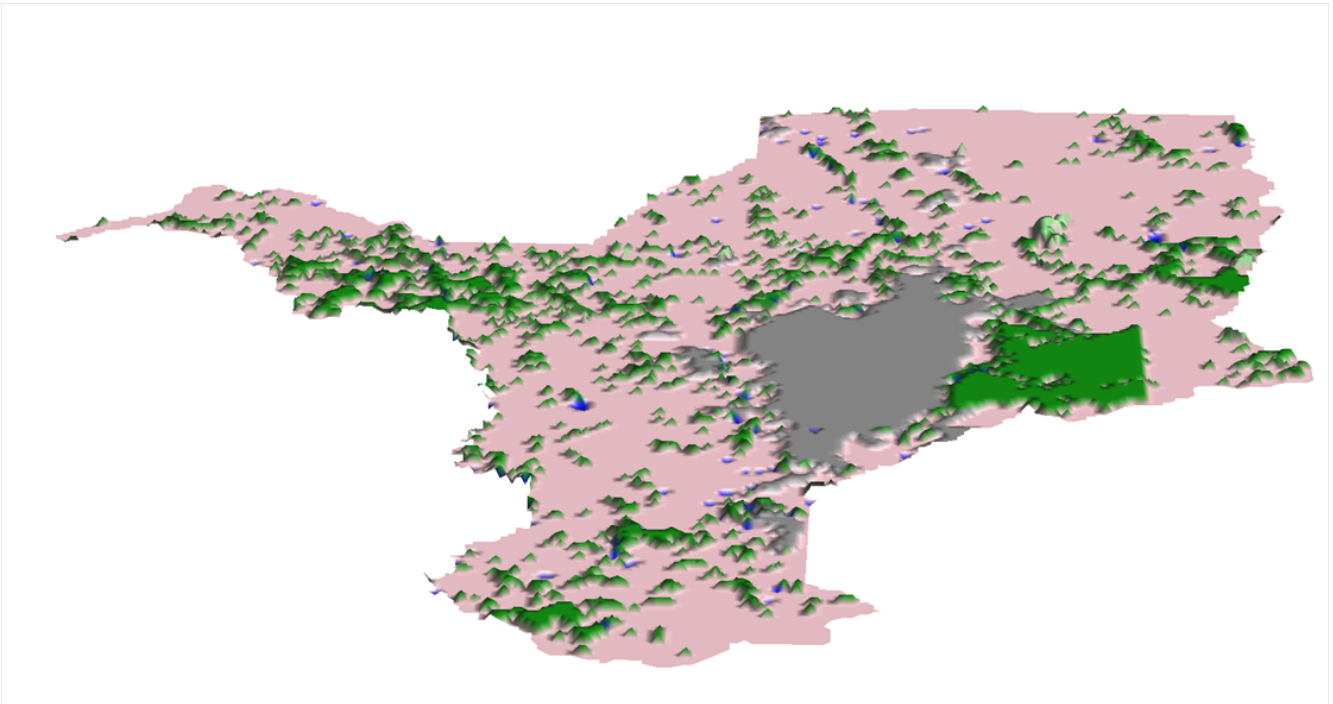
```
# Change to the code directory where you saved the program (with the version of LSMetrics you want to use)
cd "LS_METRICS/_LSMetrics_v1_0_0"

# Run LSMetrics
python LSMetrics_v1_0_0.py
```

Note!

On MS Windows, you may have to change to the partition where the code is located before changing to its directory. E.g.:

```
# If the code is on the directory "D:/"
D:
cd "D:/LS_METRICS/_LSMetrics_v1_0_0"
```

Now take a look at the Windows GUI (the GUI may be slightly different on different operational systems, but is expected to run the same way):
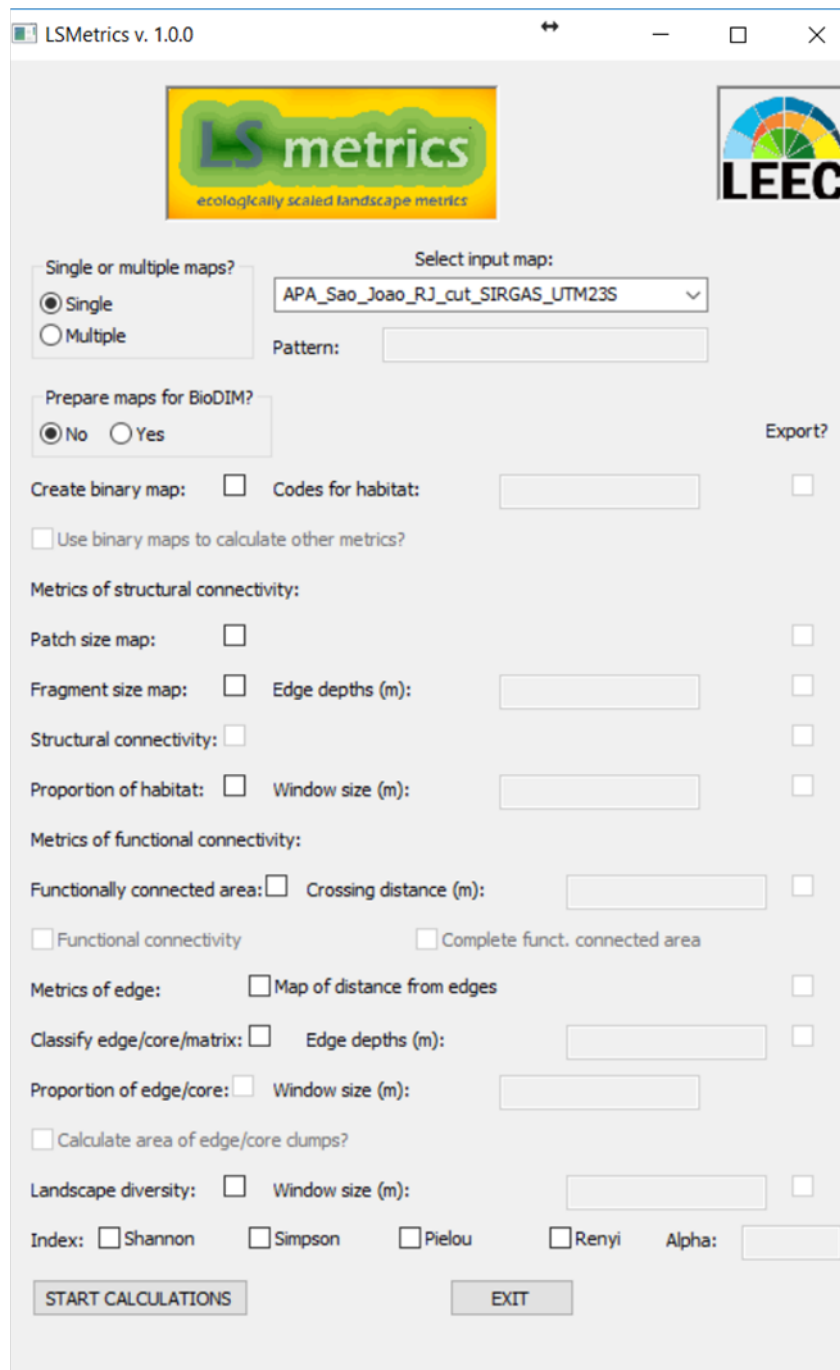
Notes on screen resolution

If the GUI does not appear completely in your screen, check your screen resolution (at least 900 pixels in the vertical direction) and your percent of text display (up to **125%**) so that the program window entirely appears. (we'll solve that soon!).

5. Running LSMetrics through GUI

Here we briefly explain how to set some important parameters used in LSmetrics. Again, make sure your input raster is using a metric coordinate reference system (CRS) by selecting the right EPSG. If your raster maps are not in a metric system EPSG, you will need to reproject them. For the reprojection, you need to know which is the SRC of your maps with projection different from your location. To do this, take a look at v.import.

Select the input map(s) and after you choose all the parameters that fit your analysis, you can click on "START CALCULATIONS". **Note that when choosing `Export`, the output of calculations (output raster maps and statistics text files) will be exported to a folder chosen by the user.**
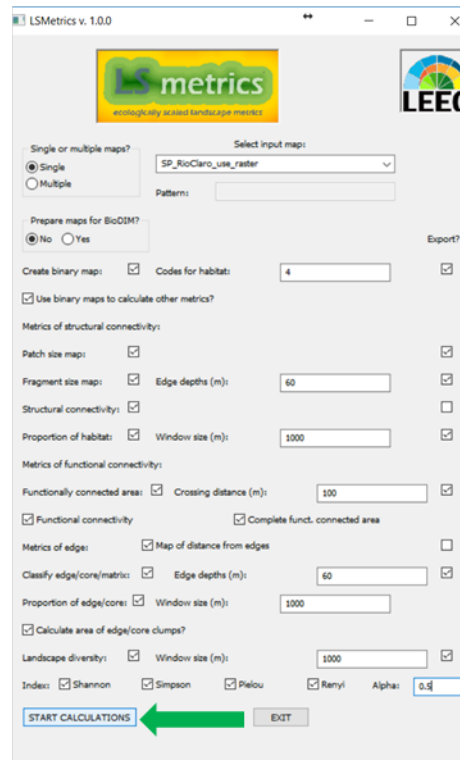
Then, select the output directory where all the rasters with the chosen metrics will be saved, as follows.
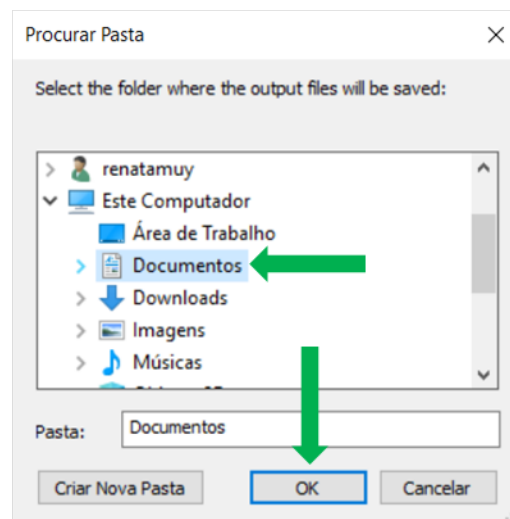
Single map or multiple maps?

LSMetrics may calculate metrics for a single or multiple maps at once. If you select "single", choose the map name in the list of maps (only maps in you current GRASS GIS mapset will appear) and select the metrics you wish to calculate.

Alternatively, you can run the selected metrics for multiple input maps in a single run, if they share some part of their names, using regular expressions. For instance, **let's say** you have the following three maps within your current mapset:

- APA_Rio_Sao_Joao_tif

- SP_RioClaro_North_tif

- SP_RioClaro_South

In this case, as some of the maps have sequences of characters in common (e.g., "tif" between the first two, and "SP_RioClaro" between the last two maps), you can choose which ones to use as LSMetrics input using that. For running the calculations for a sequence of rasters with a string common pattern in raster file name, you must use the symbol "*" (asterisk). For example, in the white box of LSmetrics (`Pattern`):

- if the file names' common pattern is all that starts with "SP", put: `SP*` (see the image below);

- if you want to select all maps that contain "forest" in any part of the file name, put: `*forest*`;

- if you want all maps that end with "SP", type: `*SP` ;

- if you want to use all maps loaded in you current mapset as input, type: `*`.
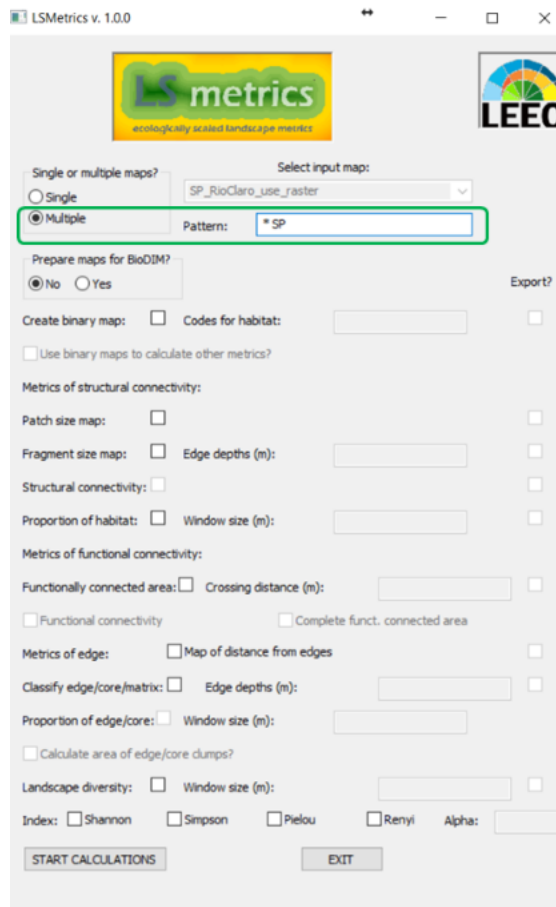
Creating binary maps

Most indices caluculated by LSMetrics are currently based on binary class (habitat/non-habitat) raster maps as input. If your map(s) are already classified this way (binary), you can use them straightforwardly as input to calculate metrics. If not, first you should select `Create binary map` and tell the app which pixel unique codes correspond to habitat. Then, you can use the resulting map as input to calculate landscape metrics by clicking in `Use binary maps to calculate other metrics`.

PS: If you select the option `Use binary maps to calculate other metrics`, you can already choose the metrics you want to calculate and generate all of them in the same run. If, instead, you create the binary map alone, you should then select the resulting map to then calculate the other metrics (in this case, unselect this option).

Binary maps are useful to investigate classes of interest and their metrics. See examples below:

This is an example of land use map that was transformed in a binary habitat map from specific codes for habitat classes (values from 15 to 20).
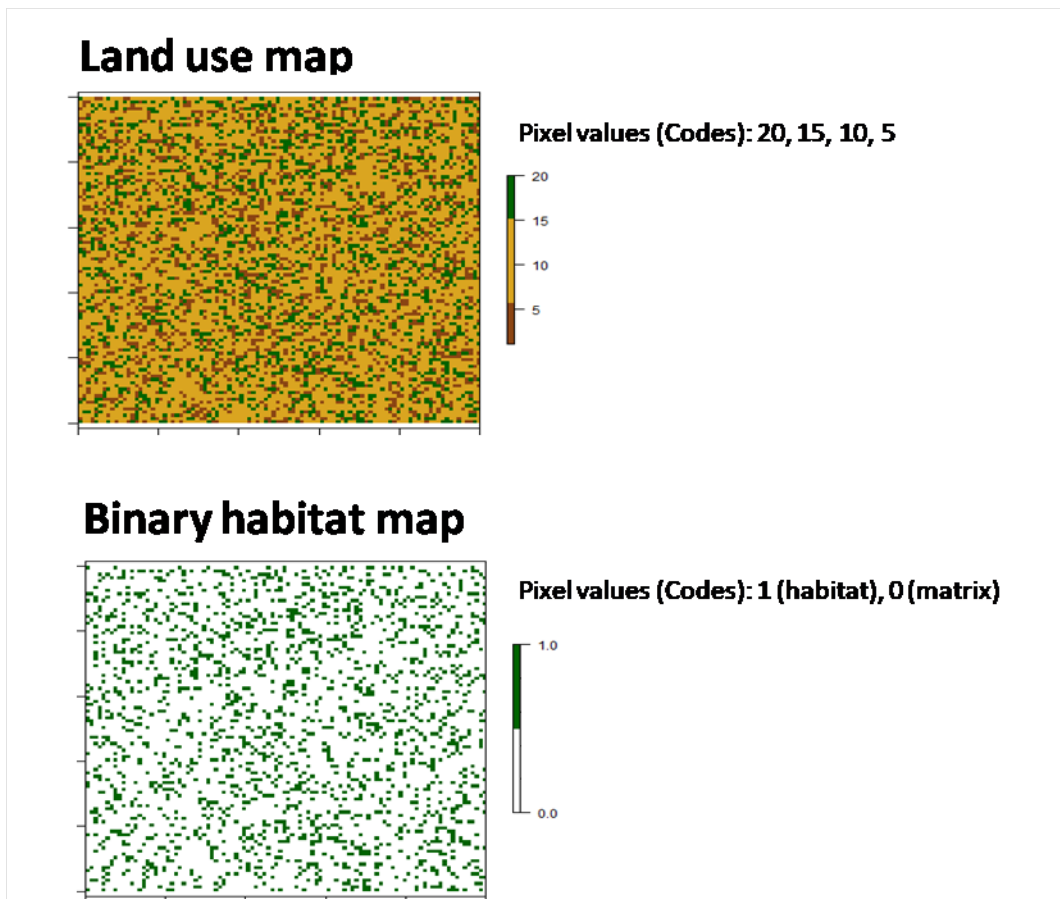
Below you may find another classic representation of binary maps. In the first, "1" (yellow) values represent the matrix, on the second the "1" (yellow) values represent the habitat areas.
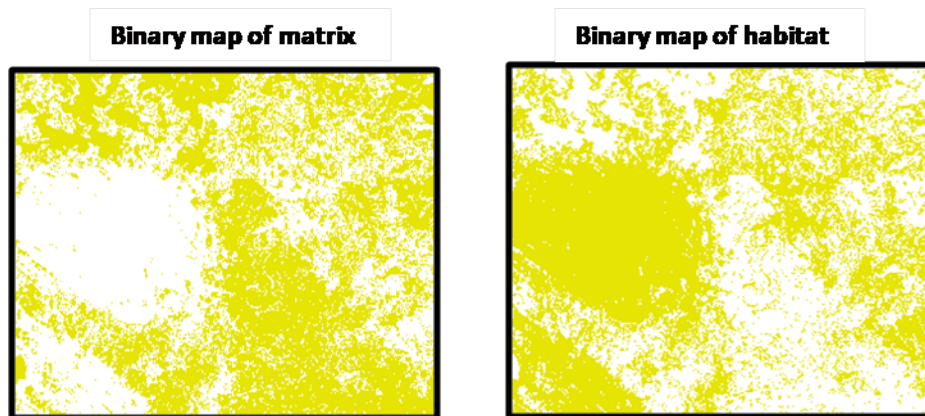
Structural connectivity metrics

Patch size

Summed area (in hectares) of one or more fragments connected by structural corridors (including the area of the corridors connecting them); if there are no fragments connected to the fragment in question, the value of this metric is equal to "fragment size" (see below). In the illustration map below, each cell has 100 m side.

Patch Size

Input raster: binary raster

ID raster output

cell value = patch id

Area raster output

Area (ha)

49

1

cell value = patch area (ha)
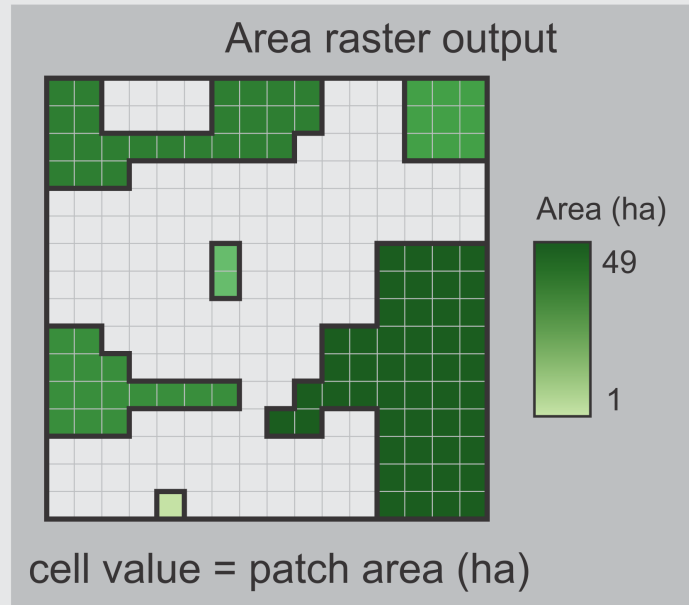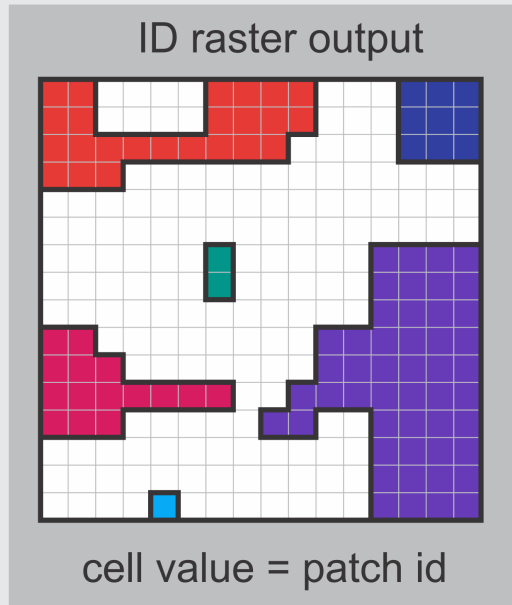
Fragment size

Area (in hectares) of any structurally isolated fragment, of any size, or the area of a fragment connected to another fragment by a structural corridor. Structural corridors are identified as parts of fragments with a width smaller than two times the specified edge depth.

The definition of what is a fragment then depends on the edge depth parameter chosen by the user.

In the illustration map below, each cell has 100 m side and the edge depth was chosen as 50 m.

Fragment Size

Input raster: binary raster
Input parameter: edge depth (meters)

ID raster output — cell value = fragment id

Area raster output — cell value = fragment area (ha)

Area (ha): 46 to 9
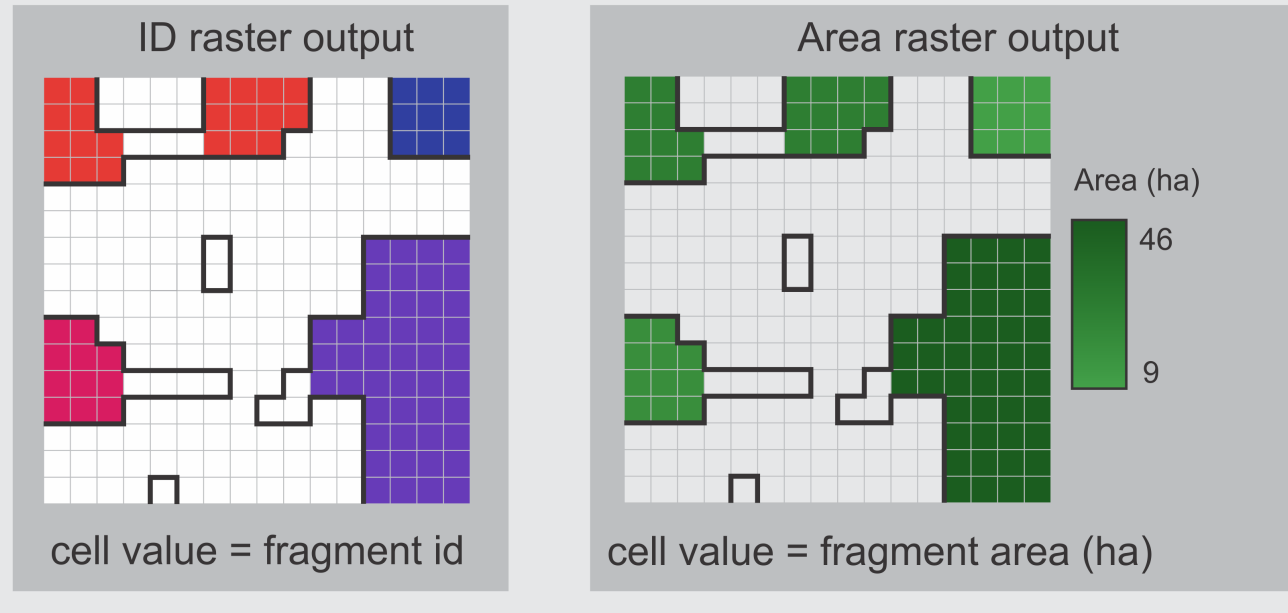
Structural connectivity

Area of habitat that is structurally (contiguously) connected to a fragment. In practice, it is the difference (in hectares) between the Patch size and the Fragment size metrics; when a patch has only one fragment, its structural connectivity will be zero.

The definition of this metric depends on what is a fragment and a structural corridor, so it also depends on the edge depth parameter chosen by the user.

In the illustration map below, each cell has 100 m side and the edge depth was chosen as 50 m.

Structural connectivity

Input raster: binary raster
Input parameter: edge depth (meters)

Area calculation of structural elements raster

E=10ha
G=11ha
F=3ha
D=11ha
B=3ha
A=55ha
C=4ha
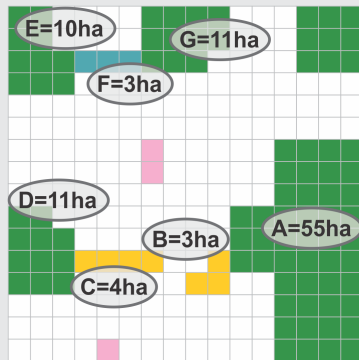
Calculation of structural connectivity:

A' = B
D' = C
E' = F+G
G' = E+F

Structurall connectivity area raster output

E'=14ha
G'=13ha
D'=4ha
A'=3ha

Area (ha)
55
0
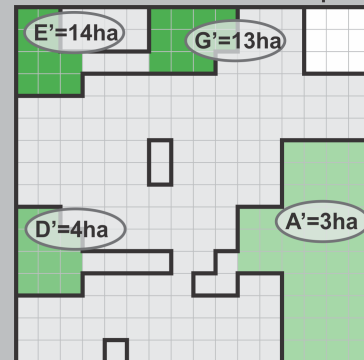
cell value = Area structurally connected

Proportion of habitat

Proportion of the target landscape class (habitat or another class(es) of interest, the one represented by the value 1 in the input binary map) within a given window around each map cell.
It depends on the size of the window chosen by the user.

How to choose the window size?   The user must decide which window size will be used to calculate metrics. It corresponds to search extent from each pixel where the calculations will be applied. It can be based on the extent of landscape perception of the target species, process or groups analyzed. It is given in meters.

Functional connectivity metrics

Functionally connected area

Represents the total amount of habitat area (in hectares) functionally available for an organism located in a patch, given a gap crossing capability of the organism. This is calculated by generating a buffer of size equal to half of the gap crossing capacity of the organism, around all patches, grouping all habitat patches close enough in the same clusters of patches, and summing up the area of all the grouped patches.

Functional connected area

Input raster: binary raster
Input parameter: gap crossing distance (meters)

ID raster output

cell value = functional patch id

Area raster output

Area (ha)

65

2
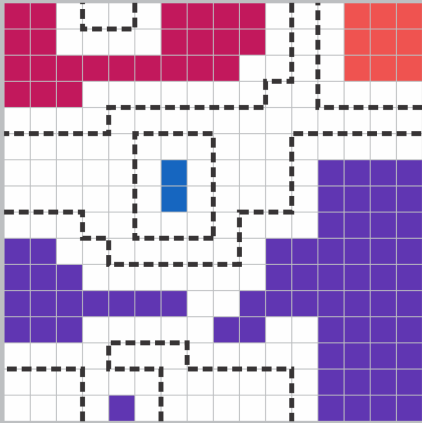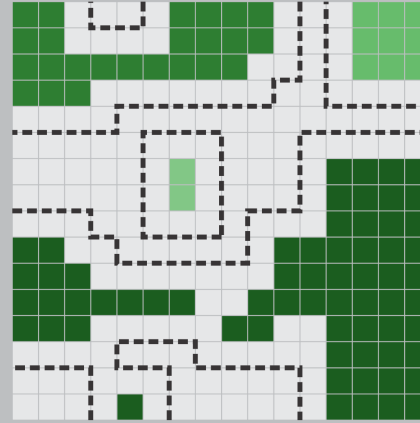
cell value = functional patch area (ha)

Functional connectivity

The amount of area functionally connected to a habitat patch, given a gap crossing capability of a species or group of interest. First, a buffer of interest equal to half of the width (in meters) that a species is able to cross is created. Then, the habitat patches that are close enough ara grouped within the same buffer. We then sum the area (ha) of all this grouped patches. We refer to these groups of nearby habitat patches as habitat **clumps**. Finally, to obtain the strict functional connectivity, we calculate the difference between each clump size (ha) and patch size (ha);

Functional connectivity

Input raster: binary raster
input parameter: gap crossing distance (meters)

Patch size raster +
gap crossing buffer
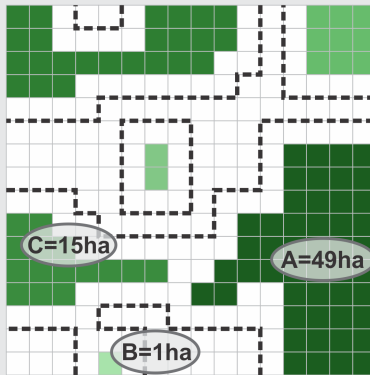
Calculation of functional connectivity:

A'=B+C
B'=A+C
C'=A+B

C=15ha
A=49ha
B=1ha

Functional connectivity
area raster output

Area (ha)
66
0

C'=50ha
A'=16ha
B'=66ha
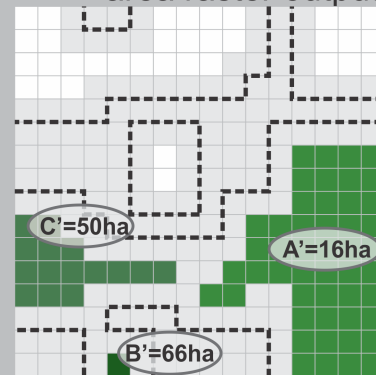
cell value = functional patch area (ha)

Complete functional connected area

The total amount of habitat functionally available for any species, given a gap crossing capability. We do all the steps for the "Functional connectivity" calculation, but do not subtract the patch size from the clump size.

Total functional connected area

Input raster: binary raster
input parameter: gap crossing distance (meters)

ID raster output — cell value = functional patch id

Area raster output — cell value = functional patch area (ha)

Area (ha)
65
2

Metrics based on the delimitation of edges

See the charts and brief explanation of each metric below:

Classification of landscape structural elements

These metrics are classifications of landscape in three or more structural elements. The simple version of this metris divides elements in three categories: core, edge and matrix. The more complex version divides elements in: core, edge, corridor, branch, stepping stone and matrix (will be available soon). See below both versions:

Classification of landscape structural elements (simplified version)

Input raster: binary raster
Input parameter: edge depth (meters)

structural elements raster output

■ core
■ edge
□ matrix
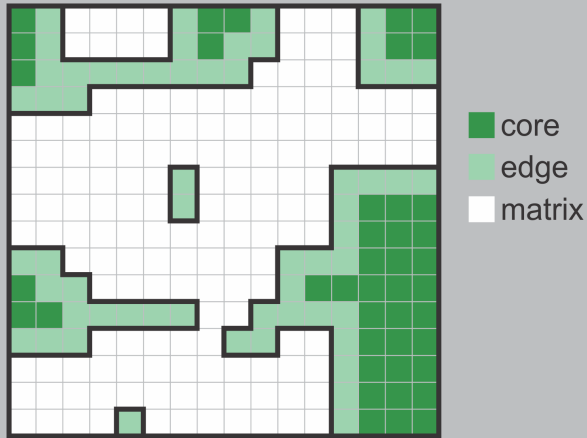
cell value = structural landscape code

statistical text output

-codes of each landscape structure

-summed area of each element

Classification of landscape structural elements

Input raster: binary raster
Input parameter: edge depth (meters)

structural elements raster output

- core
- edge
- corridor
- branch
- stepping stone
- matrix

cell value = structural landscape code
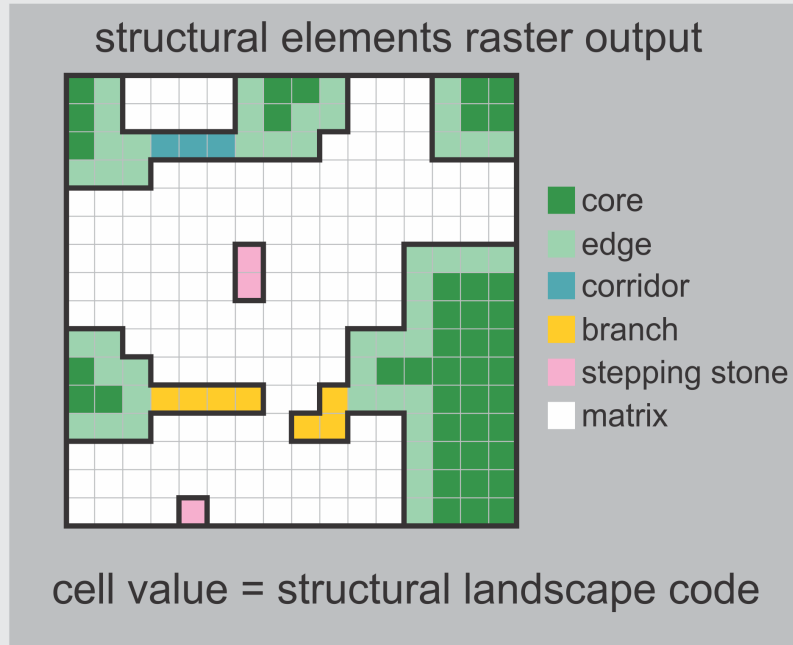
statistical text output

-codes of each landscape structure

-summed area of each element

Map of distance from edges

The output value of each pixel will represent the distance of this pixel to the nearest edge.
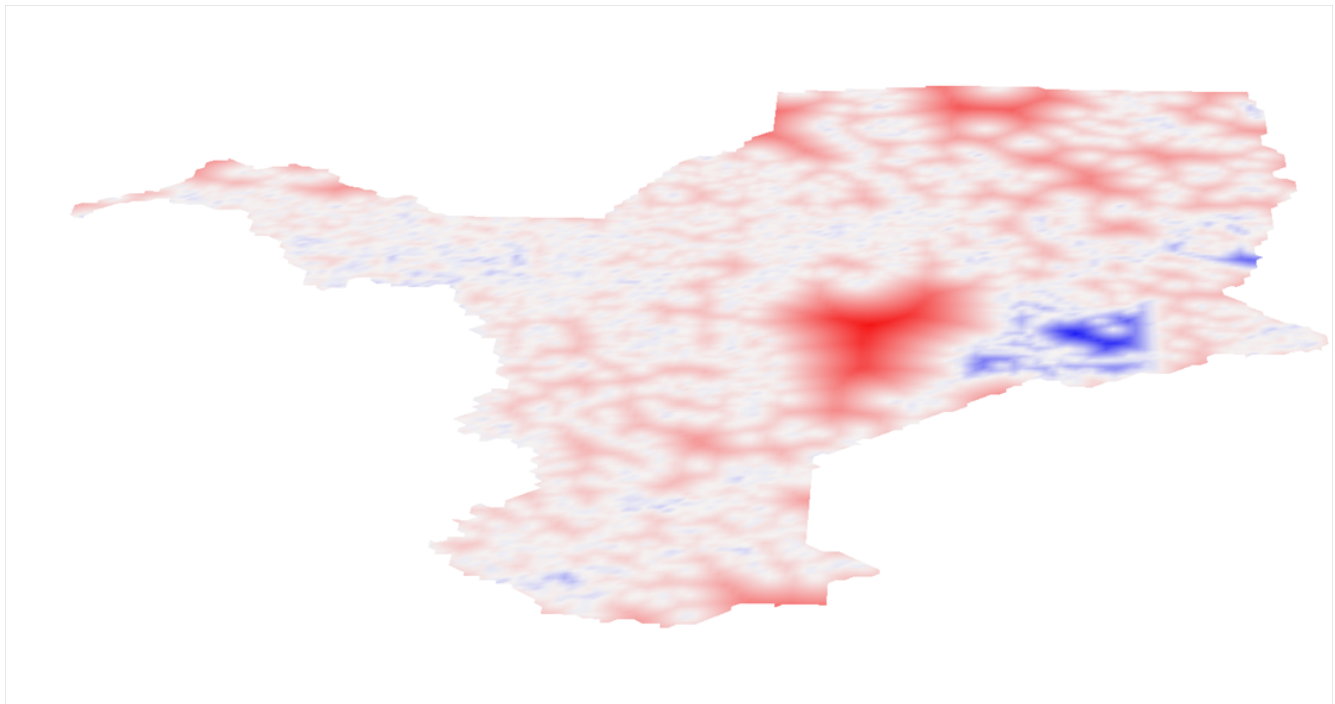
Classify edge/core/matrix

Considering a specified Edge depth, this metric classifies the pixels as belonging to three categories: edge, core and matrix. How species really use habitat area would be represented by the core area, since many species have limitations on using edges or less quality areas than their preferred habitat.

Proportion of edge/core

Percentage of habitat and edge within a search radius (Window size parameter), given a specified edge depth (Edge depths parameter).

Percentage of core

Input raster: binary raster
Input parameter: edge depth (meters)
Input parameter: window size (meters)

Proportion raster output

Percentage

100%

0
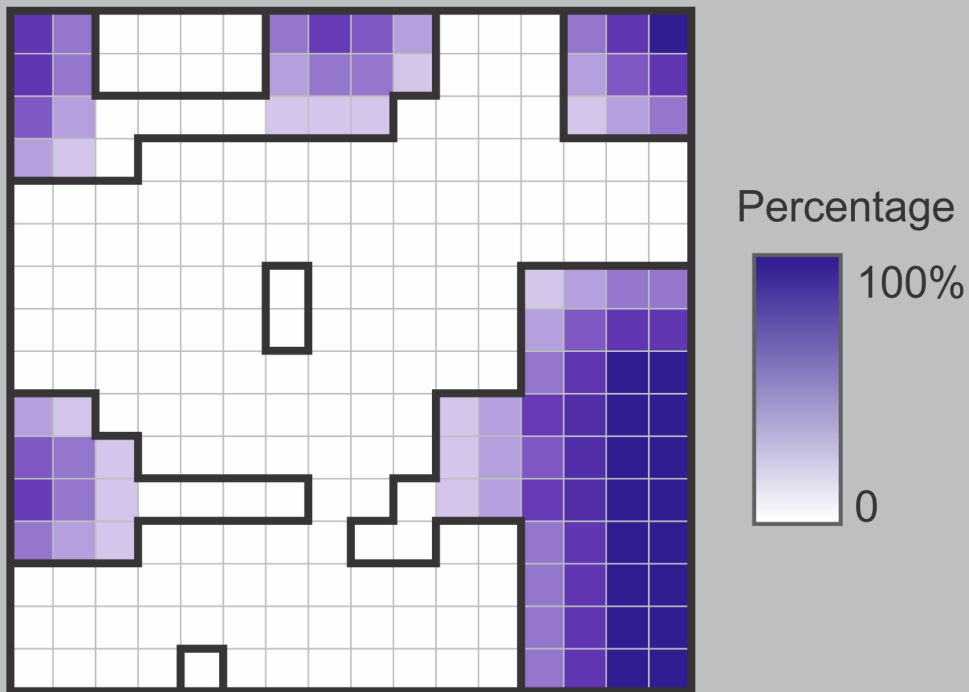
cell value = percentage of core area

Percentage of edge

Input raster: binary raster
Input parameter: edge depth (meters)
Input parameter: window size (meters)

Proportion raster output
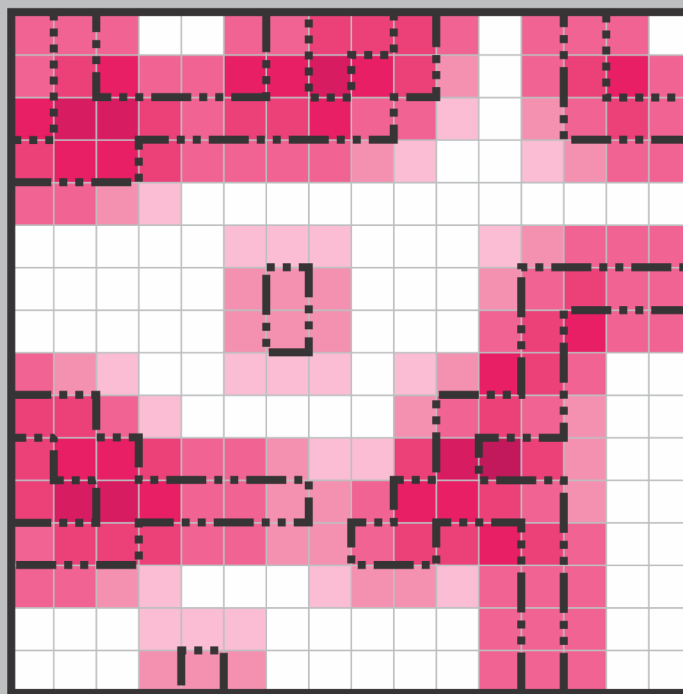
edge limit

Percentage
70%
0
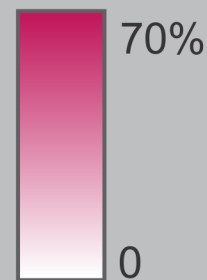
cell value = percentage of edge area

Edge depths   This parameter is a proxy for investigating the impact of edge influence on the different pixels. It estimates the distance of edge influence and should be carefully thought a priori by the user, since it will be used to calculate the output metrics. It is set in meters, and as larger the value, larger the edge influence and extent through landscape.

Calculate area of edge/core clumps?

(Achei difícil reduzir essa explicação)

Given edge and core areas were identified, contiguous cells are clumped into edge and core clumps (i.e., cells of edge and core that pertain to the same patch), and their areas are calculated (in hectares). Two maps are created for

each one (edge/core) for each landscape: an edge (core) clump ID (edge or core PID) map, which sets a distinct integer number to each clump of edge (core) cells, and a clump size map, which sets the the area of those clumps; non-edge (non-core) cells are set to NULL in both.

Core size

Input raster: binary raster
Input parameter: edge depth (meters)
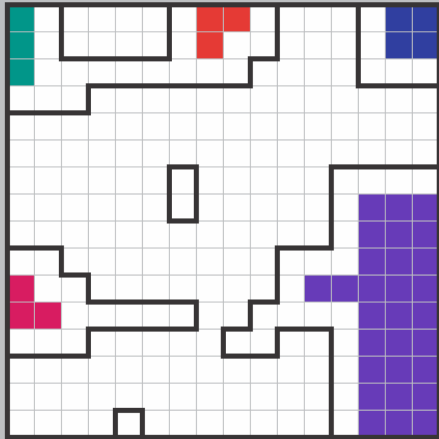
ID raster output

cell value = core id

Area raster output
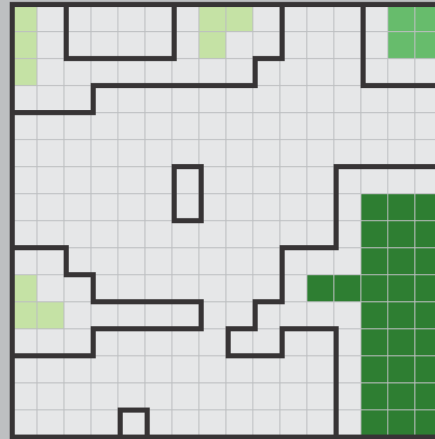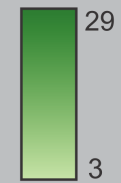
cell value = core area (ha)

Area (ha)

29

3

Edge Size

Input raster: binary raster
Input parameter: edge depth (meters)
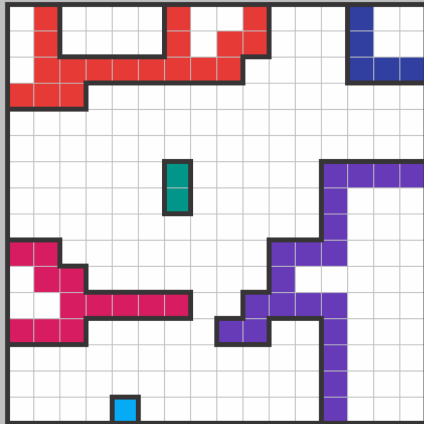
ID raster output

cell value = edge id

Area raster output

Area (ha)

20

1
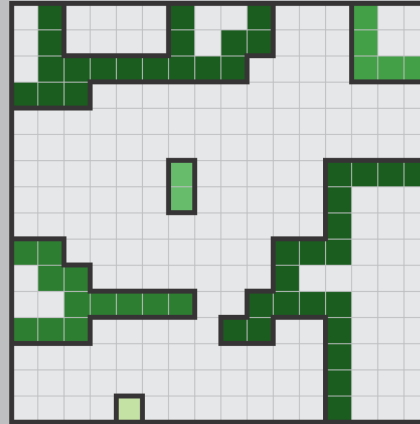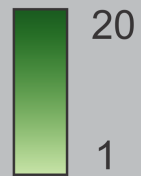
cell value = edge area (ha)

Landscape diversity metrics

Diversity indexes require multi-class raster maps. In order to calculate landscape diversity, the user must set which land use class codes are relevant for the calculation. In our example data, we have the land use for Rio Claro municipality. LSMetrics run the landscape diversity measures with **all classes**. We suggest always having more than three classes in your land use map to increase the variability in the landscape diversity measures. The user must choose the window size that will be used to calculate the diversity in landscape. In the example, we set as 1000 m and click to calculate all diversity measures. This means that the search radius will be 1000 meters.

Maps identifying patches, fragments, and functional patches

PIDs are Patch or Clump identification codes for the respective selected metrics. FIDs are identification codes for each clump generated by connectivity metrics.
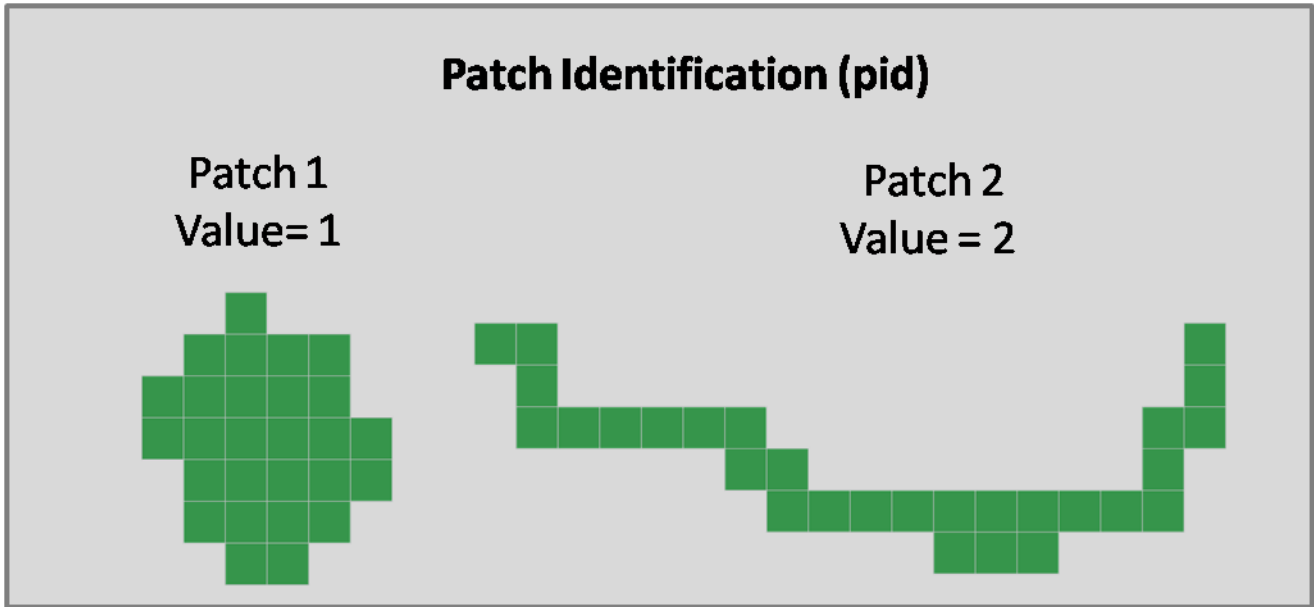
6. LSMetrics outputs

After LSMetrics runs, you will see in your screen the following message, with a sound:
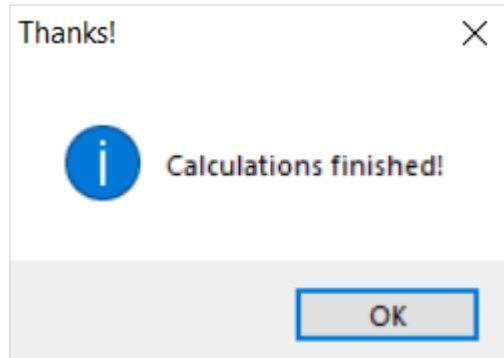
By default, LSMetrics outputs are raster maps in ".tiff" format. We will use the palette "byr" from r.colors for coloring our diversity rasters. For practical reasons, we are using different points near the state forest region of FEENA to show their values for each metrics via Query results in GRASS GIS display. If you want to visualize the values of each metric for a same spatial point, you can use r.what in the command line of GRASS GIS:

`r.what map=SP_RioClaro_use_raster_diversity_1000m_pielou_size_33@PERMANENT coordinates=241349.630457,75175`

If you choose all metrics, you will see them in the output file you´ve chosen before.

Next, we are going to briefly present a layout of each landscape metrics outputs, together with their sufix file names and query results in printscreens of GRASS GIS displays.

Take a look on the 27 output suffixes of file names for our example data:

Metric	Sufix of file name
_HABMAT	Binary raster of habitat and matrix
_HABMAT_0060m_fid	FID of structural elements map

Metric	Sufix of file name
_HABMAT_0060m_fragment_AreaHA	Fragment area in hectars
_HABMAT_0100m_func_connect_AreaHA	Functional connected area in hectars using a 100 crossing distance
_HABMAT_0060m_structural_connectivity	Classification of structural elements with a 60 m edge depth
_HABMAT_0100m_func_connect_AreaHA	Functional connected area in hectars using a 100 crossing distance
_HABMAT_0100m_func_connect_complete_AreaHA	Complete functionally connected area in hectars using a 100 window
_HABMAT_0100m_func_connect_complete_pid	PIDs of Complete functionally connected area in hectars using a 100
_HABMAT_0100m_func_connect_pid	PIDs of clumps for functional connectivity using a 100 m crossing di
_HABMAT_0100m_functional_connectivity	Functional connectivity using a 100 m crossing distance
_HABMAT_EDGE_0060m	Edge area binary map using a 60 m edge depth
_HABMAT_EDGE_0060m_AreaHA	Edge area map using a 60 m edge depth
_HABMAT_EDGE_0060m_pct_1000m	Proportion of edge using a 60 m edge depth
_HABMAT_EDGE_0060m_pid	Identification of edge cumps using a 60 m edge depth
_HABMAT_EDGE_DIST	Map of distances from edge
_HABMAT_habitat_pct_1000m	Proportion of habitat using a 1000 m window size
_HABMAT_MECO_0060m	Structural elements (edge, core, matrix)
_HABMAT_patch_AreaHA	Patch area of the habitat matrix map
_HABMAT_pid	Patch identification of the habitat matrix map
_HABMAT_CORE_0060m	Core area binary map using a 60 m edge depth
_HABMAT_CORE_0060m_AreaHA	Core area in hectares
_HABMAT_0060m_pct_1000m	Proportion of habitat using a 1000 m window size and a 60 m edge d
_HABMAT_CORE_0060m_pid	Patch identification of core areas using a 60 m edge depth value
_HABMAT_diversity_1000m_pielou_size_33	Landscape diversity using Pielou´s algorithm and a 1000 m window
_HABMAT_diversity_1000m_shannon_size_33	Landscape diversity using Shannon´s algorithm and a 1000 m windo
$HABMAT$diversity_1000m_simpson_size_33	Landscape diversity using Simpson´s algorithm and a 1000 m windo
$HABMAT$diversity_1000m_renyi_size_33_alpha_0.5	Landscape diversity using Renyis´s algorithm and a 1000 m window

Metrics of structural connectivity

Here we will show the outputs of each metric and a print of their Query results in GRASS GIS display.

Create Binary map

See this binary map of Rio Claro based on forest classes (not necessarily native forest).
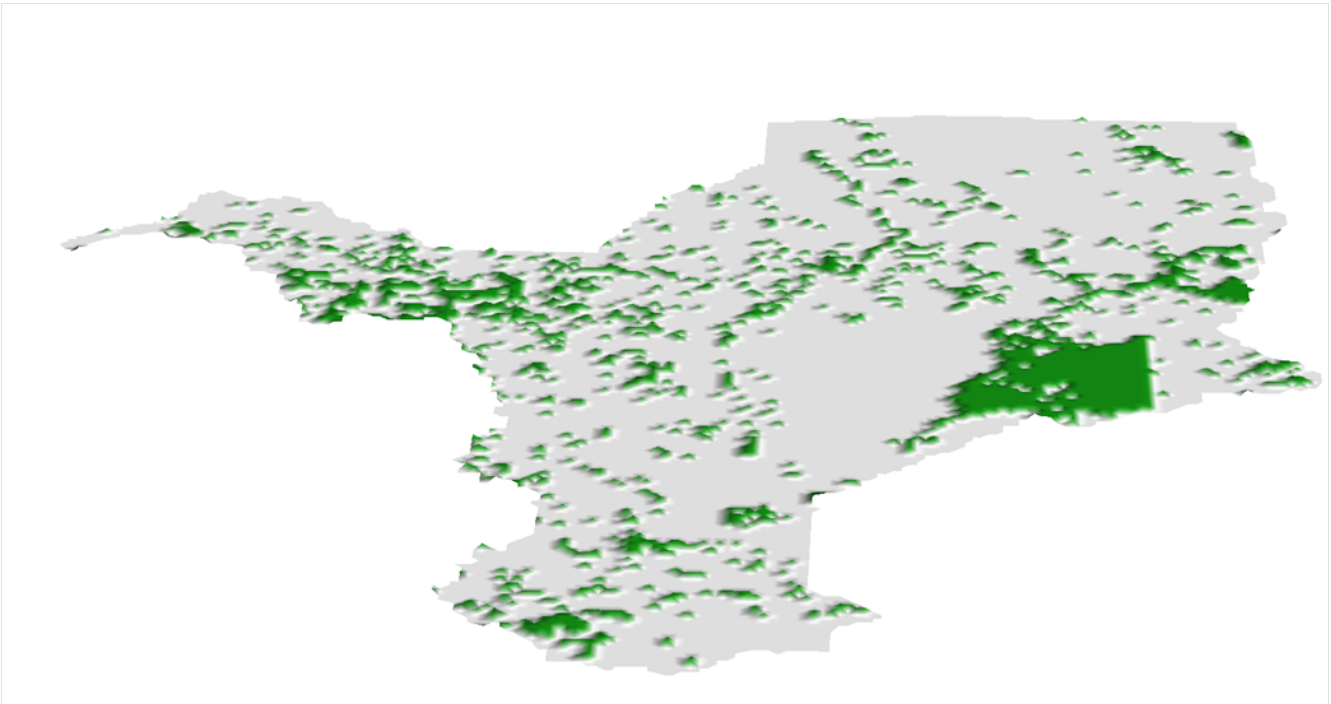
Query results are below:
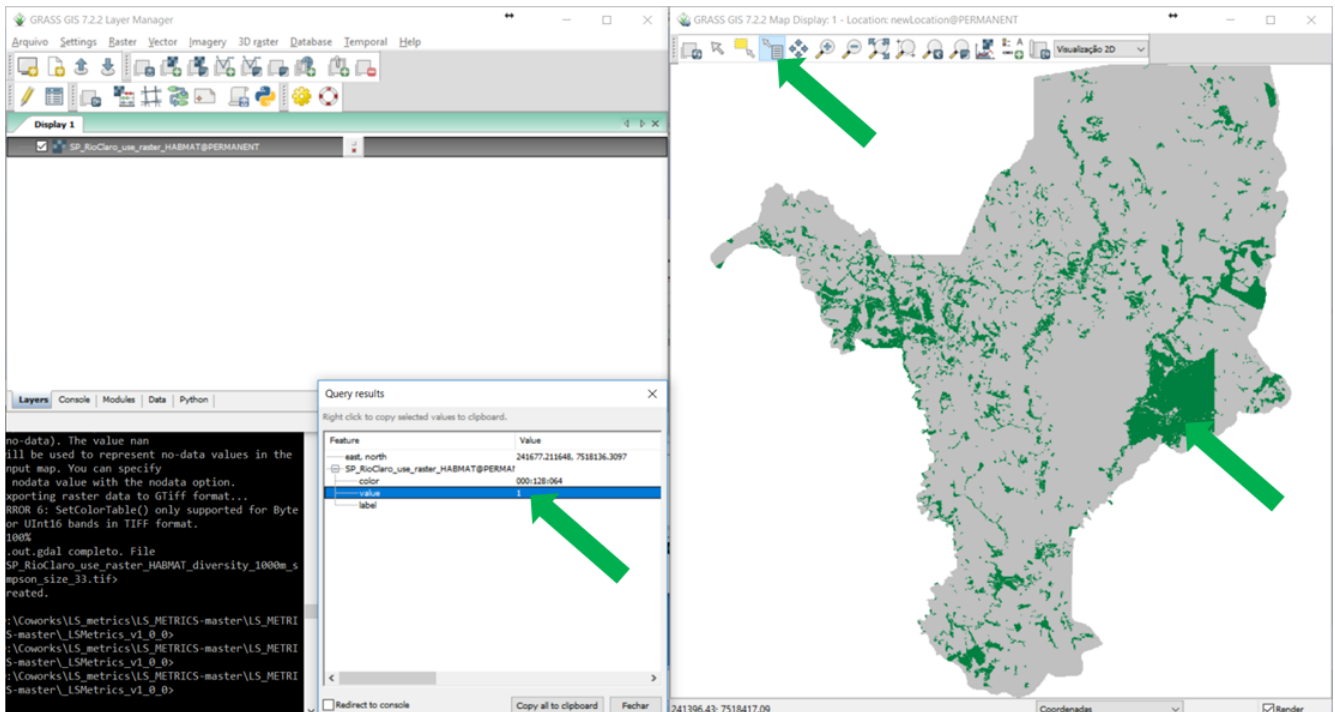
Patch size map

*patch***AreaHA**

Summed area of one or more fragments connected by structural corridors (including the area of the corridors connecting them); if there are no fragments connected to the fragment in question, the value of this metric is equal to "fragment size";
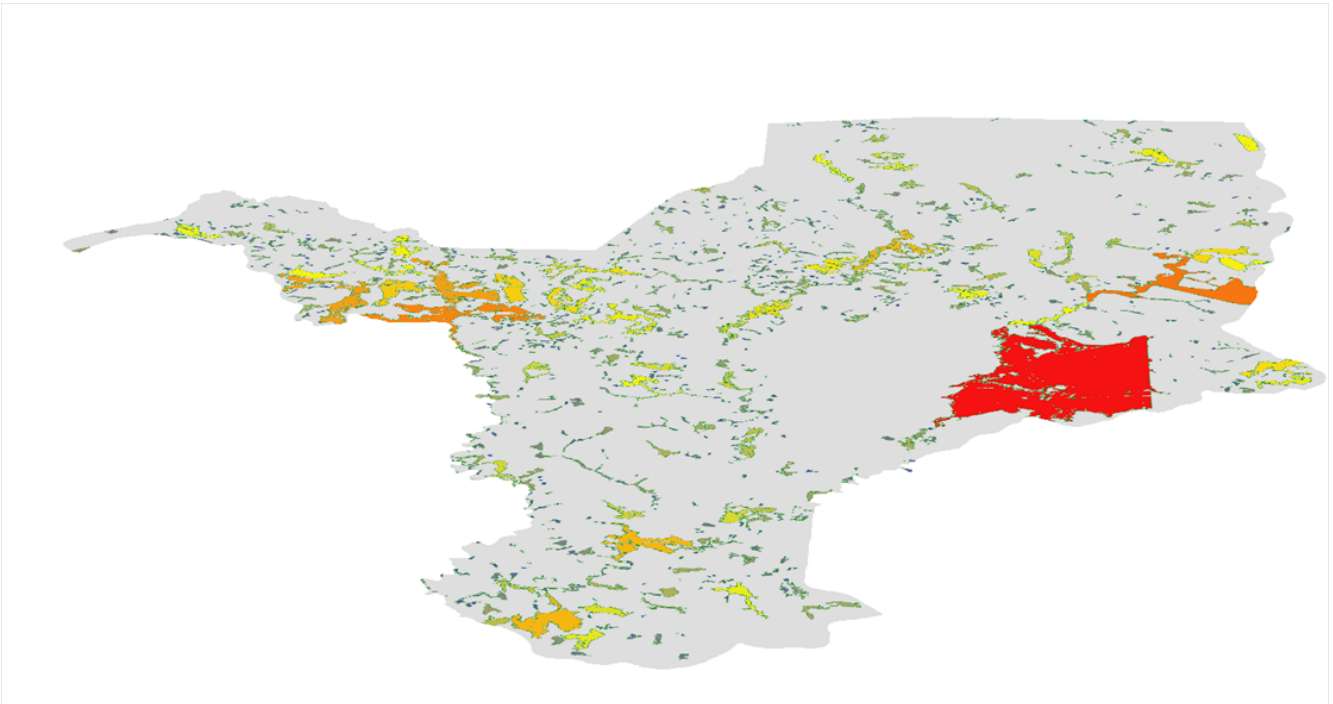
See query results below:
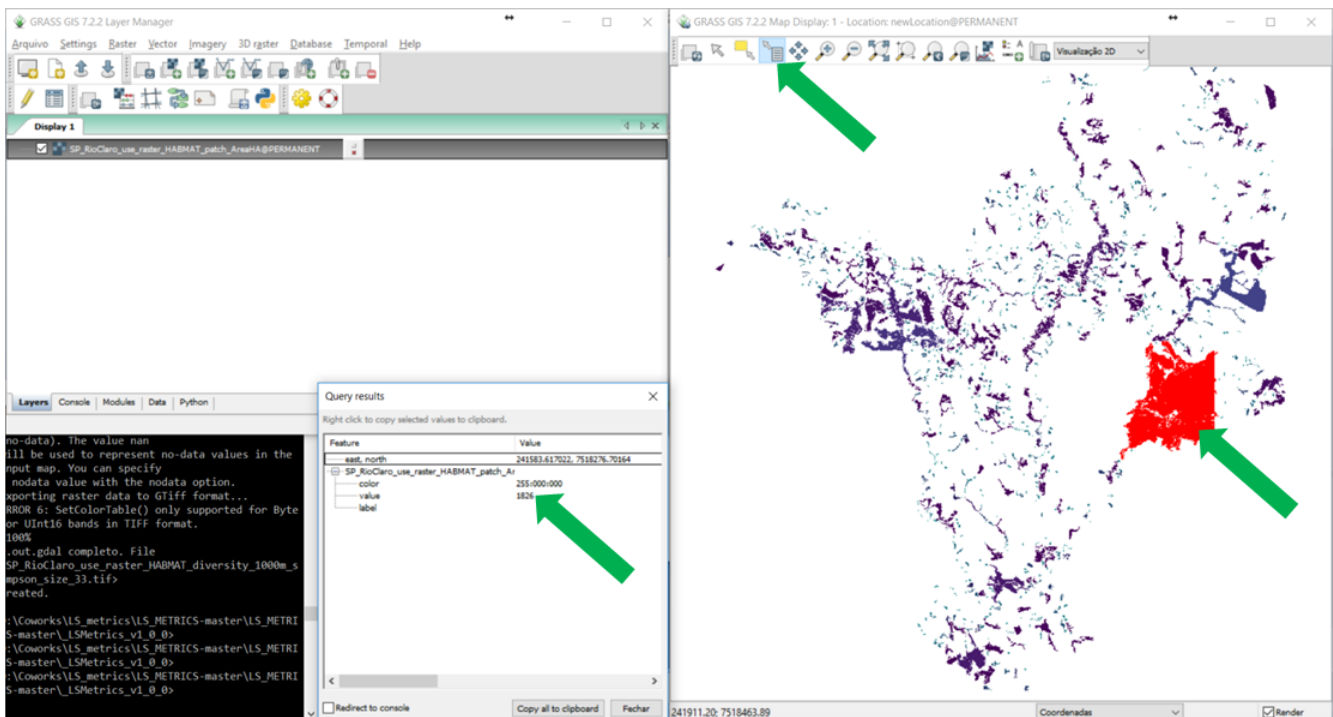
Fragment size map

*0060m*fragment__AreaHA

Area (given in ha) of any structurally isolated fragment, of any size, or the area of a fragment connected to another fragment by a structural corridor. Structural corridors are identified as parts of fragments with a width smaller than two times the specified edge depth;
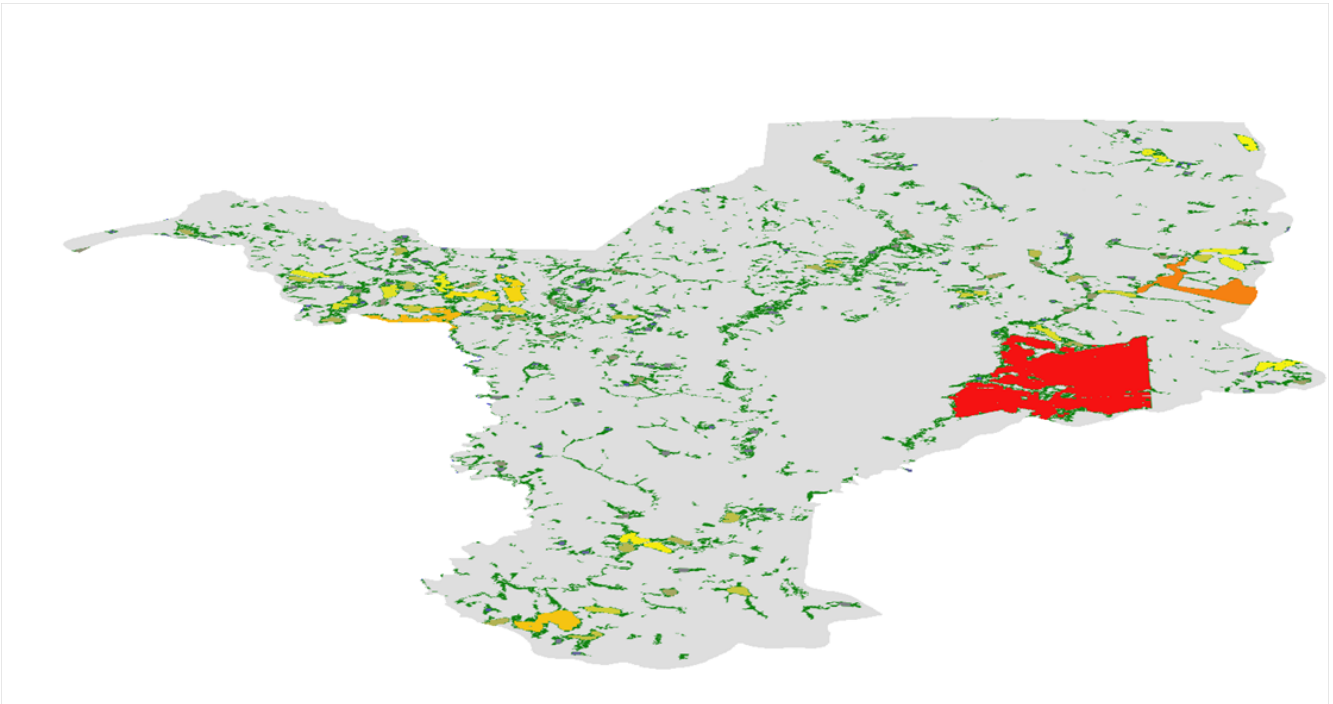
Query results are below:
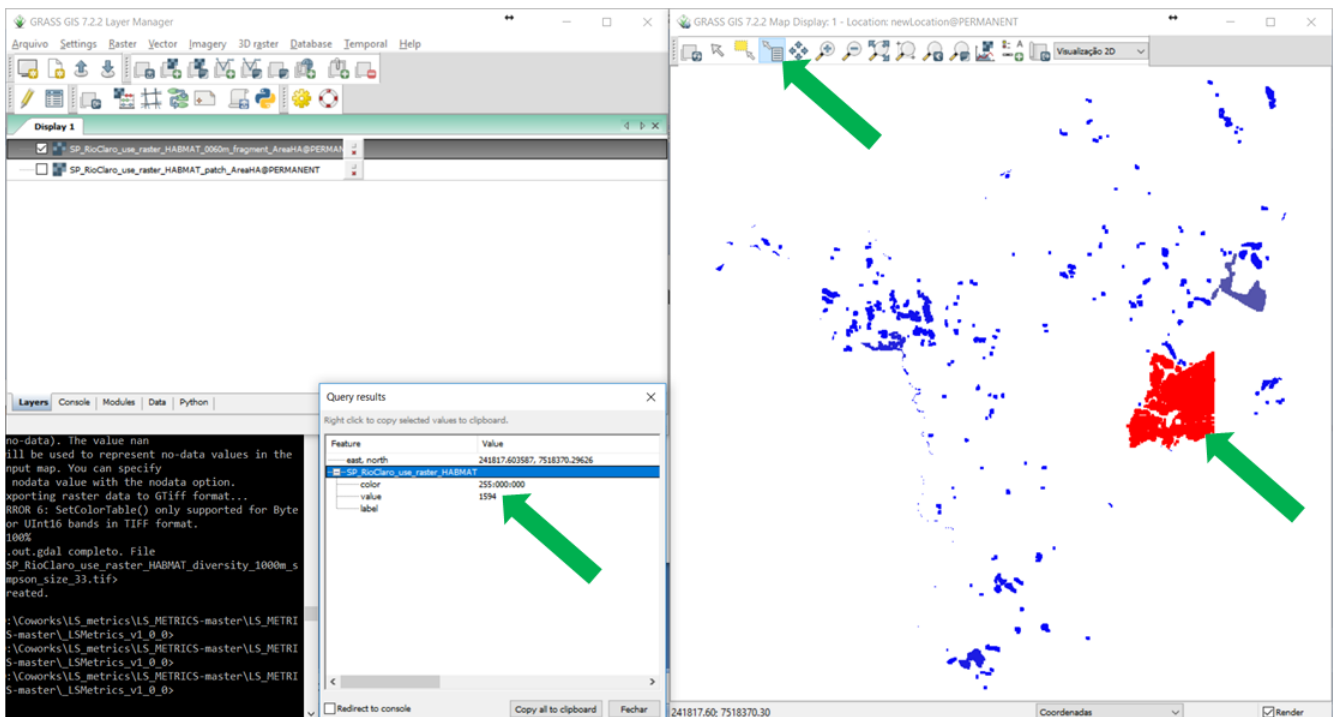
Structural connectivity

*0060m*structural_connectivity

Difference (given in ha) between the Patch size and the Fragment size metrics; when a patch has only one fragment, its structural connectivity will be zero.
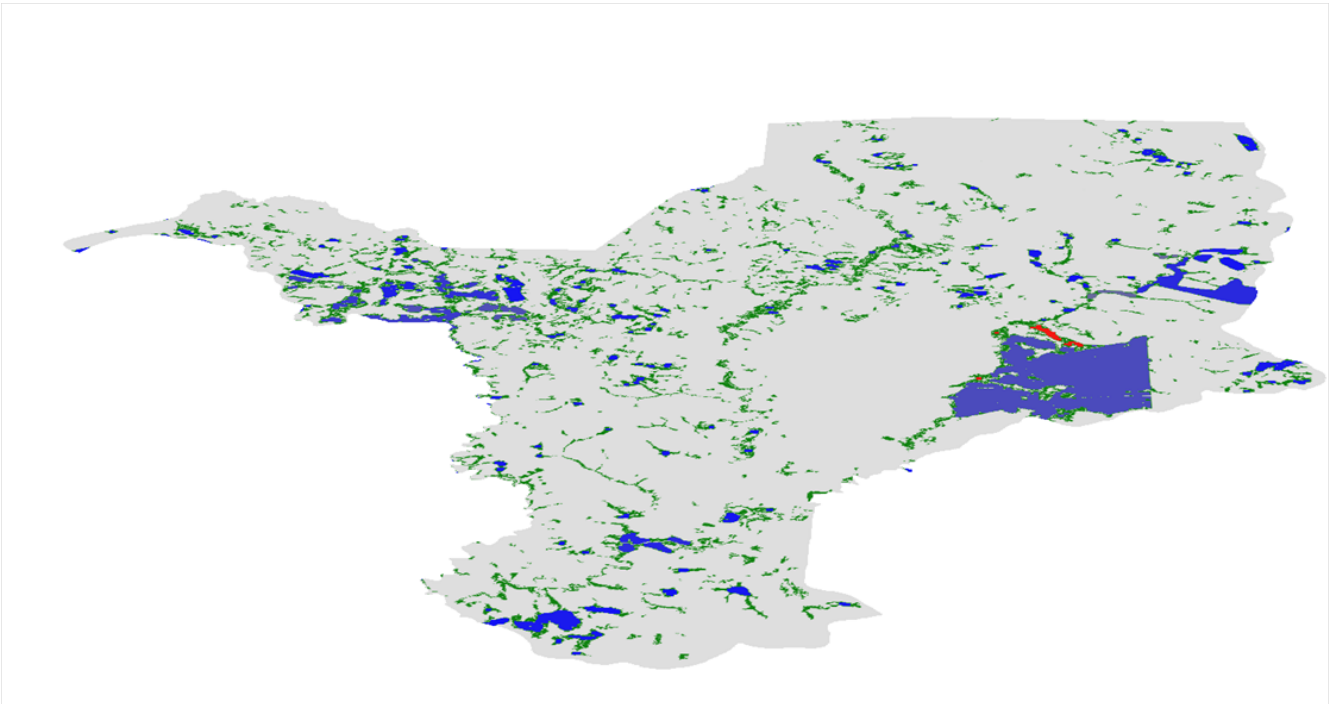
Query results are below:
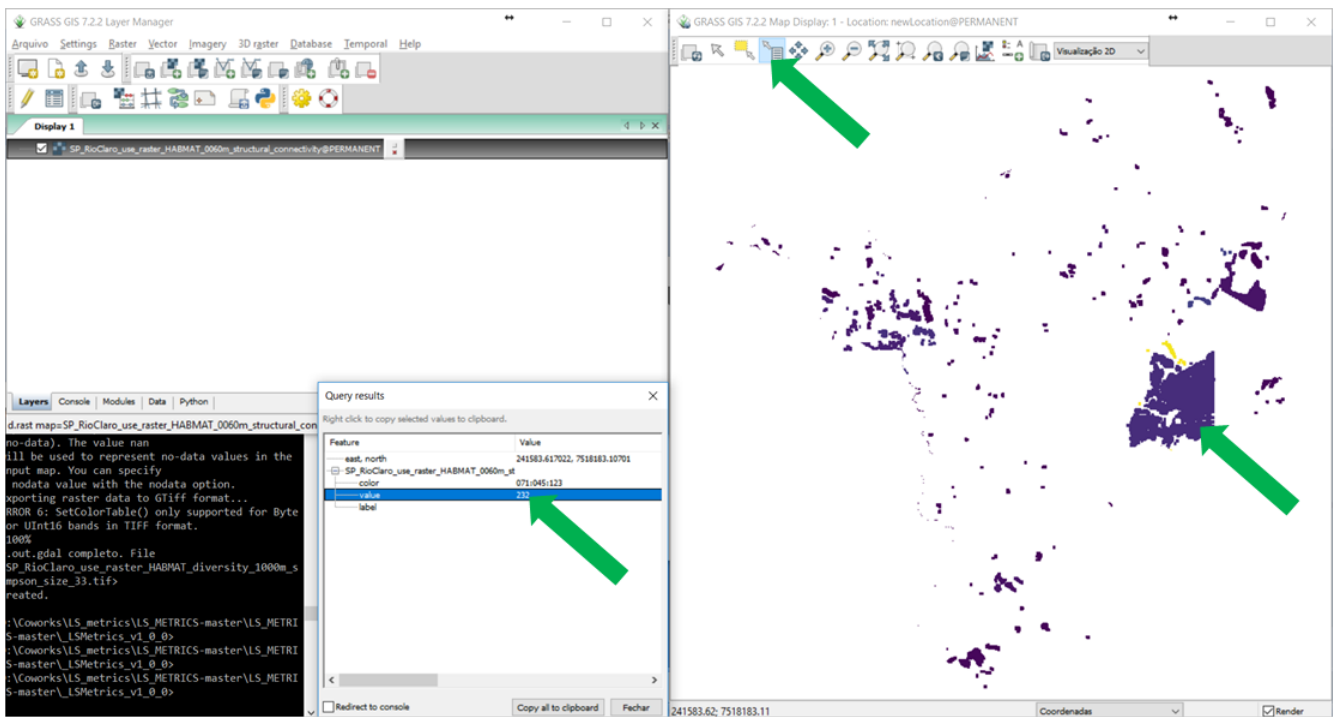
Proportion of habitat

*habitat*pct__1000m

Proportion of the target landscape classes considering a selected window size.
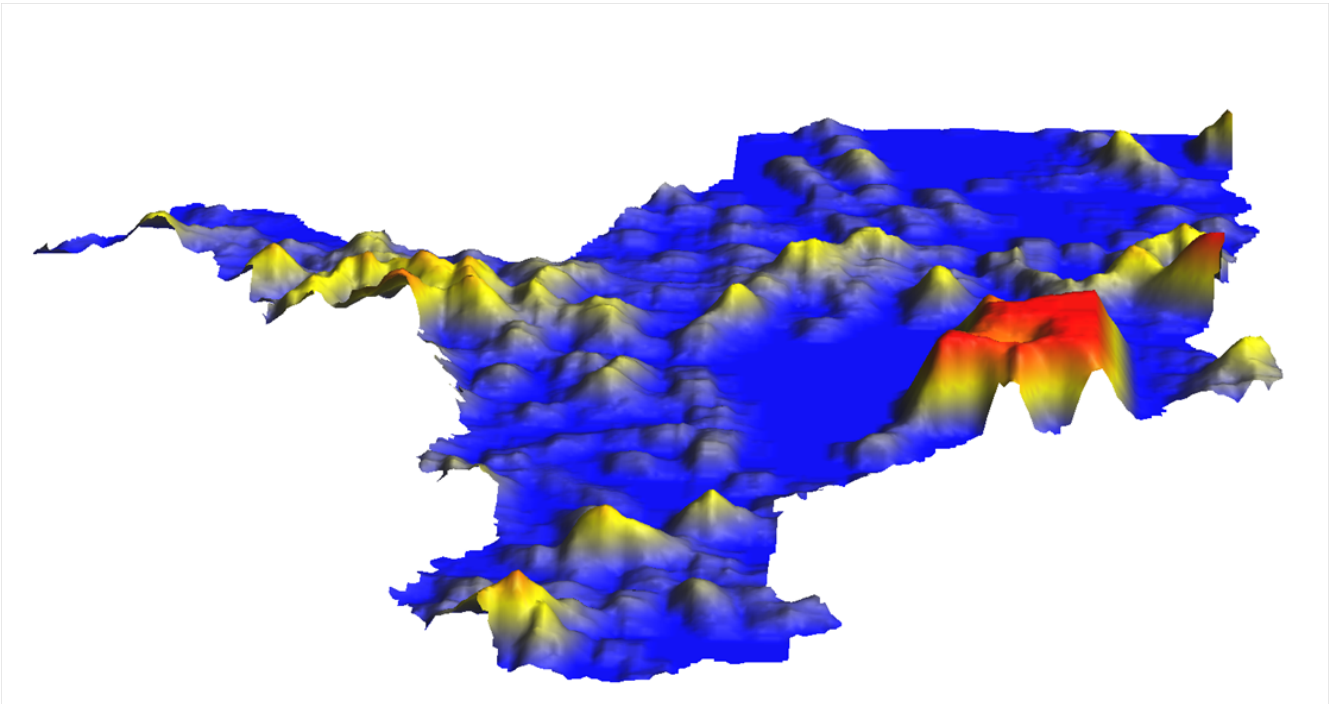
Query results are below:
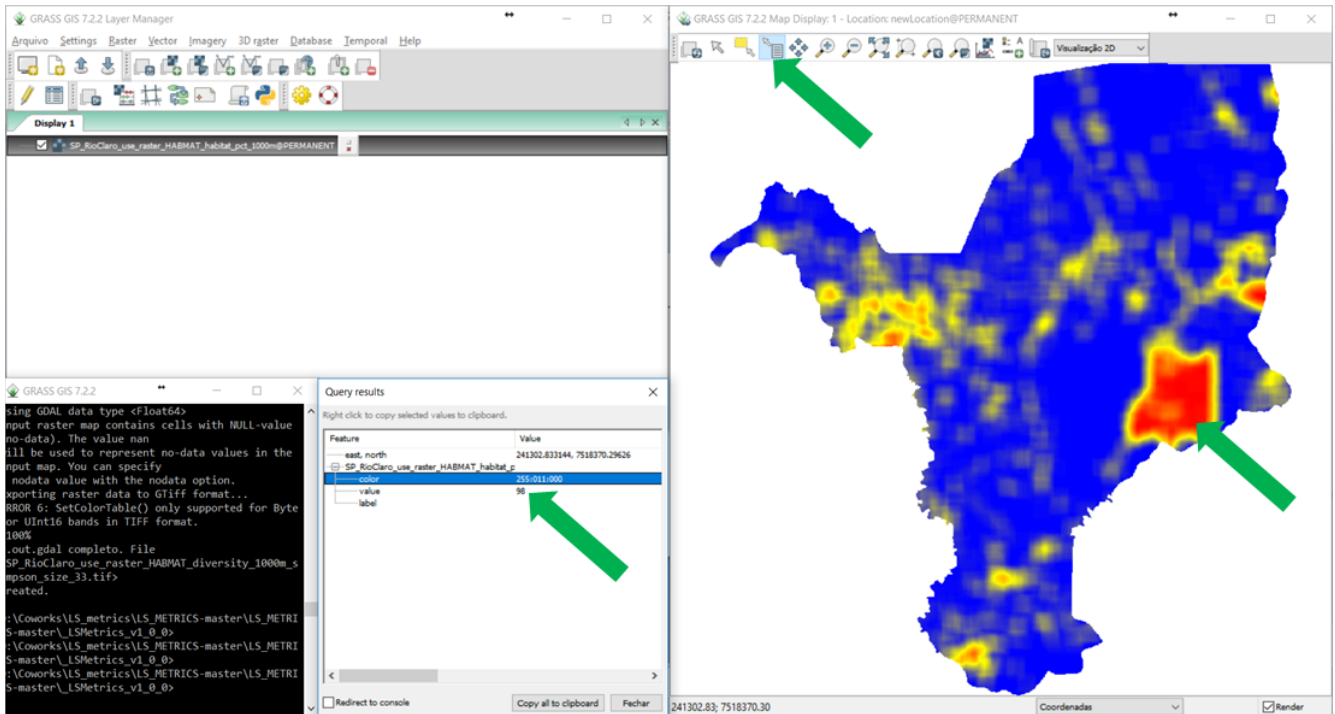
How to choose the window size? The user must decide which window size will be used to calculate metrics. It corresponds to search extent from each pixel where the calculations will be applied. It can be based on the extent of landscape perception of the target species, process or groups analyzed. It is given in meters.

Metrics of functional connectivity

Functional connectivity

The amount of area functionally connected to a habitat patch, given a gap crossing capability of a species or group of interest. First, a buffer of interest equal to half of the width (in meters) that a species is able to cross is created. Then, the habitat patches that are close enough ara grouped within the same buffer. We then sum the area (ha) of all this grouped patches. We refer to these groups of nearby habitat patches as habitat **clumps**. Finally, to obtain the strict functional connectivity, we calculate the difference between each clump size (ha) and patch size (ha);
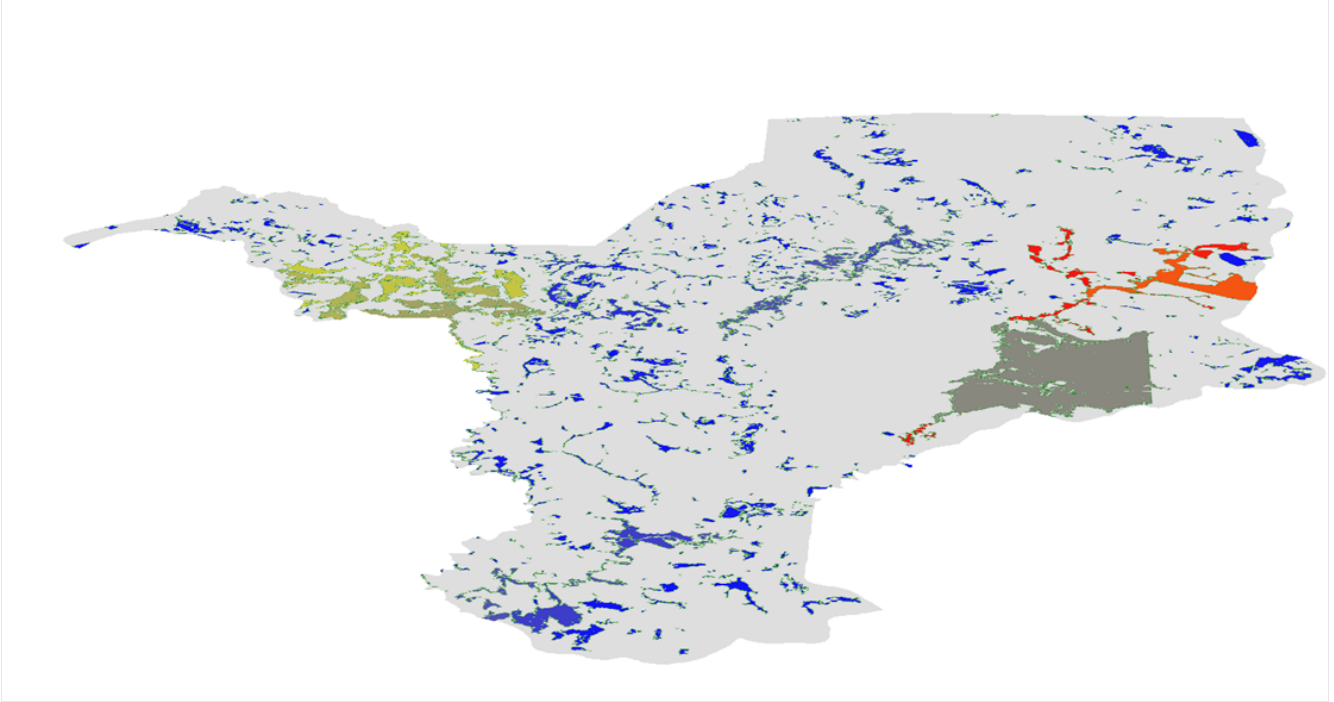
Query results are below:
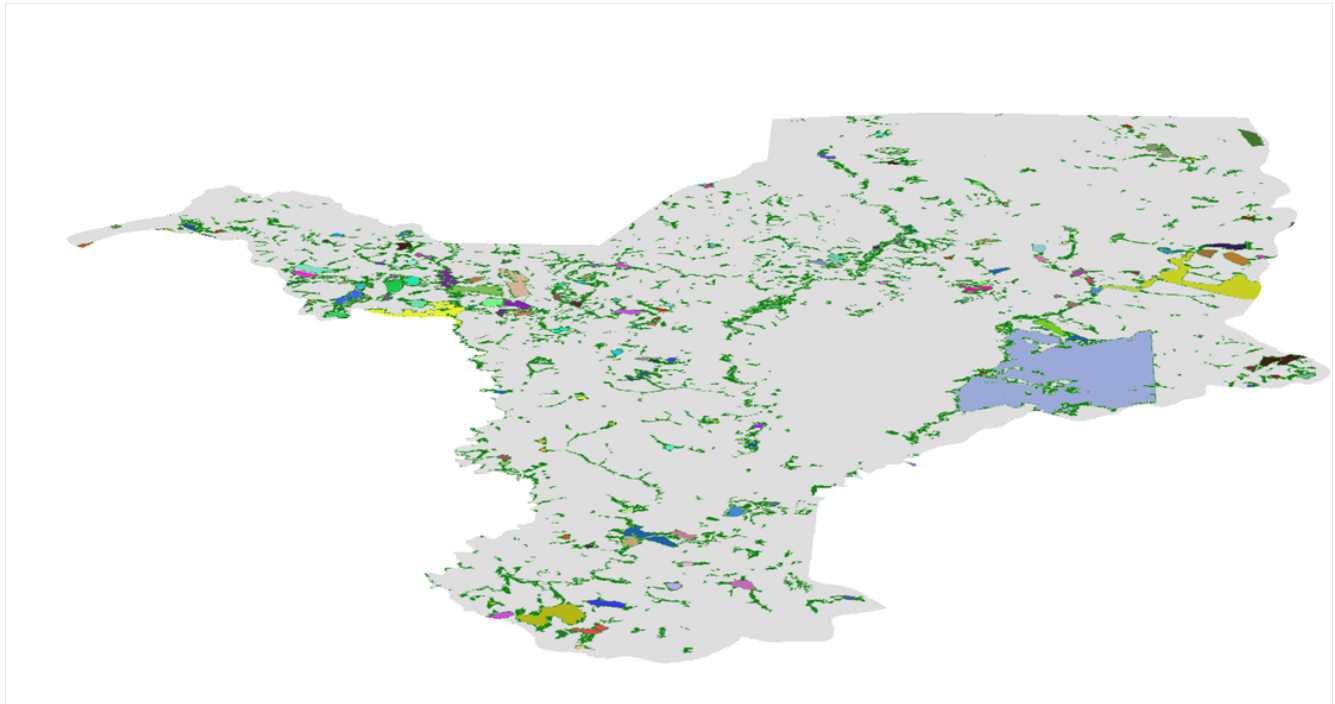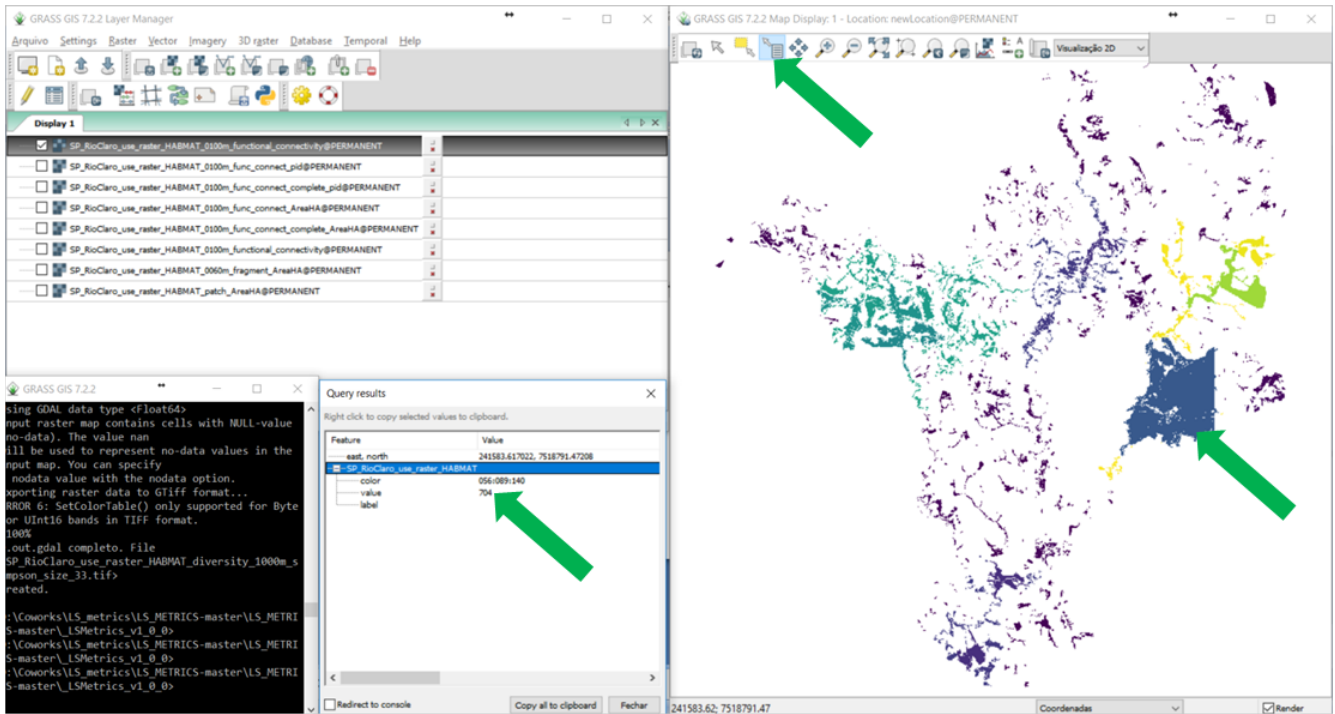
FIDs Query results are below:
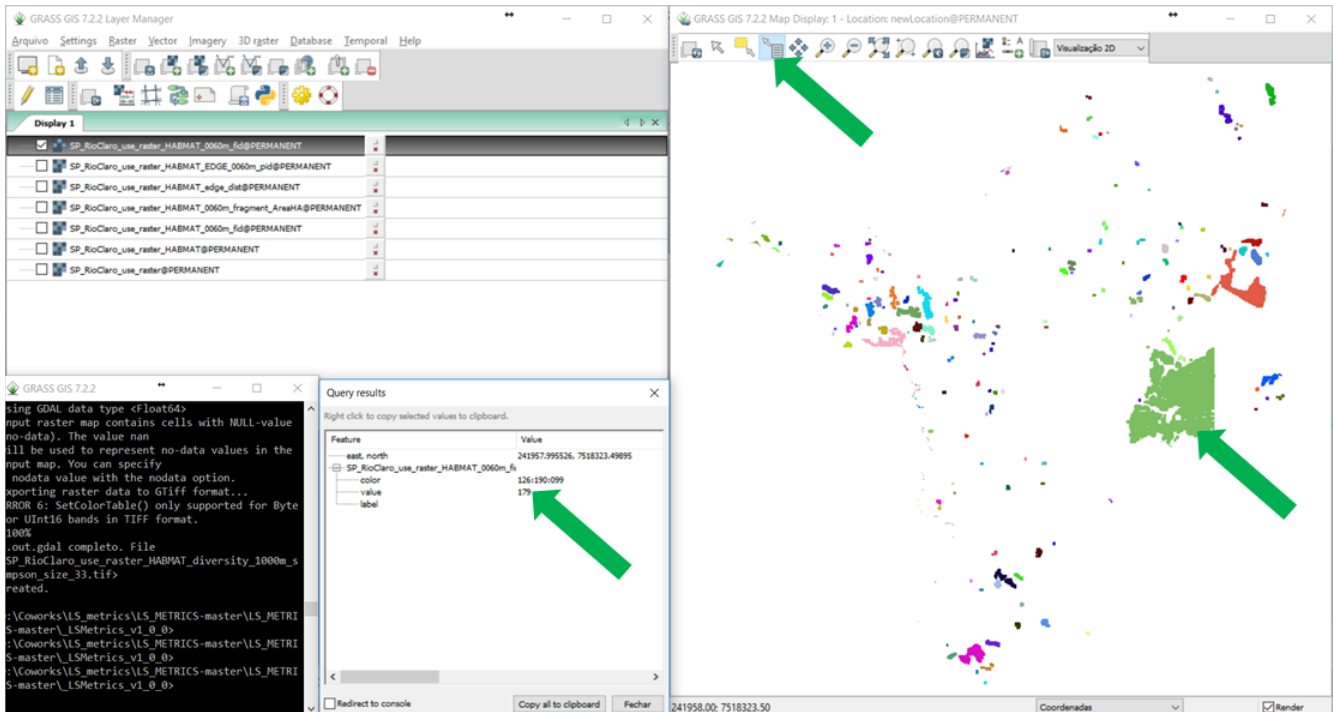
Functionally connected area

Represents the total amount of habitat area (in hectares) functionally available for an organism located in a patch, given a gap crossing capability of the organism. This is calculated by generating a buffer of size equal to half of the gap crossing capacity of the organism, around all patches, grouping all habitat patches close enough in the same clusters of patches, and summing up the area of all the grouped patches.
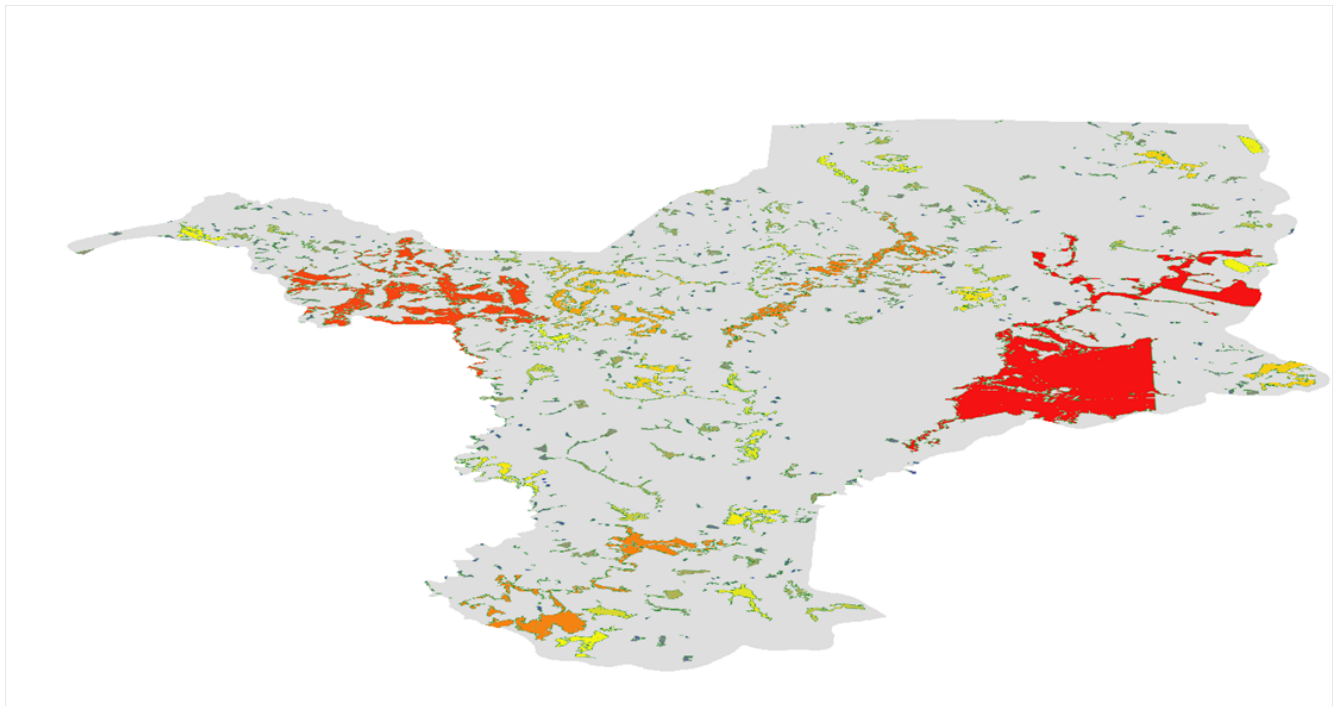
Query results are below:
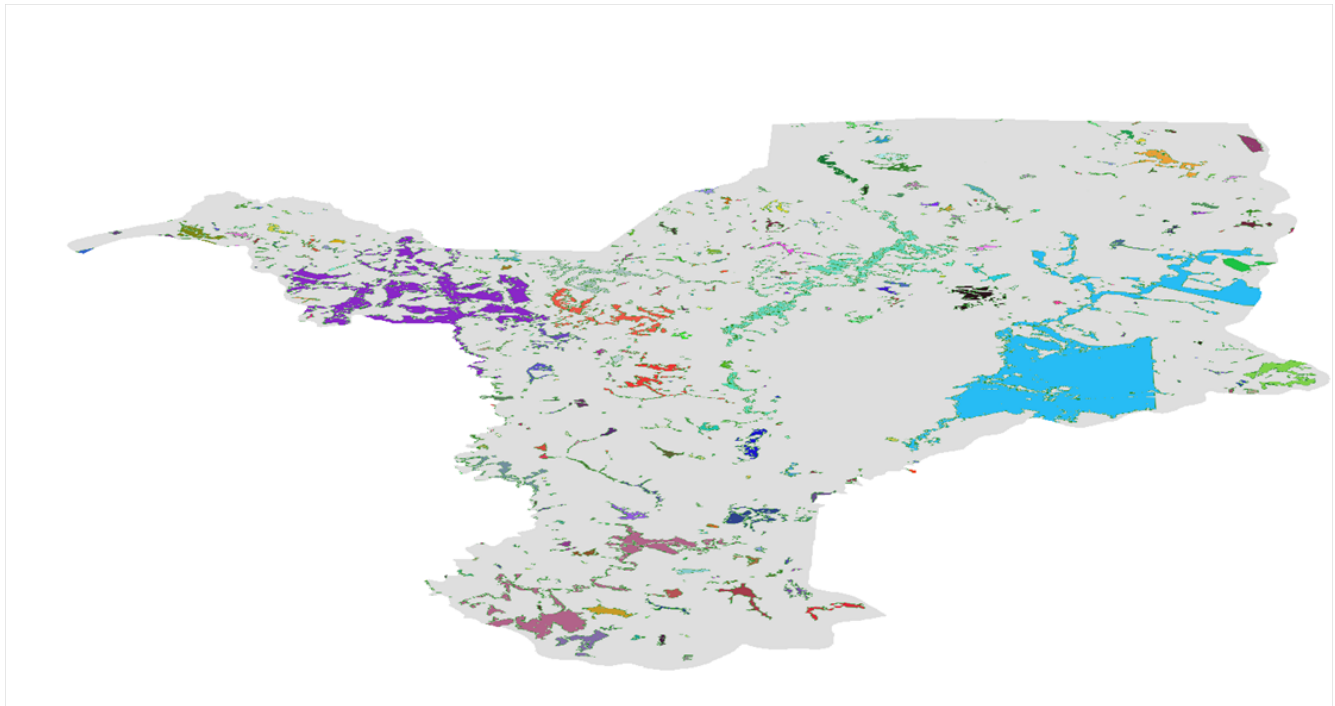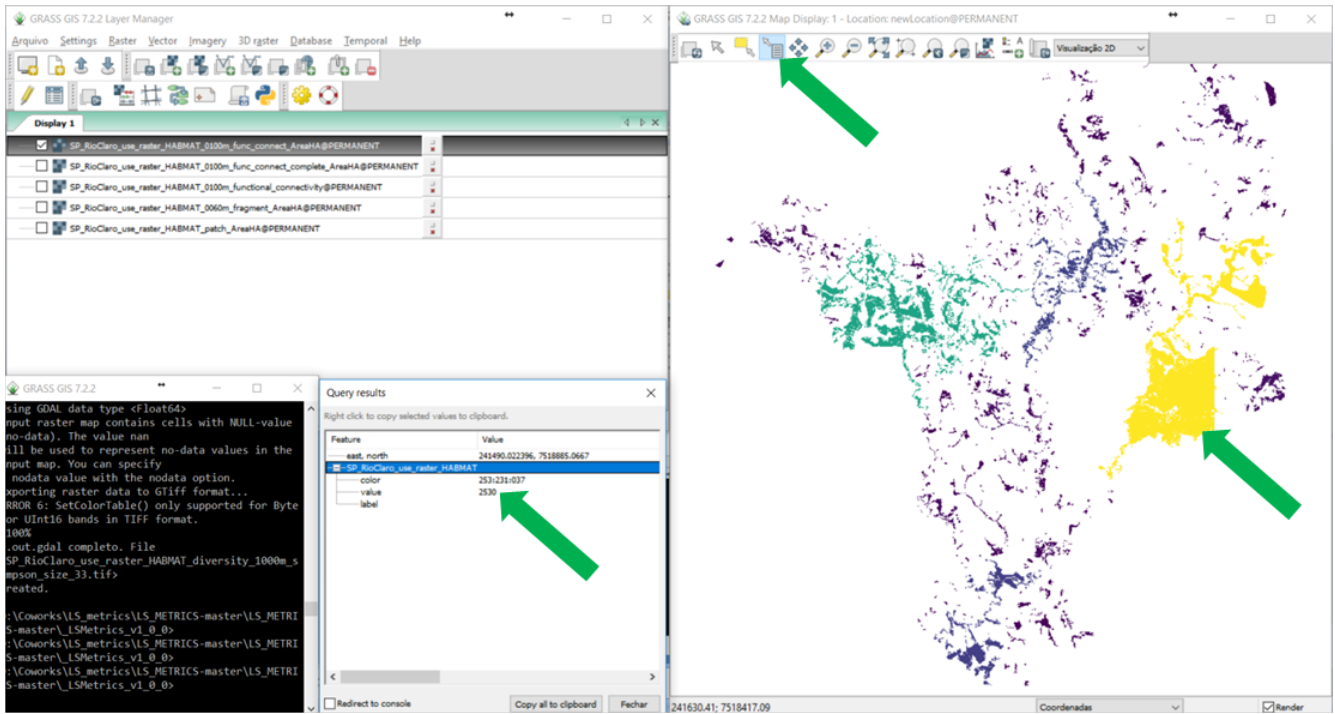
PIDs for Functionally connected area   Query results are below:
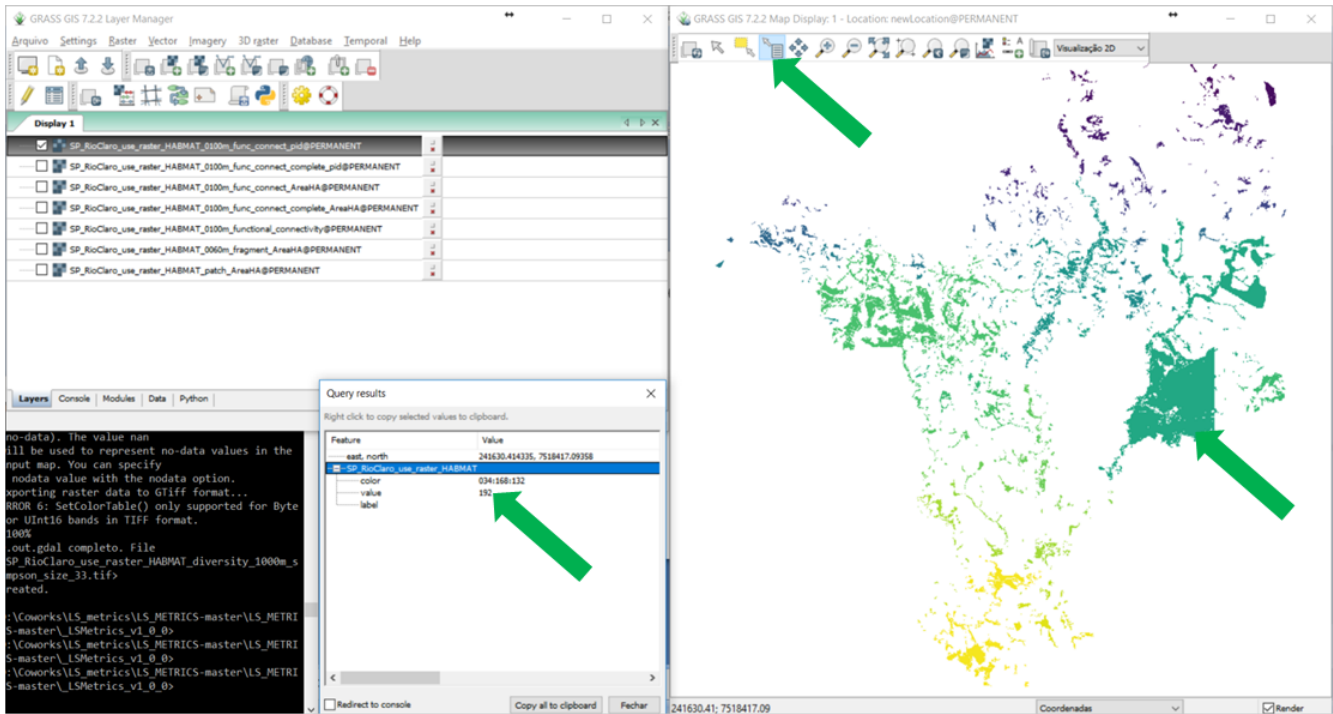
Complete functional connected area

The total amount of habitat functionally available for any species, given a gap crossing capability. We do all the steps for the "Functional connectivity" calculation, but do not subtract the patch size from the clump size.

*func*connect_complete_AreaHA

Query results are below:
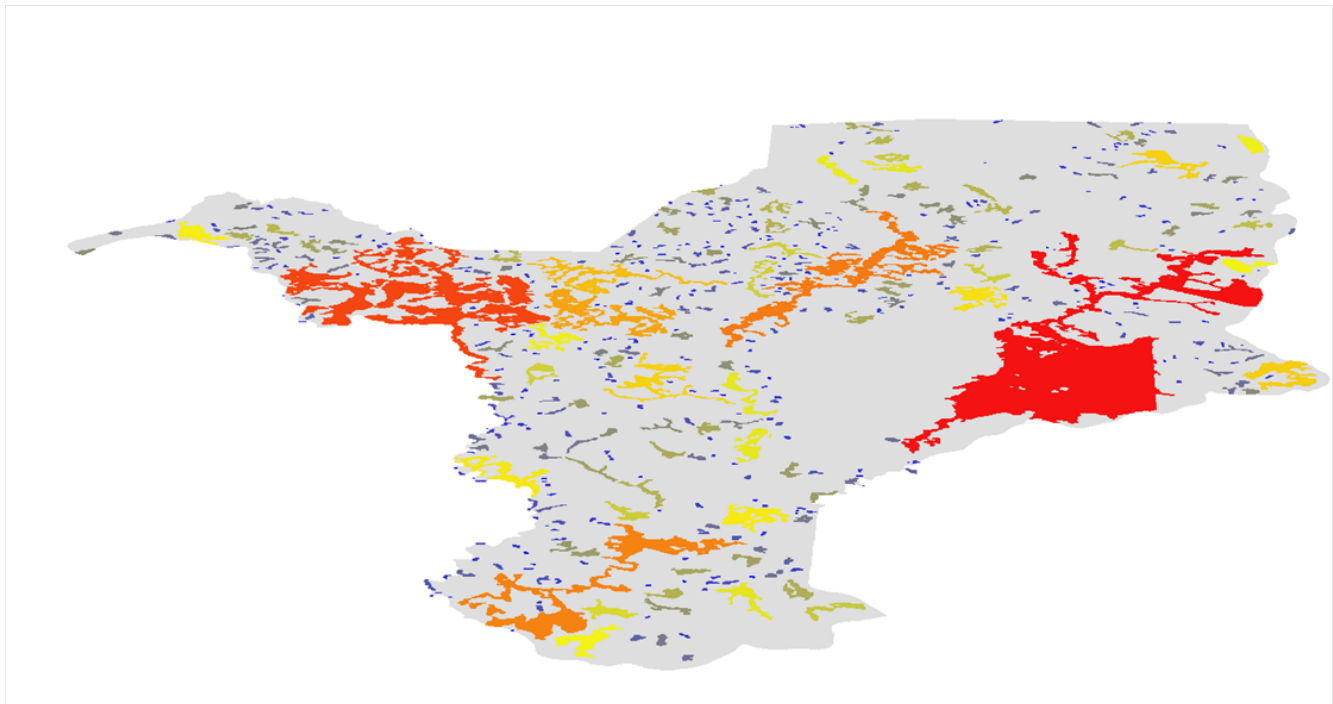
Query results are below:
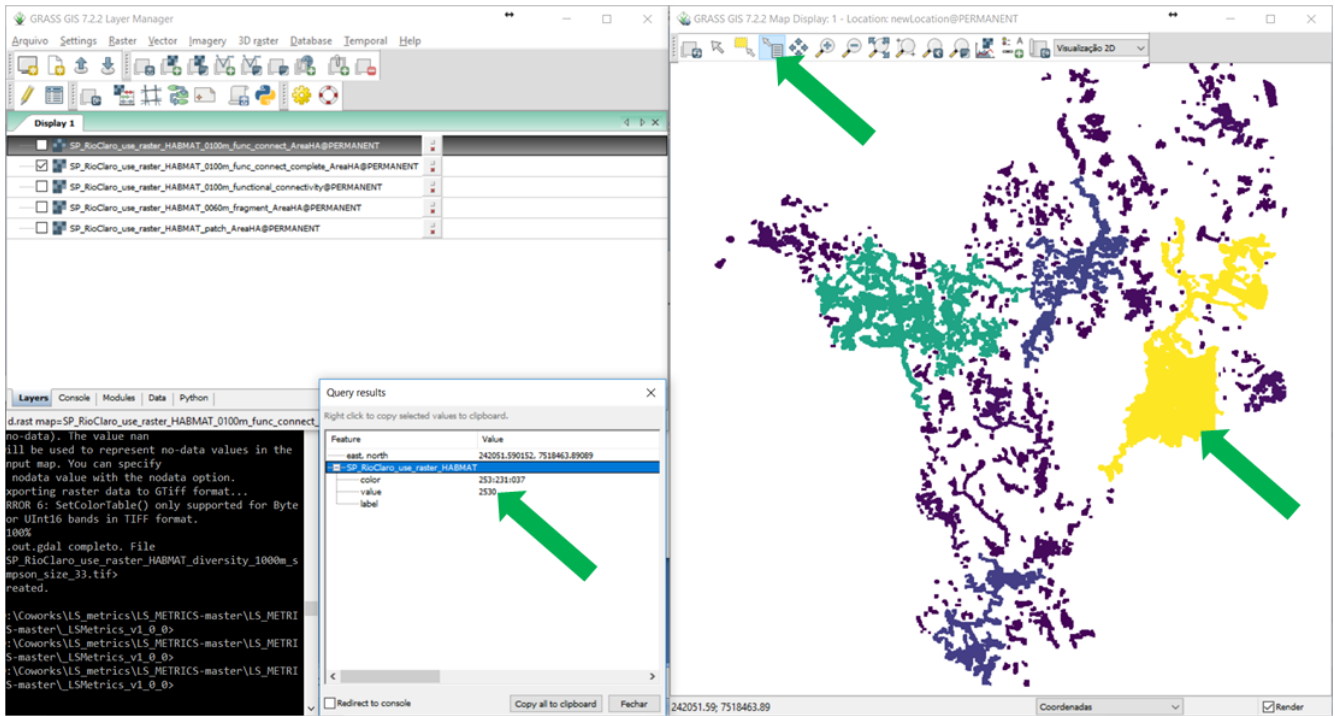
PIDs of complete functional connected area *0100*func_connect_complete_pid
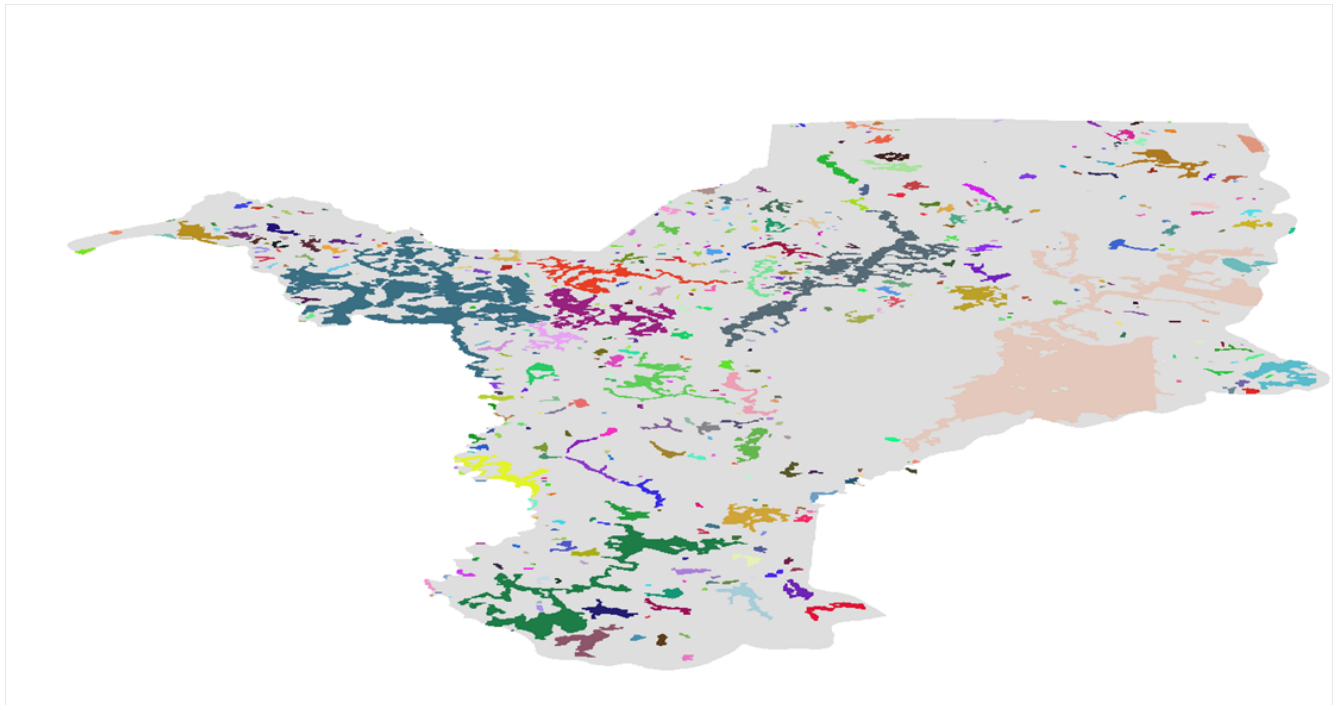
Query results are below:
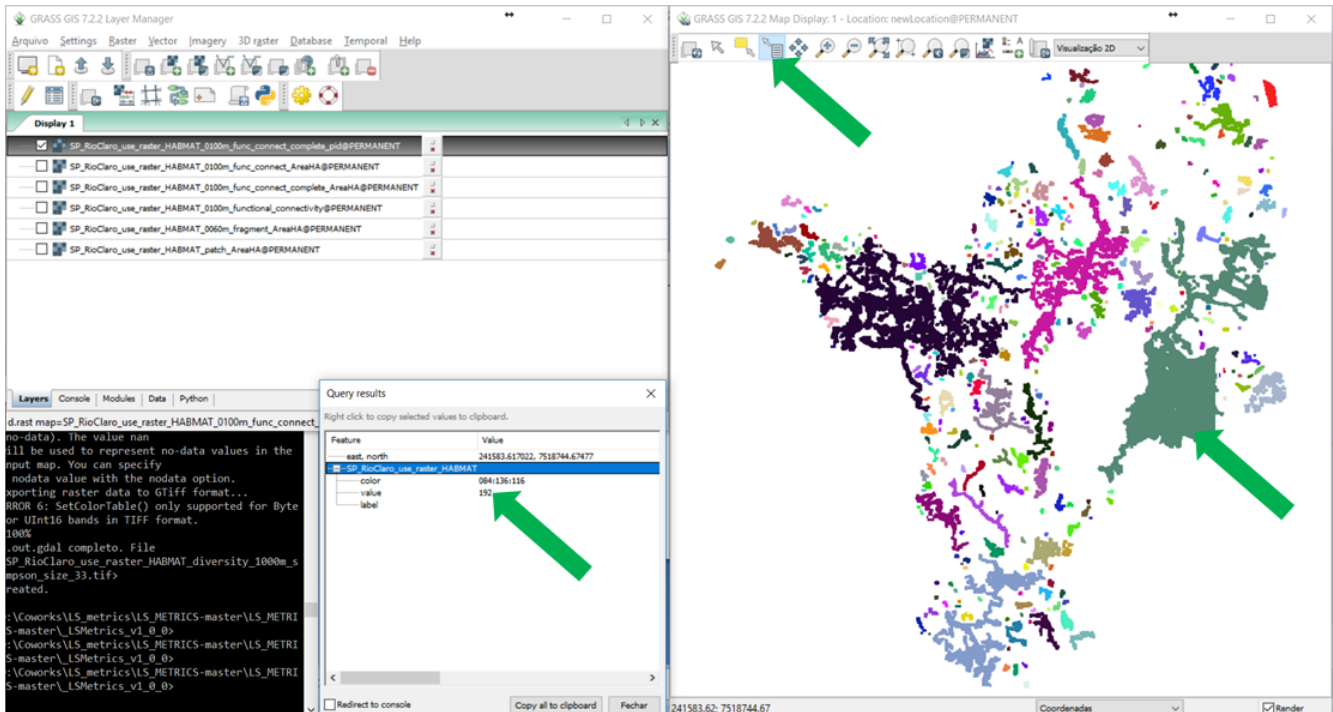
Metrics based on edges

Edge depths In order to run metrics for edge, the user must select a value for edge depths. This parameter is a proxy for investigating the impact of edge influence on the different pixels. It estimates the distance of edge influence and should be carefully thought a priori by the user, since it will be used to calculate the output metrics. It is set in meters, and as larger the value, larger the edge influence and extent through landscape.

See the charts and brief explanation of each metric below:

Map of distance from edges

The output value of each pixel will represent the distance of this pixel to the nearest edge.
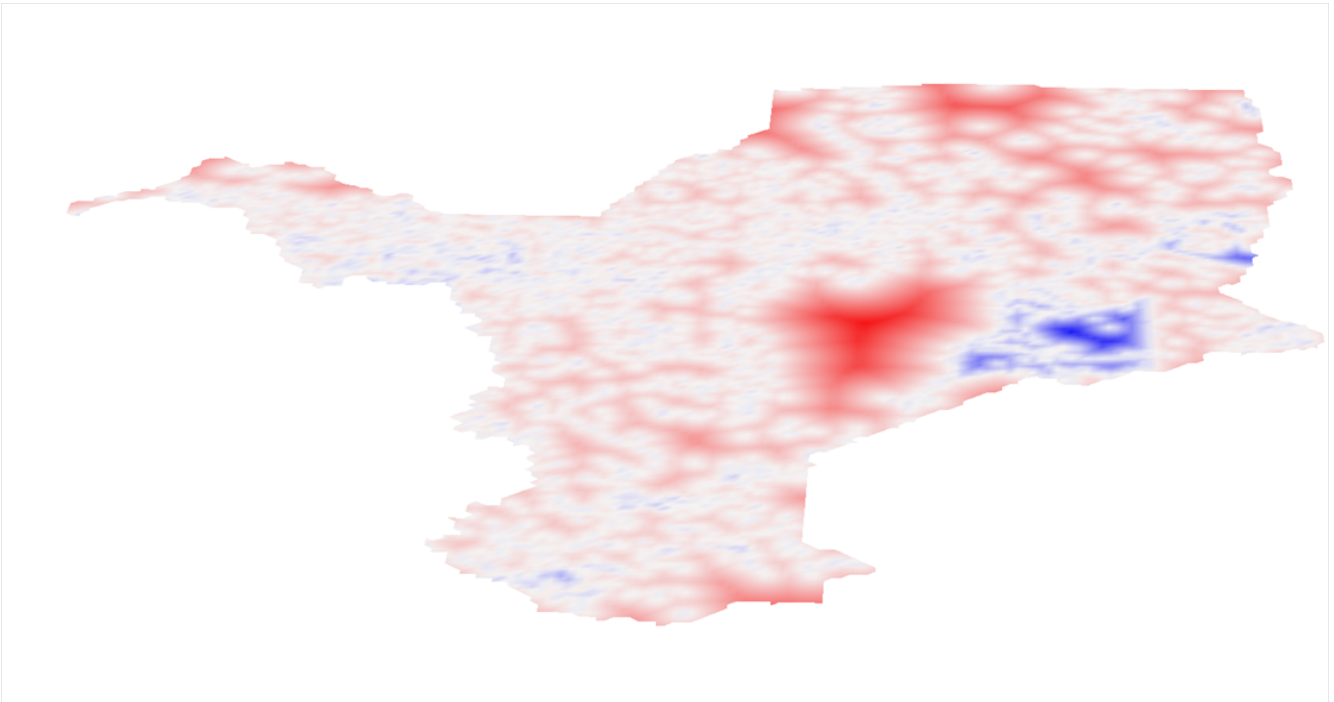
Query results are below:
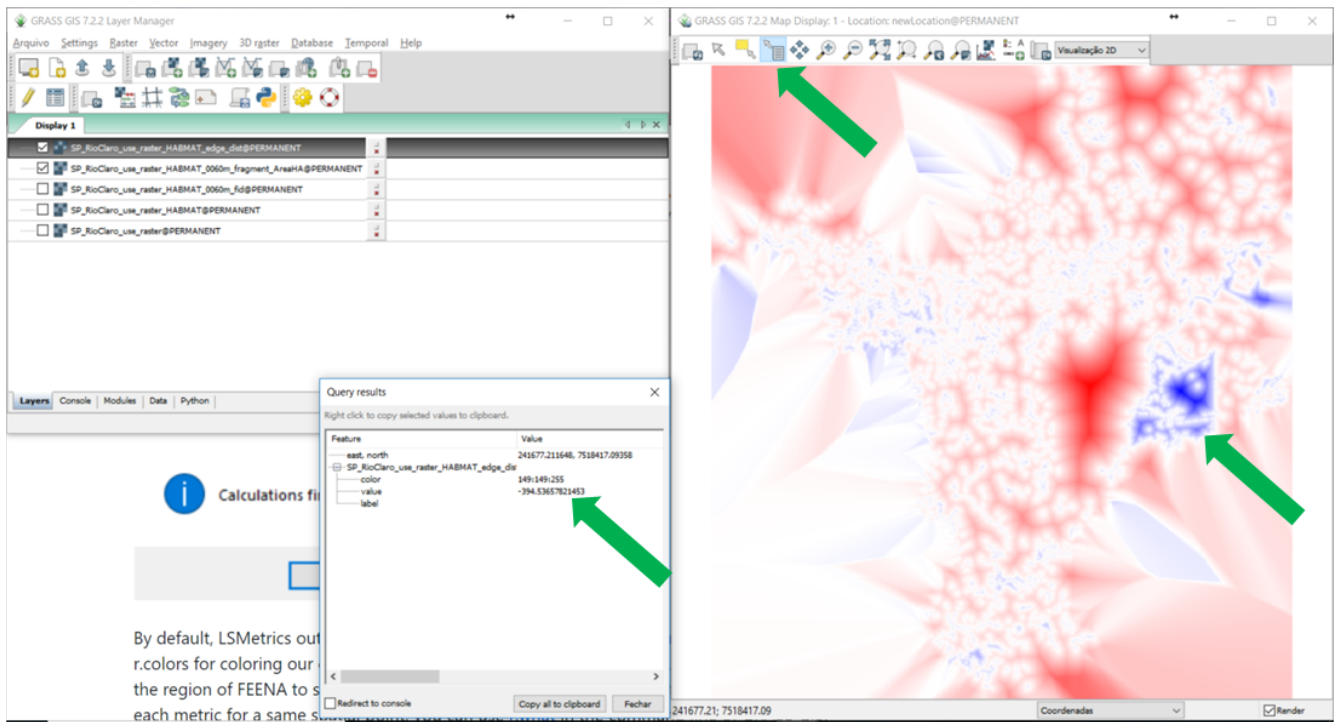
Classify edge/core/matrix (MECO)

Considering a specified Edge depth, this metric classifies the pixels as belonging to three categories: edge, core and matrix. How species really use habitat area would be represented by the core area, since many species have limitations on using edges or less quality areas than their preferred habitat.

Query results are below:

Binary maps for edge and core

Core binary maps In the core binary map, core are will be set as value "1".

Query results are below:

Edge binary maps In the edge binary maps, edge are will be set as value "1".

Query results are below:

Proportion of edge/core

Percentage of habitat and edge within a search radius (Window size parameter), given a specified edge depth (Edge depths parameter).

***HABMA*CORE_0060m_pct_1000m**
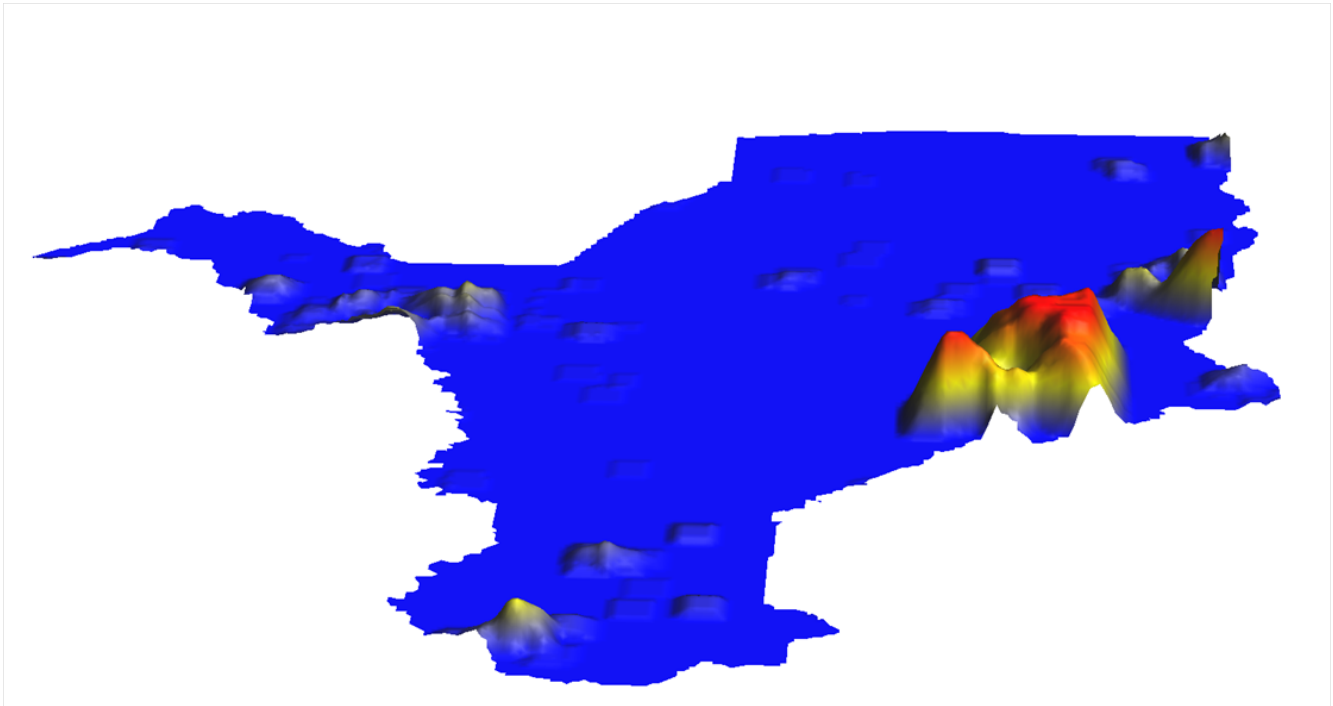
Query results are below:

*HABMAT*EDGE__0060m__pct__1000m
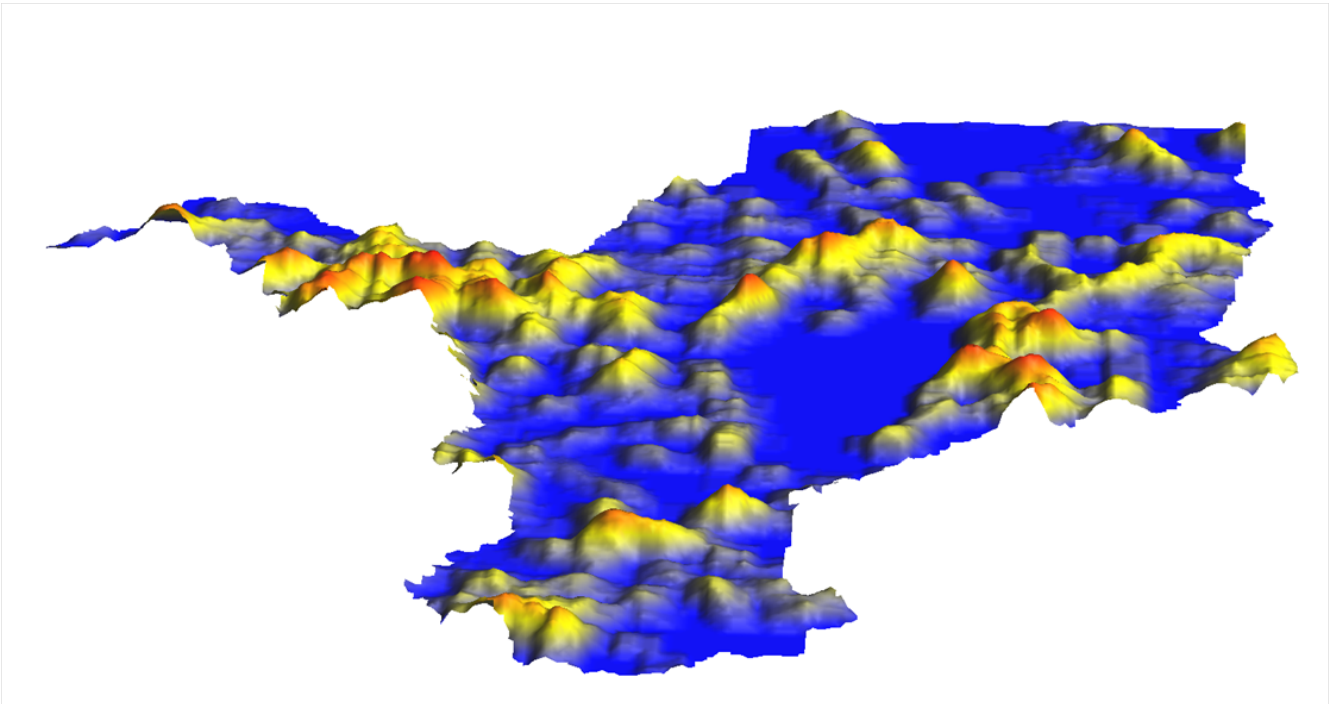
Query results are below:
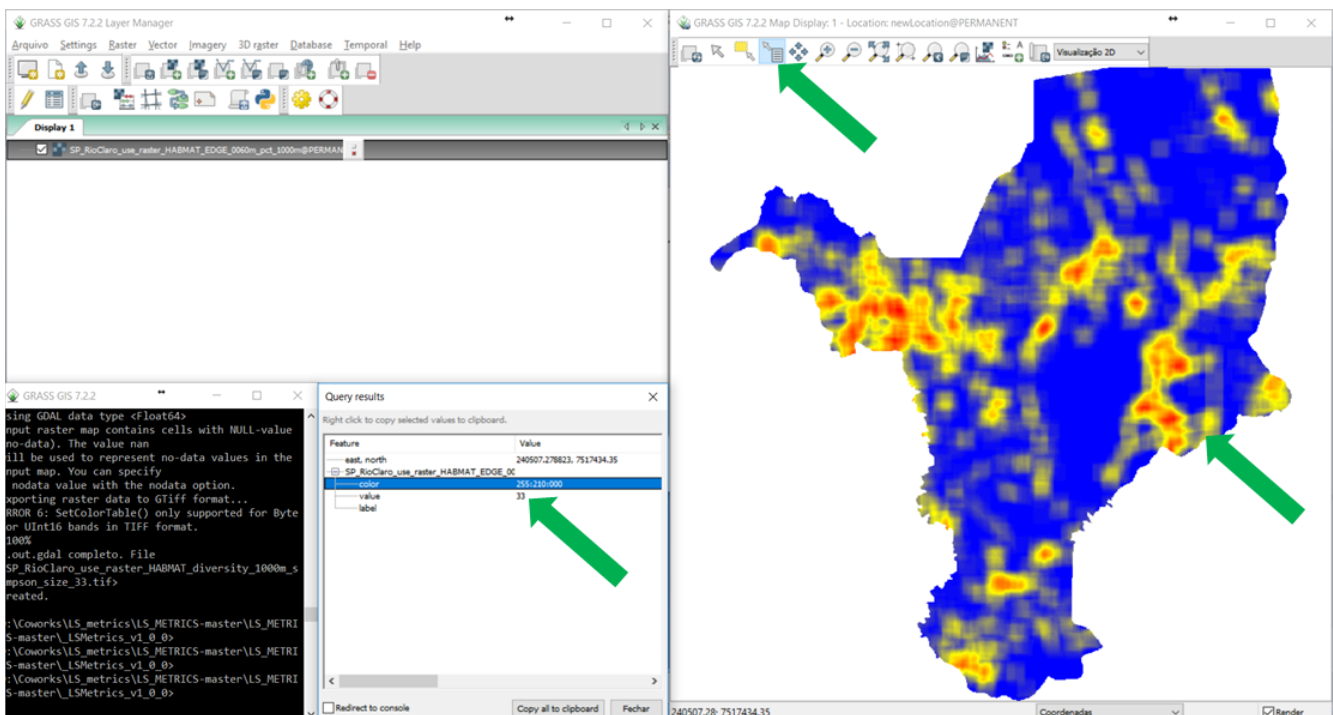
Calculate area of edge/core clumps?

Given edge and core areas were identified, contiguous cells are clumped into edge and core clumps (i.e., cells of edge and core that pertain to the same patch), and their areas are calculated (in hectares). Two maps are created for each one (edge/core) for each landscape: an edge (core) clump ID (edge or core PID) map, which sets a distinct integer number to each clump of edge (core) cells, and a clump size map, which sets the the area of those clumps; non-edge (non-core) cells are set to NULL in both.

$HABMAT$CORE__0060m__AreaHA

Query results are below:

$HABMAT$CORE__0060m__pid

Query results are below:

***HABMAT*EDGE__0060m__AreaHA**

Query results are below:

***HABMAT*EDGE_0060m_pid**

Query results are below:

Metrics of landscape diversity

LSMetrics calculates four metrics of Landscape Diversity. See the example outputs below:

Shannon

Given an extent value (or a list of values), the diversity around each pixel is calculated by computing the proportion pi of each land use inside a window of such an extent and calculating the Shannon index from it (Magurran, 2004). Therefore, the landscape diversity around a pixel depends on the number of different land use classes around it and on the amount of each class.
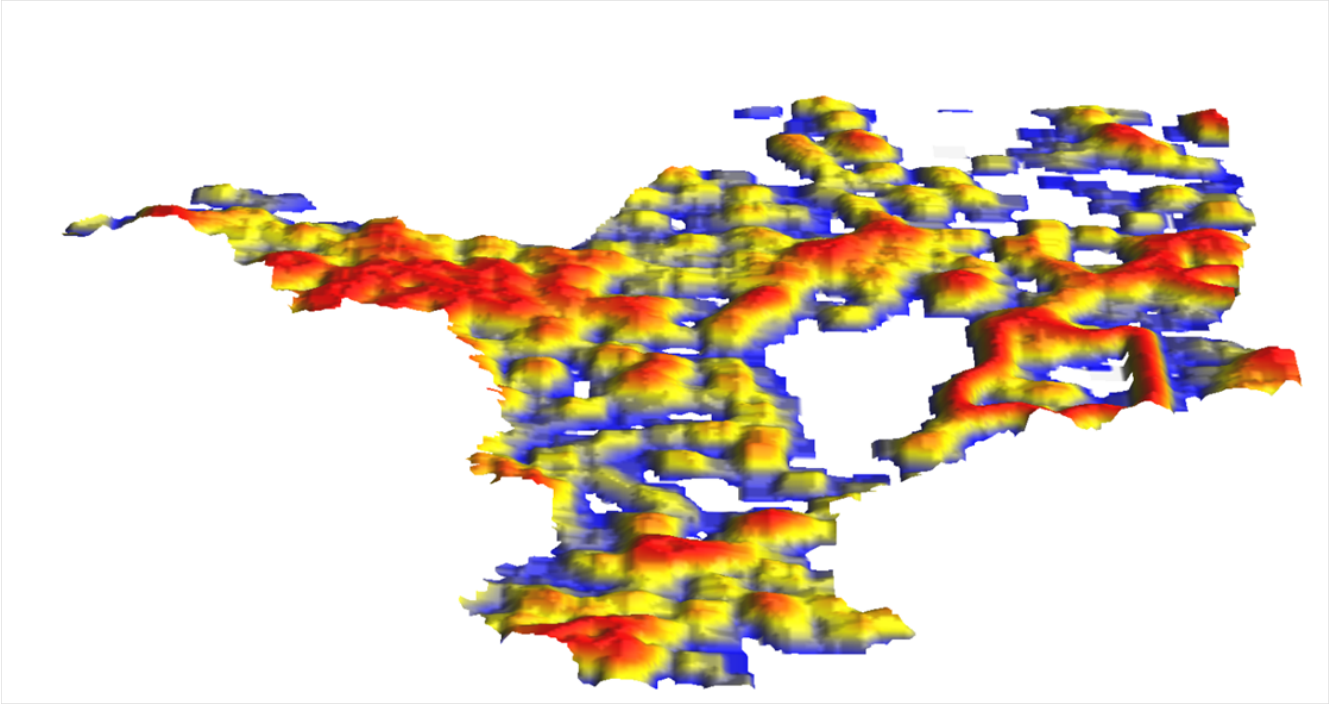
See query results below:
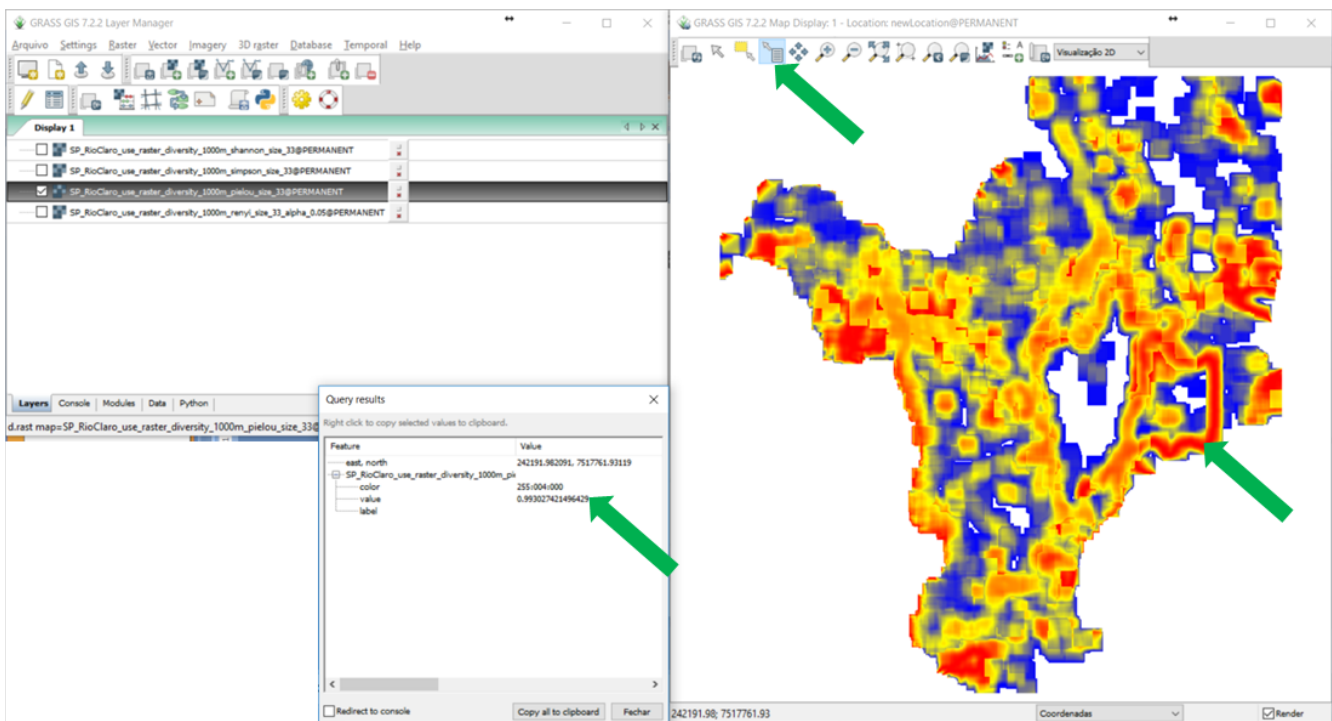
Simpson´s diversity (Simpson, 1949)

Diversity is based on the probability that two interacting individuals of a population belong to the same species. In our case, 2 patches belonging to the same land use class
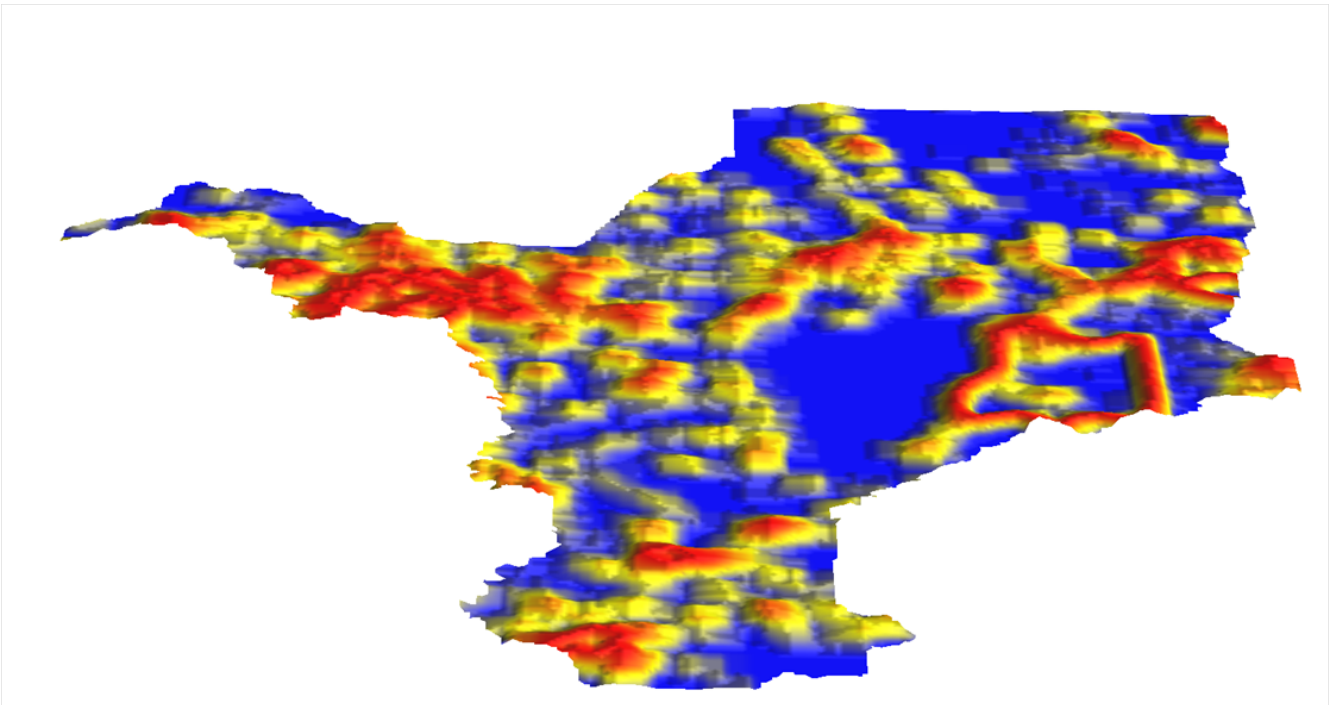
See query results below:

Pielou´s evenness (Pielou, 1966)
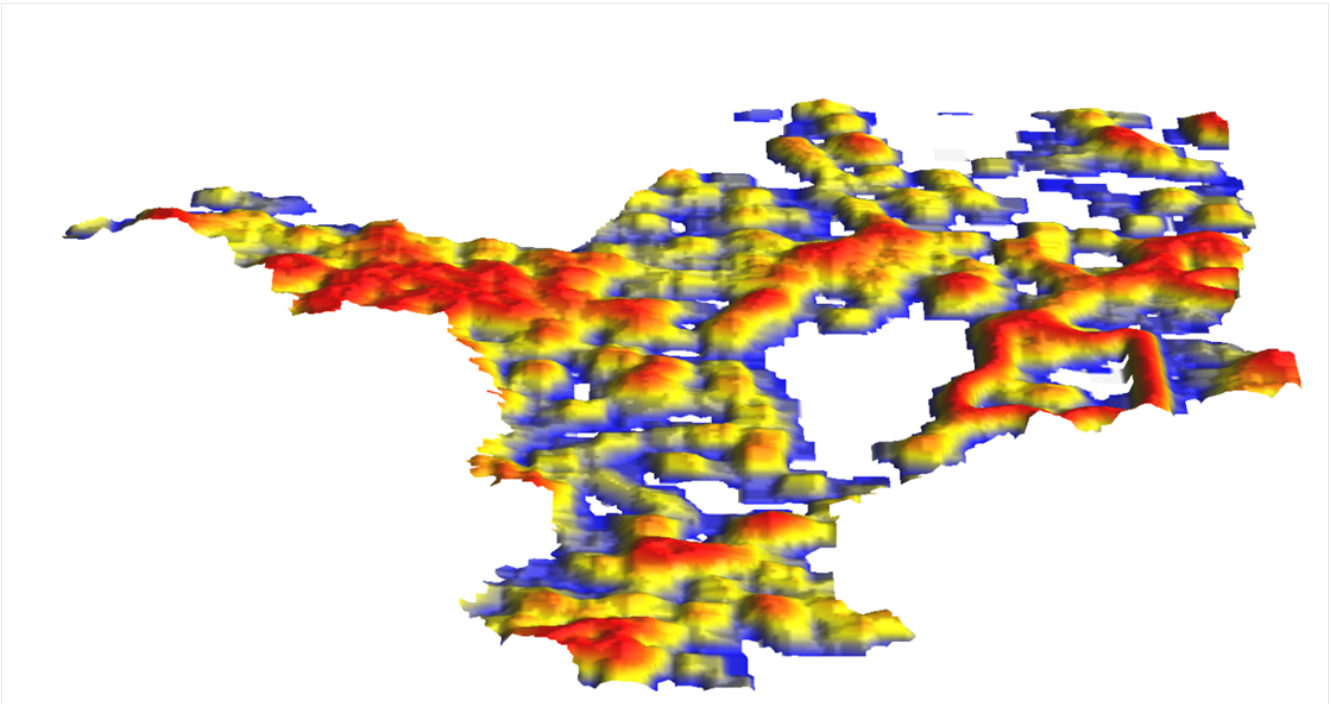
See query results below:
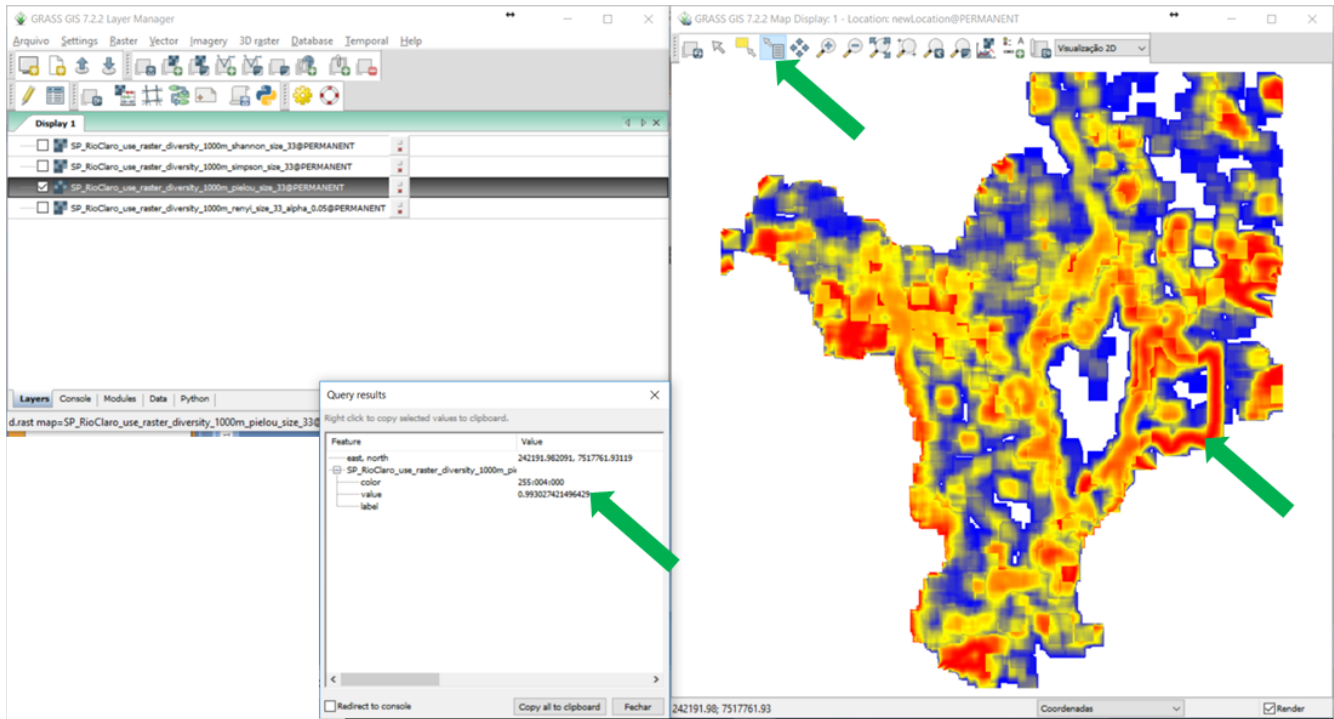
This index compares the measured diversity to the corresponding maximum value in landscape.

Renyi (Rényi, 1961)

The Rényi entropy is a generalization of the Shannon´s diversity index. Alpha of example is set as 0.5.

See query results below:

Patch ID maps

The output files with "pid" in file name are basically the patch or clumps identification. We will use the tool "Query results" in GRASS GIS to show the values attributed for the identification of a patch (pid). Note that the large green patch (The FEENA in Rio Claro) has pid equals to 9112.

Note that only habitat patches will present patch identification in the general pid files (sufix HABMAT_pid)
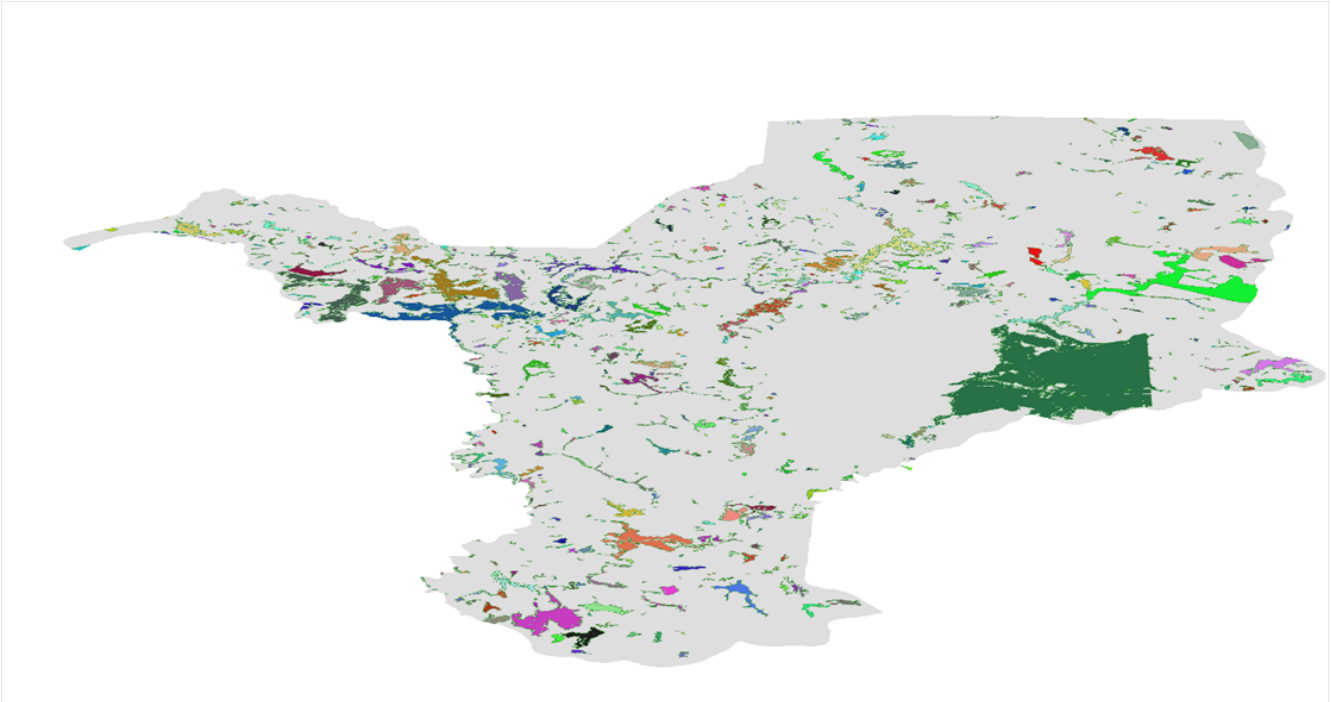
Query results are below:

Contact us

LSMetrics was developed at the Spatial Ecology and Conservation Lab (LEEC), at Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil. If you have questions, contact us at one of the e-mails below. You can also contact us if you have any errors running LSMetrics (or you can open an issue here on GitHub).

- Bernardo Niebuhr <bernardo_brandaum@yahoo.com.br>
- Milton C. Ribeiro <mcr@rc.unesp.br>
- Felipe Martello <felipemartello@gmail.com>

Contribute

You are also very welcome to contribute your own changes or new metrics to the LSMetrics tool. We are also open to dicuss the idea and how to implement other metrics needed for environmental research as well as for conservation and nature management purposes. Please submit a pull request or get in contact with us.

About LEEC lab

The LEEC lab team has developed several tools for spatial and landscape analysis:

LSMetrics

LSCorridors

Landscape analysis in R

Other publications

Take a look in our website!

2 Landscape connectivity in fragmented forests: assessing the impact of roads on Golden Lion Tamarins and proposing locations for gap restoration

Bernardo Brandão S. Niebuhr[1,2,*], Fernando Ascensão[3], Andreia Magro Moraes[1], Brenda Rocha Alexandre[4], Julia de Camara Assis[1,2], Maria Lucia Lorini[5], Milene Amâncio Alves-Eigenheer[1,2], Marcio M. de Morais-Jr[6], Carlos Ramon Ruiz-Miranda[6], Laurence Culot[2,7], Milton C. Ribeiro[1,2]

[1] Laboratório de Ecologia Espacial e Conservação, Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro, SP, Brazil

[2] Universidade Estadual Paulista (UNESP), Instituto de Biociências, Campus Rio Claro, 13506-900 Rio Claro, SP, Brazil

[3] Centre for Ecology, Evolution and Environmental Changes (CE3C), Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisbon, Portugal

[4] Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro (UFRJ), 21941-902 Rio de Janeiro, RJ, Brazil

[5] Departamento de Ciências Naturais, Instituto de Biociências, Universidade Federal do Estado do Rio de Janeiro (UNIRIO), 22290-255 Rio de Janeiro, RJ, Brazil

[6] Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense (UENF), 28015-620 Campos dos Goytacazes, RJ, Brazil

[7] Laboratório de Primatologia, Departamento de Zoologia, Universidade Estadual Paulista (UNESP), 3506-900 Rio Claro, SP, Brazil

*Corresponding author:
Bernardo Brandão S. Niebuhr
Laboratório de Ecologia Espacial e Conservação, Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista (UNESP)
Av. 24-A, 1515, Bela Vista, 13506-900 Rio Claro, SP, Brazil
e-mail: bernardo_brandaum@yahoo.com.br

AKNOWLEDGEMENTS

Abstract

Assessing structural and functional connectivity and their relation to dispersal and population persistence is one of the main tasks to manage landscapes and make them more friendly to endangered species. This is even more important for sensitive species that inhabit fragmented landscapes, in face of deforestation and a human-built infrastructure in expansion. Here we described the landscape structure of the occurrence area of an endangered arboreal primate, the Golden Lion Tamarin (GLT), estimated the effects of dirt and paved roads on the landscape connectivity, and simulated most probable routes to be used by tamarins to disperse among forest patches. We combined genetic, occurrence, and movement data, as well as expert knowledge on GLT behavior and space use, and tools to calculate landscape metrics and simulate ecological corridors. GLT occur in a highly fragmented landscape whose structure resembles that of the Atlantic Forest, but in a small extent. Pairwise genetic kinship was affected by the presence of dirt roads and highways, but not by small paved roads, that are less abundant in the landscape. The simulated connectivity was validated by presence and road crossing data: sites where GLT were detected and road sections crossed by them presented high connectivity. The simulated connectivity surface was then used to identify the forest gaps most probable to be used by GLT to move, in which the implementation of mitigation measures such as forest corridors and road crossing structures are prone to restore the connectivity between populations.

Key-words: functional connectivity; primate conservation; road ecology; ecological corridors; dispersal

2.1 Introduction

Dispersal is of utmost importance to maintain the genetic variability and the viability of wild populations (Nathan 2008; Henriques-Silva et al. 2015). For the dispersal of individuals to be effective – consisting of movement between populations and posterior reproduction – landscapes must not only be connected by structural elements such as corridors but also be functionally connected (Tischendorf & Fahrig 2000; Anderson et al. 2010). Functional connectivity is established by an interaction between species-specific endogenous factors – how organisms behave and experience the landscape, their avoidance or attraction by specific resources or landscape elements, their mating system – and spatial exogenous factors – e.g., matrix structure, physical barriers, and the isolation between habitat patches (Bowler & Benton 2005). Recent studies have demonstrated a negative correlation between

animal dispersal success and the presence of these spatial exogenous factors (e.g., Castilho et al. 2011; Mickelberg 2011; Koen et al. 2012; Soare et al. 2014; Mullins et al. 2015). As a consequence, the gene flow between populations tends to decrease and there may be a decrease in the evolution potential and in the probability of persistence of the metapopulation, particularly in fragmented landscapes and in face of climate changes (Mbora & McPeek 2010; Reed et al. 2011; Kool et al. 2013; Meyer et al. 2014).

Physical barriers are exogenous spatial factors that may isolate wild populations, impeding or drastically reducing dispersal between them (Mader 1984). Examples of barriers are human-built linear structures such as roads, channels, railways and power lines (Mader 1984; Trombulak & Frissell 2001). Primates and other arboreal animals may be highly endangered when human-built linear structures fragment their habitats (Vié et al. 2001; Williams & Vaughan 2001; Teixeira et al. 2013), because they depend on forest continuity to disperse (Arroyo-Rodríguez & Dias 2010; Estrada et al. 2017). Thus, the success of primate dispersal between habitat patches will depend upon the primate's ability to cross non-habitat gaps in the landscape (da Silva et al. 2015). Previous studies have reported that *Alouatta guariba clamitans* was suffering mortality during crossing attempts on a small rural road (Teixeira et al. 2013), and that *Sapajus nigritus* was subject to road kills in a single way paved road but their mortality decreased after road widening (Ciocheti et al. 2017). This indicates that roads tend to be highly resistant to arboreal primate movements for causing mortality or avoidance behavior. Despite the presence of roads throughout all landscapes where arboreal primates occur, little (or none) studies have quantified their influence on the primate's dispersal (but see, e.g., Moraes et al. 2018), or have tested best designs of crossing structures in order to increase the efficiency in primate crossing between both sides of the roads (e.g., Teixeira et al. 2013). These studies are important to plan conservation and to eliminate roads to act as potential barriers to primate population connectivity.

Golden Lion Tamarins (*Leontopithecus rosalia*, GLT) are an example of a Neotropical arboreal primate highly endangered by habitat loss and fragmentation (Kierulff et al. 2008) and naturally structured in small family groups (3-14 individuals) that hardly accept new disperser individuals (Baker et al. 1993, 2008). The reduction of gene flow occur more rapidly when populations of tamarins are distributed in fragmented landscapes (Di Fiore & Valencia 2014), as it is the prevailing state of their occurrence area within the Atlantic Forest (Ribeiro et al. 2009). An important exogenous factor that fragments the GLT occurrence region and negatively affects their dispersal potential are roads (Moraes et al. 2018). Currently, the widening of the federal highway (BR-101) that subdivides the occurrence area of GLT in two

portions (Procópio de Oliveira et al. 2008a) threatens the persistence and conservation of their populations; there is even the possibility that the widening of BR-101 will permanently isolate the GLT populations in two areas to the South and North of the highway. Moraes et al. (2018) showed that roads may be one of the main factors of GLT population fragmentation, but did not measure the influence of different types of roads according to width, traffic intensity, and other factors.

Our aim here was to assess the landscape connectivity of the GLT occurrence area, understand how connectivity is affected by different types of roads (dirt roads, small paved roads, and large paved roads as highways), and propose places to restore connectivity between patches and GLT populations. We accomplished that by using landscape remote sensing maps, literature data on GLT biology and ecology, genetic data on GLT populations as well as expert knowledge on GLT landscape preferences and use of space. GLT is an ideal model species to do so for four reasons: (i) they are a sort of "closed" metapopulation – almost all GLT populations that live in the wild occur in the same area, so it is possible to evaluate their whole landscape; (ii) the landscape where they occur is divided by a highway that is being widened, and is crossed by many other small paved and dirt roads; (iii) there are more than 30 years of data on the ecology of this species, which is not the case of most endangered species around the globe; (iv) there are several other species in the same area threatened by similar reasons: one critically endangered, one endangered, nine vulnerable, and eleven near threatened. This means that some measures of connectivity restoration such as corridor design may benefit not only the GLT but also other endangered species.

Our working hypotheses are the following (Fig. 1). 1) Paved roads (and especially large ones, such as the highway, which present an intense traffic) have a higher effect on the disruption of connectivity than dirt roads (Fig. 1A). This is translated into a smaller mean kinship between individuals found in patches separated by paved roads. On the other hand, connectivity is higher (and kinship larger) when there are no roads between patches. 2) The connectivity is higher in patches where GLTs were detected (Fig. 1B) and in road zones often crossed by the GLT (hence, where road kill rates are also high; Fig. 1C).

A How do the road type affect connectivity?

B How is connectivity related to GLT presence?

C Does the fauna cross roads in places with higher connectivity?
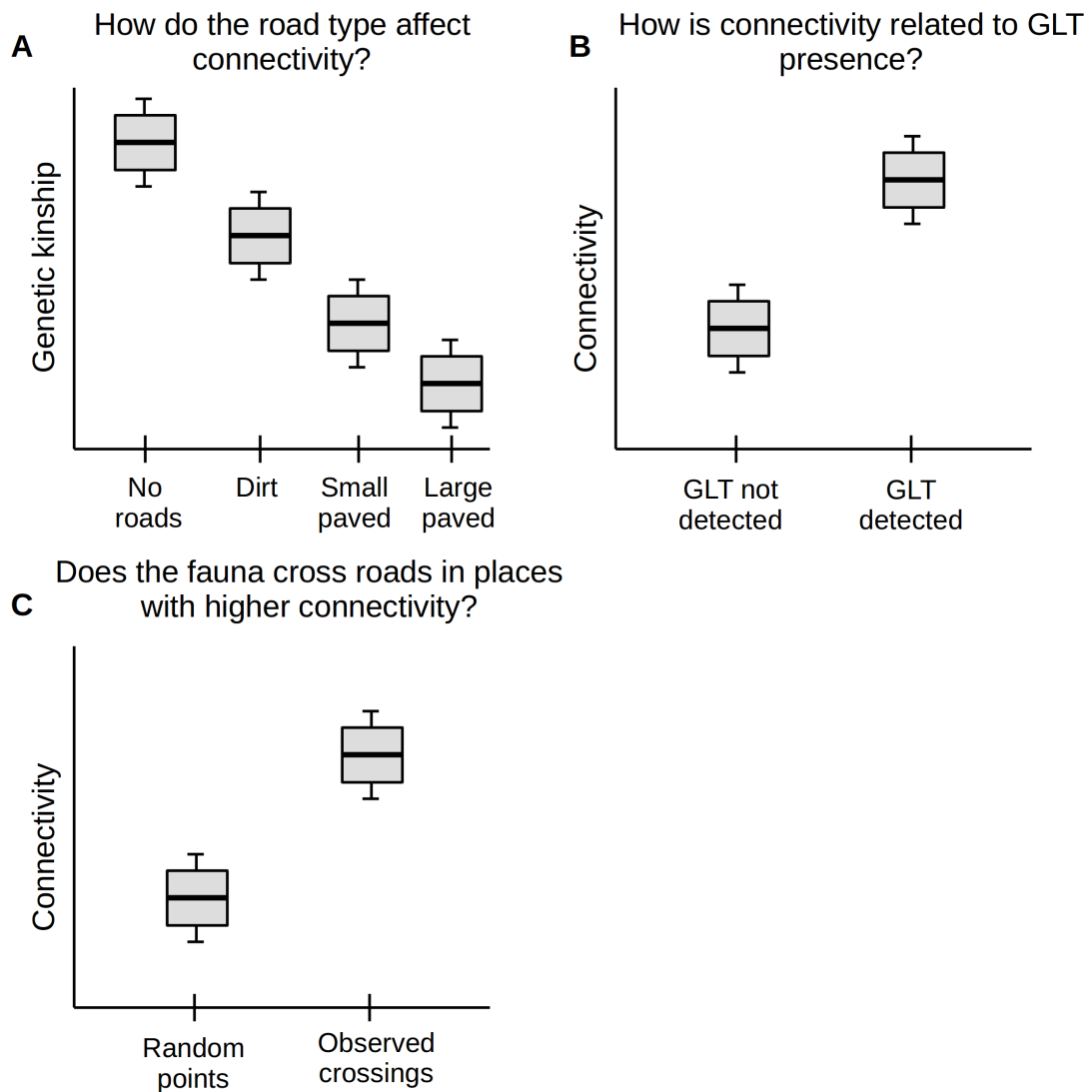
Figure 1. Hypotheses regarding the landscape connectivity of GLT occurrence region. (A) Genetic kinship (hence connectivity) is smaller between patches separated by paved roads, compared to patches separated by dirt or no roads. (B) Simulated landscape connectivity tend to be higher in patches where GLT were detected (C) and in zones of the roads often crossed by GLT.

2.2 Methods

2.2.1 Study Area and Study Species

The study species was the Golden Lion Tamarin (*Leontopithecus rosalia*), an endangered primate species with a very restricted distribution in the Atlantic Forests of South America, in the state of Rio de Janeiro. GLT are small (nearly 600 g, Dietz et al. 1994) and

territorial primates, which live in small groups and feed mainly on fruits and invertebrates (Dietz et al. 1997; Procópio de Oliveira et al. 2008a). Their social groups are mainly monogamous, although polygyny may be observed, mainly in isolated forest patches (e.g., Dietz & Baker 1993; Coelho 2009). Although they can adapt relatively well to secondary and degraded forests, they are very sensitive to habitat loss and fragmentation and these habitat modification processes are widespread in their occurrence region (Procópio de Oliveira et al. 2008a; Moraes et al. 2018).

The landscape used as the study region comprises the São João River Basin (SJRB), the Biological Reserve União, and a region of 5 km around these areas, in which almost all golden lion tamarins living in the wild may be found (Fig. A1). The 5 km-buffer area was included to consider the landscape influence on the connectivity of habitat patches inhabited by GLT, and its size was chosen to represent the order of magnitude of maximum distance dispersed by GLT (around 6 km; Mickelberg 2011; Paula 2013). Information on spatial data and composition of the land use map used here may be found in Appendix A.

2.2.2 A general view of landscape connectivity

Based on the land use map for the study region, the amount and proportion of each land use class in the landscape was calculated. Then, three landscape metrics were calculated for forests: (i) patch area, (ii) functionally connected area (or cluster size), and (iii) edge area. The functionally connected area is the summed area of all forest patches closer than a gap crossing distance, i.e., the average distance an organism has the ability to cross between patches. For a more general view of the landscape connectivity, we evaluated multiple values of the gap crossing capability, so that we could assess functional connectivity for GLT and other species that inhabit the landscape. Gap crossing capacity also varies with matrix type, but for a more general assessment of landscape connectivity, not considering the specificity of different species, the effect of matrix was not accounted in this step. For edge area we used a multi-scale approach and quantified the amount of forest that was located at different distances from the edges between forests and any kind of matrix. The calculations were performed within GRASS GIS using the package LSMetrics (Niebuhr et al. 2018, Chapter 1).

2.2.3 Effects of road type on connectivity

We used the pairwise genetic kinship between individuals as a proxy to functional connectivity. Genetic kinship is a measurement at the individual level that represents how related each pair of individuals are, expressing the potential gene flow or connectivity

between the individuals' locations. Genetic data was based on 14 microsatellite loci developed for the genus *Leontopithecus* and was extracted from 201 individuals sampled between 2007 and 2013 (Fig. A1C). Genetic kinship was calculated using SPAGeDi (Hardy & Vekemans 2002). A complete description of genetic analysis may be found at Moraes et al. (2017, 2018). For each pair of individuals, we recorded the kinship (response variable), the distance between their sampling locations, the management category of the individuals (native, reintroduced from captivity, translocated from isolated patches), and whether there were roads (and which kind of road – dirt roads, small paved roads, or the BR101 highway) in a straight line linking the locations.

Moraes et al. (2018) have shown that kinship for GLT depends on the the distance between the sampling points. As GLT populations are composed of unmanaged individuals born in the wild, individuals translocated between forest patches, and individuals reintroduced from captivity (Kierulff et al. 2012), they also found an effect of the management category on kinship: pairs of individuals of the same management category (or their descendants) are expected to be more closely related than individuals managed differently. Taking that into account, we first fitted a generalized linear model (GLM) to GLT kinship considering the effects of management and Euclidean distance. To remove the effect of these variables, we then used the residuals (the unexplained part) of the kinship to test the effect of road type on connectivity, through a new GLM approach. We also performed the analyses considering only observations (comparisons between a pair of individuals) whose locations were closer than 10km. This is the range for which distance affects genetic kinship, and beyond this distance road presence and type is probably a less important factor determining the relatedness between individuals. Analyses were performed within R 3.3.1 (R Development Core Team 2016) and all scripts and data are available at the GitHub repository (see Appendix A).

2.2.4 Functional connectivity and corridor simulation

To understand functional connectivity and assess the most probable routes of dispersal between populations, we simulated ecological corridors considering the resistance of the landscape elements to the movement of GLT. As detailed knowledge on the movement of GLT are available only at small within territory scale (Dietz et al. 1997; Procópio de Oliveira et al. 2008b) and information on dispersal routes is scarce (but see Paula 2013), here we used expert knowledge to determine the resistance of different habitat types to the movement of GLT. Expert knowledge is an approximation of an unknown information that is estimated by researchers and technicians with experience with a given species or ecosystem, that is widely

used in conservation sciences when raw data is unavailable (Martin et al. 2012; McBride & Burgman 2012).

Given the land use map of the study area, twelve experts (8 researchers, 4 field experts) were interviewed and asked "What is the resistance of each land cover to the movement of Golden Lion Tamarins?" They were asked to rank each land use type with a resistance value between 1 and 100, in which 1 represents a low resistance (higher likelihood of movement, if GLTs face this type of land use) and 100 represents a high resistance (low movement likelihood). These resistance values were crossed with land use and elevation to generate the final resistance map. Elevation was considered to account for the low occurrence probability of GLT over 550 m of altitude (Kierulff & Rylands 2003). A complete description of the expert knowledge survey and the calculation of the resistance surface may be found in Appendix B.

The resistance surface was used to simulate ecological corridors and assess functional connectivity through Circuitscape, a package that uses circuit theory to estimate the potential flow of organisms between locations in a landscape (McRae et al. 2008; McRae & Shah 2011). First the resulting connectivity map was validated by comparing the simulated connectivity with sites where GLT were or not detected, and sites along the BR101 highway where GLT were or not observed crossing the road. Then, the map was used to identify places for gap restoration between habitat patches crossed by roads, considering the most probable GLT routes. Data on GLT detection and road crossing were collected by the Golden Lion Tamarin Association (Associação do Mico Leão Dourado, AMLD) and are described in details in Appendix C.

2.3 Results

2.3.1 Landscape structure and connectivity

The area of occurrence of GLT is dominated by pasture (~ 58% of the landscape) and forest (~ 35%). The remaining 7% of the whole area is distributed among the other classes – mainly water and urban areas (Table A1). Therefore, simplifying the landscape as a binary landscape with only two classes – forest and pasture – is not too coarse for many environmental assessments. This supports the fact that many of the landscape metrics described here are based on a binary view of the study region. However, some of the other land use classes such as roads and urban areas, although occupying only a little part of the

whole area, may be very important to determine landscape connectivity for different species (as for the GLT, as shown here and in Moraes et al. 2018).

Almost half of the forest in the study area is located within a single large patch of nearly 50,000 ha, in the northern part of the region. On the other hand, 90% of the patches are smaller than 50 ha, and their summed area accounts for only 10% of the forest in the landscape (Fig 2A). Nearly 11,840 ha of forest are located within the two Biological Reserves inhabited by GLT – 5,100 ha of forest inside Poço das Antas Biological Reserve, covering 68% of its area, and 6,740 ha inside the Biological Reserve União, covering 87% of its area.

The expected cluster size is very small for organisms that have low ability to cross matrix gaps, mainly because of the great number of isolated small patches in the landscape (Fig. 2B). This is the case of the GLT: according to field observations, they can generally cross ~100m of pasture between forest patches (Mickelberg 2011), and it is rare that they cross longer distances. For the landscape to be more connected and present high functionally connected area, organisms must be able to cross more than 1,000 m – as the maned wolf (*Chrysocyon brachyurus*), for instance (Paula 2016). More than 40% of the forest is located at less than 100 m from forest edges, and 70% of forest areas are within 250 m from them (Fig. 2C). This is a reflex of the high fragmentation level in the landscape.
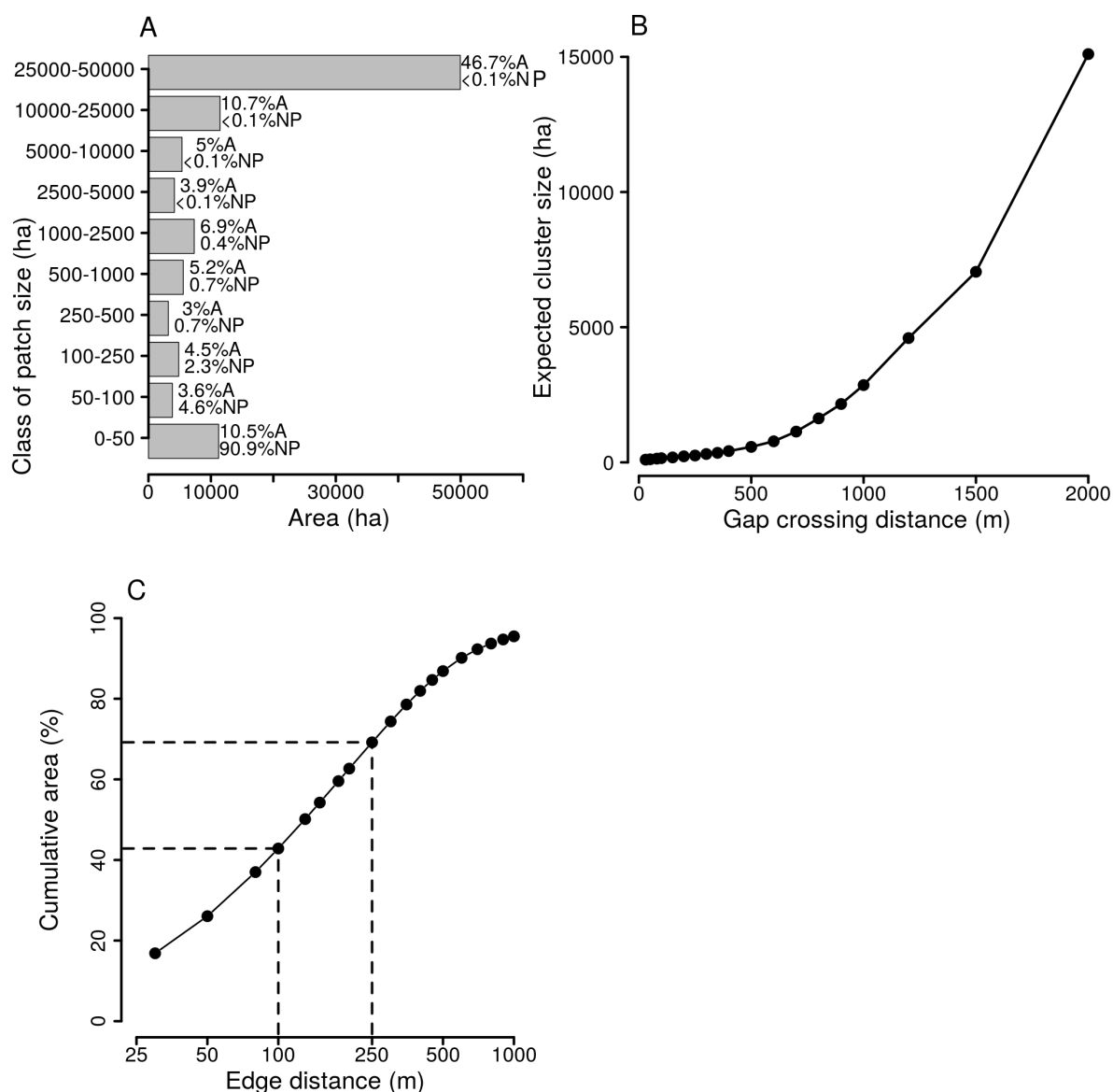
Figure 2. Landscape metrics of the study area. (A) Distribution of forest patch sizes; the percentage of the whole forest area (%A) and of the number of patches (%NP) that correspond to each class is shown to the right of each bar. (B) Expected cluster size (functionally connected area) for organisms with capacities of crossing different distances in the matrix (gap crossing capacity). (C) Proportion of the forest area that is located at different distances from the edges between forest and matrix.

2.3.2 Road effects on connectivity

We found an effect of roads on the expected kinship between individual GLT, even though there is much variation within each class: mean kinship decreases mainly when there are dirt roads (Expected kinship E(k) = -0.143, $p < 0.001$) and large paved roads (E(k) = -0.007, $p = 0.002$), compared to when there are no roads between the location of individuals

(E(k) = 0.018, *p* < 0.001; Fig. 3). The effect is opposite for smaller paved roads (E(k) = 0.058, *p* < 0.001), but this may be a sampling issue – small paved roads are more scarce between occupied forest patches of the landscape and sampling size was 10 times smaller for these roads (n = 190 against n > 2000 all other categories). This indicates there is a general effect of roads on the connectivity between populations, but that road type is not so important – what matters is if there are or not roads between patches.
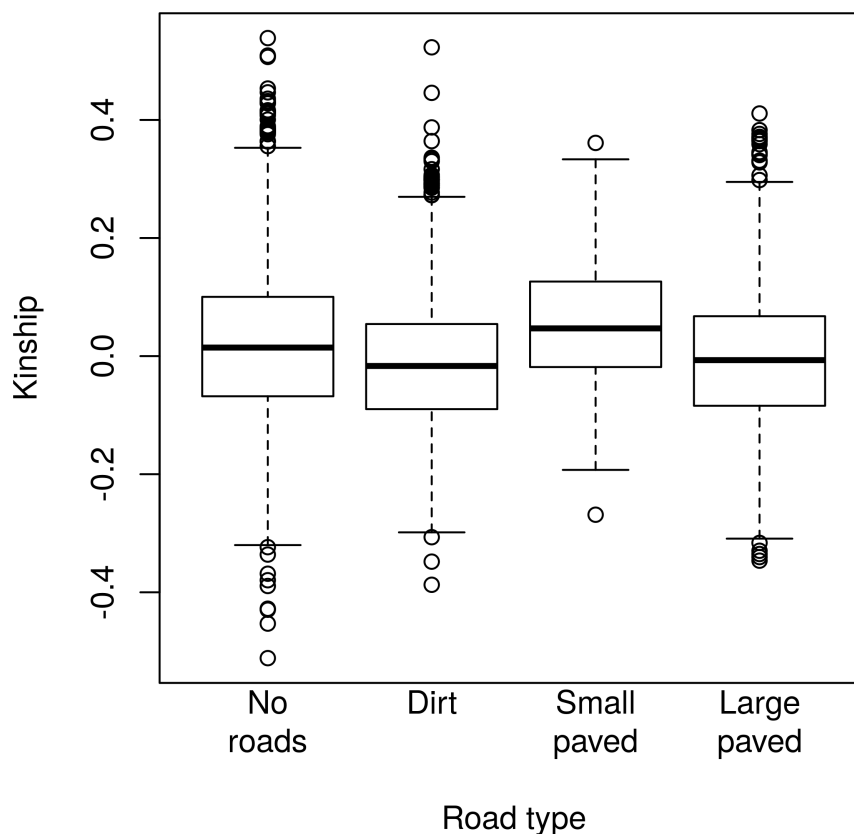
Figure 3. Effect of road type on the genetic kinship among GLT individual. Kinship is smaller for dirt and large paved roads.

2.3.3 Dispersal routes for Golden Lion Tamarins

Functional connectivity assessed via flow simulation showed preferential routes in more forested areas where the distance between patches is small and roads and urban areas are absent, as expected (Fig. 4A). Simulated connectivity across roads was higher in places where GLT crossings were observed (Mann-Whitney U = 272, *p* = 0.005; mean connectivity (SE) = 0.106 (0.009)), compared to random locations along the roads (mean connectivity (SE) = 0.069 (0.008); Fig. 4B, 4D). Connectivity was also higher for sites where GLT were present, compared to sites where they were not detected, although the pattern is not so strong Mann-

Whitney U = 1253, *p* = 0.049; mean connectivity (SE) = 0.061 (0.004) for detection sites, 0.052 (0.004) for non-detection sites; Fig. 4C).

The positive response of the simulated connectivity to GLT presence and crossings patterns indicates this flow surface may be useful for indicating gaps between forest patches to be restored by structural elements such as corridors and crossing structures, in the case of roads. This is exemplified in Fig. 4B for the BR101 highway that crosses the landscape from East to West. The selection of the road sections with highest connectivity, such as many of the places where GLT were observed crossing and other sites with high forest cover around the road, are good candidates to be selected for the application of mitigation measures to decrease the probability of road kills and increase the success in the dispersal of individuals moving from one side to the other of the highway.
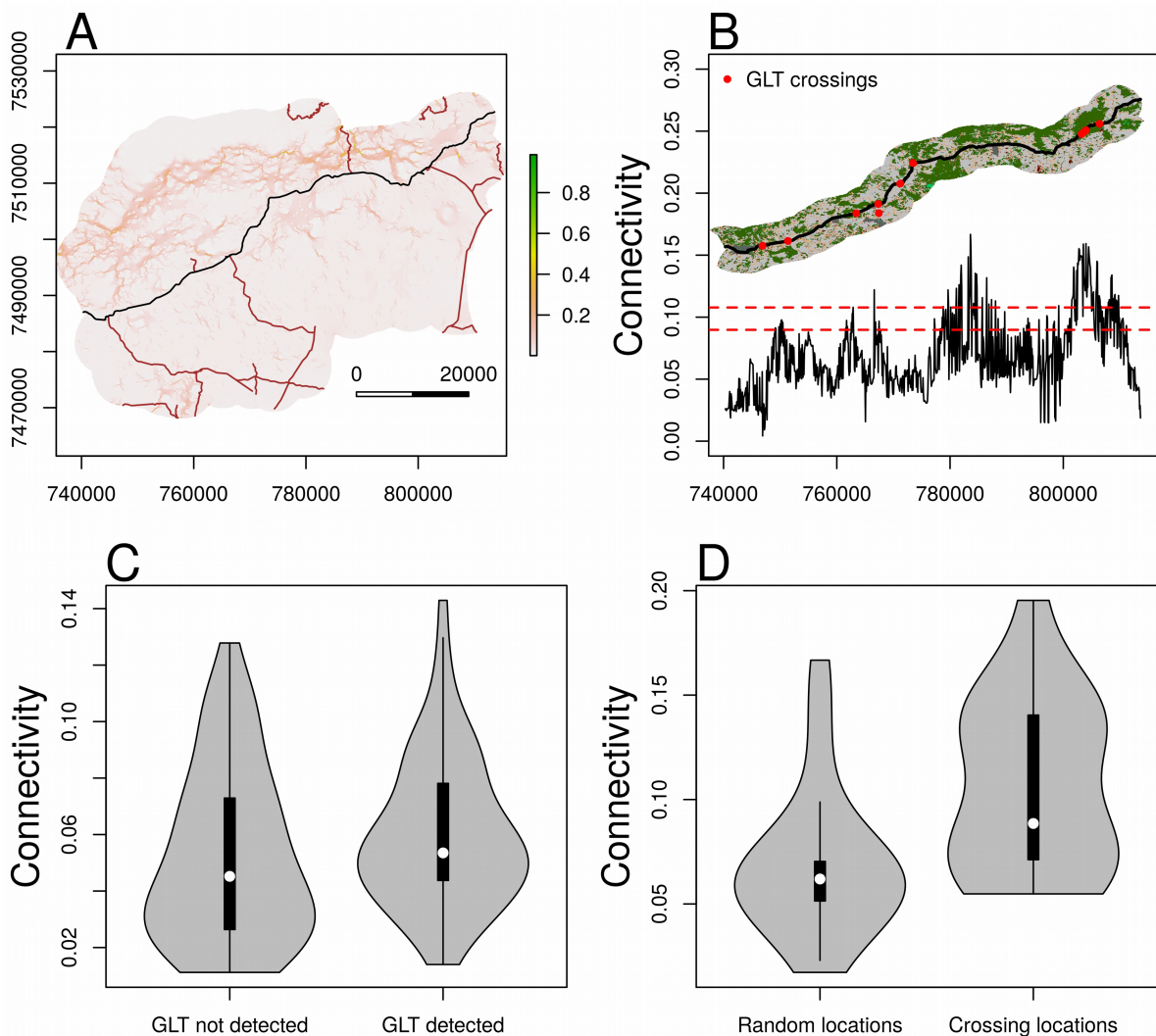
Figure 4. GLT landscape connectivity simulated through circuit theory. (A) Connectivity surface, with the highway shown in black and small paved roads in brown. (B) Connectivity

values along the BR101 highway, an illustration of the land cover around it (green for forest and light grey for pasture), and the locations of GLT crossings (red dots). The red dashed lines show the 80% and 90% percentiles of connectivity values along the highway. Highest values indicate a greater chance of these places being used as routes by GLT. Comparison of connectivity values between sites where GLT were and were not detected (C), and between road sections where GLTs were observed crossing and random locations along the roads (D).

2.4 Discussion

Assessing and increasing landscape connectivity and identifying opportunities to restore habitat connections and ultimately increase dispersal success and the persistence of populations is a vital task in conservation biology. Here we accomplished that by assessing the landscape structure of the occurrence area of the endangered Golden Lion Tamarins, unveiling the effect of roads over the dispersal between populations, and simulating functional connectivity to indicate gaps for restoration along roads. We found an effect of dirt and large paved roads on genetic kinship, and showed that sites with a higher landscape functional connectivity correspond to the ones occupied by tamarins and used by them to cross roads.

The landscape inhabited by GLT is highly fragmented, dominated mainly by small forest patches and by pasture, an inhospitable matrix to GLT. Since most patches are small and the average isolation between them is high, mainly in the Southern part of the study area, the forest area accessible to most organisms is small, on average, even for those species that can cross several hundred meters in open matrix. This is the case for most endangered species that occur in the region (see Appendix D; Brito et al. 2004; Araújo et al. 2008; Pacheco et al. 2010). Besides the GLT, most endangered mammals (e.g., *Bradypus torquatus* and *Hylaeamys oniscus*) and birds (e.g., *Myrmotherula minor* and *Cotinga maculata*) found in the study area have a small gap crossing capacity, which functionally connected area small. Only larger animals such as manned wolfs (*Chrysocyon brachyurus*), jaguars (*Panthera onca*), and Channel-billed toucans (*Ramphastos vitellinus*) may assess a larger forest area in such a landscape (Table D1).

These elements together – distribution of patch sizes, functionally connected area, and distance from forest to edges – make the GLT occurrence area a kind of small extent replicate of the whole Atlantic Forest (see Ribeiro et al. 2009), regarding landscape structure (although the proportion of habitat is higher). This makes the landscape an interesting model to understand the relation between landscape structure, landscape processes, biodiversity patterns, and the functioning of ecosystems (which is much harder to be considered for the

complete Atlantic Forest). This also puts the study area as an ideal landscape to understand how landscape structure elements such as roads affect dispersal and connectivity between populations, what we aimed here.

We found an overall road effect on GLT connectivity: individuals tended to be more genetically different when there were roads between them, even after removing the effect of distance and management. However, the type of road was not a decisive factor – kinship was smaller for pairs of individuals separated by both dirt roads and highways. This was in accordance to what we expected – roads are indeed a barrier that makes the effective dispersal of GLT more difficult (Moraes et al. 2018), but contradicted our expectation that paved roads would affect kinship more strongly than dirt roads.

There are two reasons why the effect of dirt roads may have been unexpectedly strong. First, the effect is real – what matters is the distance the animal has to cross over open spaces, and some dirt roads may be more exposed than paved roads, where the crossing places are more close to forest patches. The hypothesis that dirt roads affect kinship less than paved roads is based on the assumption that dirt roads are located in areas with forest on both sides and are easier to traverse, but that may not be the case in many situations. There are at least a few wide unpaved roads not adjacent to forest patches in the landscape, as well as some narrow paved roads. The other reason is that we may not have an adequate sampling design on both sides of the BR101 highway to understand the effect of this traffic intense road on dispersal and connectivity. Another unexpected result was an absence of effect of small paved roads on kinship. We believe this may be a sampling effect – at the same time the sampling size was much smaller for this kind of road, there is only a few small paved roads between forest patches occupied by GLT. This limitations points out to the need in performing well designed landscape studies to assess the effects of the highway on the dispersal and connectivity of GLT populations. Another point to be considered is traffic intensity and speed. We assumed dirt roads have less traffic than paved roads as well as reduced average speed for their structure and configuration, but this may not be true, mainly when comparing dirt and small paved roads.

Functional connectivity was higher on places where GLT cross the roads, compared to random road locations, what indicates that sites with high connectivity may be a surrogate for corridors or routes got GLT, between both sides of roads. On the other hand, functional connectivity was not so high in forest patch sites where GLT occur, in comparison to sites where they were not detected. Connectivity is expected to be linked to dispersal events and movement routes (With et al. 1997; King & With 2002), and also to animal occurrence, but

may not be a determinant factor to the establishment of territories by animals (what matters for occupancy may be patch size, the larger scale habitat amount, or the resource abundance, for instance; Magioli et al. 2015; Regolin et al. 2017). This difference in connectivity between detection and non-detection sites is not so surprising if we consider that these sites represent territories and not dispersal routes.

In any case, the observation of higher occupancy probability and road crossings in sites with high simulated connectivity indicate that the functional connectivity surface may be a good tool to indicate places with a high crossing probability by GLT – and, therefore, to apply measures that minimize the effects of roads over populations. The same expert knowledge data used here was also used to show that landscape resistance is one of the most important variables determining the dispersal patterns and genetic structure of GLT (Moraes et al. 2018), what reinforces the potential usage of this connectivity surface to conservation. This is also reinforced by the fact that the implementation of crossing structures in these places and barriers around them may stimulate GLT and other organisms to cross roads using such crossing structures, as well as prevent them to cross in other dangerous places (Kramer-Schadt et al. 2004; Ascensão et al. 2013). GLT experts interviewed here indicated that large overpasses with a high vegetation structure are the ideal type of crossing element to be used by GLT and other arboreal animals to cross, and that underpasses or canopy overpasses (a type of thin structure linking canopies at both sides of the road) won't probably be used by them, at least in roads with an intense traffic such as the BR101 highway.

The BR101 highway is currently being widened, what offers new threatens to GLT and also new perspectives on road ecology research. The results found here and the functional connectivity map presented may be used as tools to select places for the implementation of structures that link patches and increase the connectivity between populations at both sides of the highway. We suggest this data is crossed with other information (e.g. relief, land cost, owner's will on collaborating) to define where to build crossing structures. At the same time, such efforts must be followed by a good design of the structures and a systematic monitoring of its usage by the fauna in the long term. At the same time, as the effect of dirt roads was also strong on the connectivity between populations, efforts must not be restricted to large roads. We suggest the use of the connectivity surface for also selecting gaps for forest restoration, through revegetation and implementation of crossing structures in dirt roads and the surrounding matrix areas. The implementation of these measures may increase dispersal success for GLT but may also benefit many other endangered species that co-occur and are less or equally sensible to forest fragmentation as the golden lion tamarins.

Supporting Information

Appendix A – Description of spatial data and landscape metrics

Appendix B – Landscape resistance surface for the Golden Lion Tamarins

Appendix C – Description of GLT detection and crossing data

Appendix D – Threatened species on the Golden Lion Tamarin occurrence area

2.5 References

Anderson CD, Epperson BK, Fortin MJ, Holderegger R, James PMA, Rosenberg MS, Scribner KT, Spear S. 2010. Considering spatial and temporal scale in landscape-genetic studies of gene flow. Molecular Ecology **19**:3565–3575.

Araújo RM de, Souza MB de, Ruiz-Miranda CR. 2008. Densidade e tamanho populacional de mamíferos cinegéticos em duas Unidades de Conservação do Estado do Rio de Janeiro, Brasil. Iheringia, Série Zoologia **98**:391–396.

Arroyo-Rodríguez V, Dias PAD. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology **72**:1–16.

Ascensão F, Clevenger A, Santos-Reis M, Urbano P, Jackson N. 2013. Wildlife-vehicle collision mitigation: Is partial fencing the answer? An agent-based model approach. Ecological Modelling **257**:36–43.

Baker AJ, Bales K, Dietz JM. 2008. Sistema de acasalamento e dinâmicas de grupo em micos-leões. Pages 251–284in D. G. Kleiman and A. B. Rylands, editors.Micos leões: biologia e conservação. MMA/Smithsonian Institution, Brasília.

Baker AJ, Dietz JM, Kleiman DG. 1993. Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. Animal Behaviour **46**:1091–1103.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews **80**:205–225. Available from http://doi.wiley.com/10.1017/S1464793104006645.

Brito D, Oliveira LC, Mello MAR. 2004. An overview of mammalian conservation at Poço das Antas Biological Reserve, southeastern Brazil. Journal for Nature Conservation **12**:219–228.

Castilho CS, Marins-Sá LG, Benedet RC, Freitas TO. 2011. Landscape genetics of mountain lions (*Puma concolor*) in southern Brazil. Mammalian Biology **76**:476–483.

Ciocheti G, de Assis JC, Ribeiro JW, Ribeiro MC. 2017. Highway widening and underpass effects on vertebrate road mortality. Biotropica **49**:765–769.

Coelho AS. 2009. Reintrodução do mico-leão-dourado, Leontopithecus rosalia, em fragmentos: Sucesso reprodutivo, interações inter-grupais em corredores e conflito social. Universidade Estadual do Norte Fluminense.

da Silva LG, Ribeiro MC, Hasui É, da Costa CA, da Cunha RGT. 2015. Patch size, functional isolation, visibility and matrix permeability influences neotropical primate occurrence within highly fragmented landscapes. PLoS ONE **10**:1–20.

Di Fiore A, Valencia LM. 2014. The Interplay of Landscape Features and Social System on the Genetic Structure of a Primate Population: An Agent-Based Simulation Study Using "Tamarins." International Journal of Primatology **35**:226–257.

Dietz JM, Baker AJ. 1993. Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. Animal Behaviour **46**:1067–1078.

Dietz JM, Baker AJ, Miglioretti D. 1994. Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (Leontopithecus rosalia). American Journal of Primatology **34**:115–132.

Dietz JM, Peres CA, Pinder L. 1997. Foraging ecology and use of space in wild golden lion tamarins (*Leontopithecus rosalia*). American Journal of Primatology **41**:289–305.

Estrada A et al. 2017. Impending extinction crisis of the world's primates: why primates matter. Science Advances **3**:e1600946.

Hardy OJ, Vekemans X. 2002. SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Molecular Ecology Notes **2**:618–620.

Henriques-Silva R, Boivin F, Calcagno V, Urban MC, Peres-Neto PR. 2015. On the evolution of dispersal via heterogeneity in spatial connectivity. Proceedings of the Royal Society B **282**:20142879. Available from http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2014.2879.

Kierulff MCM, Ruiz-Miranda CR, Oliveira PP de, Beck, Martins A, Dietz JM, Rambaldi DM, Baker AJ. 2012. The Golden lion tamarin *Leontopithecus rosalia:* a conservation success story. International Zoo Yearbook **46**:36–45.

Kierulff MCM, Rylands AB. 2003. Census and distribution of the golden lion tamarin (*Leontopithecus rosalia*). American Journal of Primatology **59**:29–44.

Kierulff MCM, Rylands AB, de Oliveira MM. 2008. Leontopithecus rosalia.

King AW, With KA. 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? Ecological Modelling **147**:23–39.

Koen EL, Bowman J, Garroway CJ, Mills SC, Wilson PJ. 2012. Landscape resistance and American marten gene flow. Landscape Ecology **27**:29–43.

Kool JT, Moilanen A, Treml EA. 2013. Population connectivity: Recent advances and new perspectives. Landscape Ecology **28**:165–185.

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U. 2004. Fragmented landscapes, road mortality and patch connectivity: Modelling influences on the dispersal of Eurasian lynx. Journal of Applied Ecology **41**:711–723.

Mader HJ. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation **29**:81–96.

Magioli M, Ribeiro MC, Ferraz KMPMB, Rodrigues MG. 2015. Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest. Animal Conservation **18**:499–511.

Martin TG, Burgman MA, Fidler F, Kuhnert PM, Low-Choy S, Mcbride M, Mengersen K. 2012. Eliciting expert knowledge in Conservation Science. Conservation Biology **26**:29–38.

Mbora DNM, McPeek MA. 2010. Endangered species in small habitat patches can possess high genetic diversity: the case of the Tana River red colobus and mangabey. Conservation Genetics **11**:1725–1735. Available from http://link.springer.com/10.1007/s10592-010-0065-0.

McBride MF, Burgman MA. 2012. What is expert knowledge, how is such knowledge gathered, and how do we use it to address questions in Landscape Ecology? Pages 11–38in A. H. Perera, C. A. Drew, and C. J. Johnson, editors.Expert knowledge and its application in Landscape Ecology. Springer, New York. Available from http://link.springer.com/10.1007/978-1-4614-1034-8.

McRae BH, Dickson BG, Keitt TH, Shah VB. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology **89**:2712–2724.

McRae BH, Shah VB. 2011. Circuitscape User Guide. Available from http://www.circuitscape.org.

Meyer ALS, Pie MR, Passos FC. 2014. Assessing the exposure of lion tamarins (Leontopithecus spp.) to future climate change. American Journal of Primatology **76**:551–562.

Mickelberg J. 2011. Understanding and managing isolation in a fragmented population of golden lion tamarins, Leontopithecus rosalia. Available from http://digilib.gmu.edu/jspui/handle/1920/6337 (accessed August 9, 2014).

Moraes AM, Ruiz-Miranda CR, Galetti Jr. PMG, Niebuhr BBS, Alexandre BR, Muylaert R de L, Grativol A, Ribeiro JW, Ferreira A, Ribeiro MC. 2018. Landscape resistance influences effective dispersal of endangered golden lion tamarins within the Brazilian Atlantic Forest. Submitted.

Moraes AM, Ruiz-Miranda CR, Ribeiro MC, Grativol AD, da S. Carvalho C, Dietz JM, Kierulff MCM, Freitas LA, Galetti PM. 2017. Temporal genetic dynamics of reintroduced and translocated populations of the endangered golden lion tamarin (Leontopithecus rosalia). Conservation Genetics **0**:1–15. Springer Netherlands.

Mullins J, Ascensão F, Simões L, Andrade L, Santos-Reis M, Fernandes C. 2015. Evaluating connectivity between Natura 2000 sites within the montado agroforestry system: a case study using landscape genetics of the wood mouse (*Apodemus sylvaticus*). Landscape Ecology **30**:609–623.

Nathan R. 2008. An emerging movement ecology paradigm. Proceedings of the National Academy of Sciences of the United States of America **105**:19050–19051.

Niebuhr BBS, Martello F, Ribeiro JW, Vancine MH, Muylaert R de L, Campos VEW, dos Santos JS, Tonetti VR, Ribeiro MC. 2018. Landscape Metrics (LSMetrics): a spatially explicit tool for calculating connectivity and other ecologically-scaled landscape metrics. To be submitted to Environmental Modelling & Software.

Pacheco JF, Nascimento I, Astor DC, Cesar CB. 2010. Avifauna da Reserva Biológica de Poço das Antas, Silva Jardim, RJ. Atualidades Ornitológicas **157**:55–74.

Paula RC de. 2016. Adequabilidade ambiental dos biomas brasileiros à ocorrência do lobo-guará (Chrysocyon brachyurus) e efeitos da composição da paisagem em sua ecologia espacial, atividade e movimentação. Universidade de São Paulo.

Paula VR de. 2013. Comportamento de dispersão dos micos-leões-dourados (Leontopithecus rosalia, LINNAEUS, 1766) reintroduzidos e seus descendentes nascidos em vida livre.

Procópio de Oliveira P, Grativol AD, Ruiz-Miranda CR, editors. 2008a. Conservação do mico-leão-dourado: Enfrentando os desafios de uma paisagem fragmentada. Universidade Estadual do Norte Fluminense Darcy Ribeiro press, Campos dos Goytacazes, RJ, Brazil.

Procópio de Oliveira P, Kierulff MCM, Lapenta MJ. 2008b. Dieta e áreas de uso de micos-leões-dourados na Reserva Biologica União, RJ. Pages 40–57in P. Procópio-de-Oliveira, A. D. Grativol, and C. R. Ruiz-Miranda, editors.Conservação do mico-leão-dourado: enfrentando os desafios de uma paisagem fragmentada. Universidade Estadual do Norte Fluminense Darcy Ribeiro, Campos dos Goytacazes.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/.

Reed DH, Teoh VH, Stratton GE, Hataway RA. 2011. Levels of gene flow among populations of a wolf spider in a recently fragmented habitat: Current versus historical rates. Conservation Genetics **12**:331–335.

Regolin AL et al. 2017. Forest cover influences occurrence of mammalian carnivores within Brazilian Atlantic Forest. Journal of Mammalogy **98**:1721–1731.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation **142**:1141–1153.

Soare TW, Kumar A, Naish KA, O'Donnell S. 2014. Genetic evidence for landscape effects on dispersal in the army ant Eciton burchellii. Molecular Ecology **23**:96–109.

Teixeira FZ, Printes RC, Fagundes JCG, Alonso AC, Kindel A. 2013. Canopy bridges as road overpasses for wildlife in urban fragmented landscapes. Biota Neotropica **13**:117–123.

Available from http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1676-06032013000100013&lng=en&tlng=en.

Tischendorf L, Fahrig L. 2000. On the usage and measurement of landscape connectivity. Oikos2 **90**:7–19.

Trombulak SC, Frissell CA. 2001. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14**:18–30.

Vié J-C, Richard-Hansen C, Fournier-Chambrillon C. 2001. Abundance, use of space, and activity patterns of white-faced sakis (Pithecia pithecia) in French Guiana. American Journal of Primatology **55**:203–221. Available from http://onlinelibrary.wiley.com/doi/10.1002/ajp.1055/full%5Cnhttp://www.ncbi.nlm.nih.gov/pubmed/11748693.

Williams HE, Vaughan C. 2001. White-faced monkey (*Cebus capucinus*) ecology and management in neotropical agricultural landscapes during the dry season. Revista de Biologia Tropical **49**:1199–1206.

With KA, Gardner RH, Turner MG. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos **78**:151–169.

Appendix A – Description of spatial data and landscape metrics

Here we described the sources of data and the geographical information system (GIS) manipulations made to create a map of land use for the Golden Lion Tamarin occurrence region. Besides, we presented the methods and some results regarding the calculation of landscape metrics for this region. All data and Python and R code may be found at the GitHub repository: https://github.com/LEEClab/ms_connectivity_roads_GoldenLionTamarins.

The landscape used as the study region comprises the São João River Basin (SJRB), the Biological Reserve União, and a region of 5 km around these areas, in which almost all golden-lion tamarins (GLT) living in the wild may be found.

The main land use map used here was classified by the Brazilian Foundation for Sustainable Development (FBDS – http://www.fbds.org.br/) through visual interpretation of RapidEye satellite images collected between 2013 and 2015, with 5 m resolution, for the whole Altlantic Forest. It presented the classes forest, water, non-forest natural areas, silviculture, urban areas, and antropic areas (the last one was not used here). The FBDS land use map was complemented with the map of urban areas made by SOS Mata Atlântica in their annual Atlas of the Atlantic Forest for 2013-2014 (SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais 2014) and the class agriculture from a land use map produced by the researcher Vinicius S. Seabra, using images from 2010 (Seabra 2012). Both maps were based on LANDSAT satellite images and present a resolution of 30 m. Roads were mapped by the Brazilian Institute of Geography and Statistics (IBGE – https://ww2.ibge.gov.br/) using a geographic ratio of 1:25000 (pixel size of nearly 10 m) and divided into paved and unpaved roads. Here we also distinguished the BR-101 highway from the other paved roads, since the former is larger, presents a more intense traffic, and has been widened in the period 2010-2018. The width of roads was 30 m for the highway, 16 m for the other paved roads, and 10 m for the dirt roads. To be combined, all vectorial maps were rasterized with 5 m resolution and reprojected to Universal Transverse Mercator (UTM) projection, zone 23 S, Datum WGS-84. All the GIS operations to combine maps were done within GRASS GIS v. 7.2.2 (GRASS Development Team 2017).

The final land use map consisted of the combination of the classes described above (Fig. A1). All areas that did not match one of those classes were considered pasture, the main type of matrix in the region (Seabra 2012). When there was an overlap between classes of different sources, priority was given to the ones extracted from more precise maps. This combination resulted in the following classes, presented in order of priority: BR-101 highway,

paved roads, water, forest, non-forest natural areas (humid areas, *restinga*, mangroove), urban areas, silviculture, dirt roads, agriculture, and pasture. The area and proportion of each land use class are shown in Table A1.
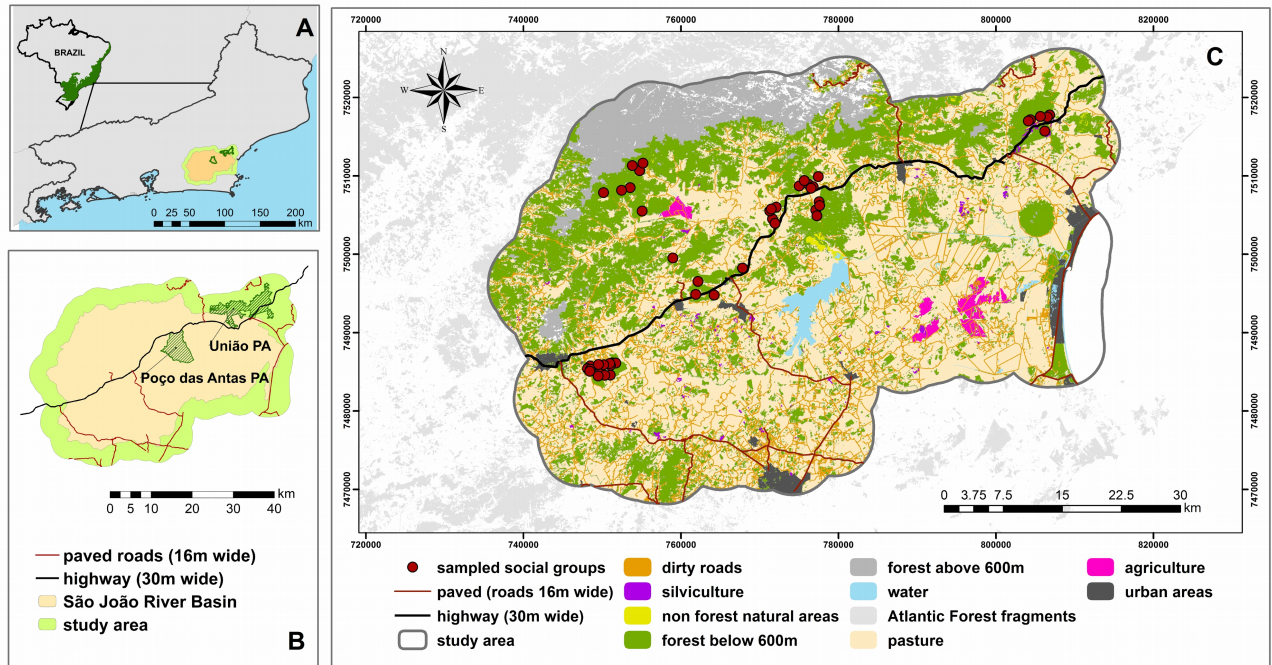
Figure A1. Land use map of the study area, the São João River Basin (SJRB), the União Protected Area, and their surroundings. (A) Location of the study area within the Rio de Janeiro State, in the Atlantic Forest (in green), in southeastern Brazil. (B) Zoom to the study area, highlighting the location of SJRB, the main protected areas (PA), and the larger roads. (C) Complete land use map used in this study and location of the sampling groups used for genetic analysis. Forest areas above 600 m of altitude were shown in a different color since they are hardly used by golden lion tamarins. Maps in UTM projection, Zone 23 S, Datum WGS-84.

Table A1. Total area and proportion of the whole landscape that correspond to each land use class.

Land use class	Area (ha)	Proportion (%)
BR-101 highway	292.93	0.09
Other paved roads	360.46	0.11
Water	5446.76	1.63
Forest	119,003.93	35.59
Non-forest natural areas	1073.81	0.32
Urban areas	6918.74	2.07
Silviculture	1266.16	0.38
Dirt roads	3922.39	1.17
Agriculture	2912.47	0.87
Pasture	193,162.46	57.77
Whole study area	334,360.11	100.00

Appendix B – Landscape resistance surface for the Golden Lion Tamarins

In the Appendix B we described the creation of the resistance surface, used as input to simulate ecological corridors for Golden Lion Tamarins. A resistance surface is a spatial layer that represents the lack of likelihood, the risk, or difficulty of an organism moving through different parts of a landscape (McRae 2006). The resistance surface was created in two steps: (i) the definition of resistance values for each land use type, based on expert knowledge; and (ii) calculation of landscape resistance, taking into account expert knowledge information and altitude. All the data and the code to analyze and generate the resistance map may be found at the GitHub repository.

B1) Expert knowledge data

As detailed knowledge on the movement of GLT are available only at small within territory scale (e.g., Dietz et al. 1997, Procópio de Oliveira et al. 2008) and information on dispersal routes is scarce (but see Paula 2013), here we used expert knowledge to determine the resistance of different habitat types to the movement of GLT. Expert knowledge is an approximation of an unknown information that is estimated by researchers and technicians with experience with a given species or ecosystem, that is widely used in conservation sciences when raw data is unavailable (Martin et al. 2012, McBride and Burgman 2012).

Given a land use map of the study area, twelve experts (8 researchers, 4 field experts) were interviewed and asked "What is the resistance of each land cover to the movement of Golden Lion Tamarins?". They were asked to rank each land use type with a resistance value between 1 and 100, in which 1 represents a low resistance (higher likelihood of movement, if GLT face this type of land use) and 100 represents a high resistance (low movement likelihood). Besides the land use types classified in the land use map used here (BR-101 highway, paved roads, water, forest, non-forest natural areas, urban areas, silviculture, dirt roads, agriculture, and pasture), we assessed the resistance of four types of fauna crossing structures to structurally link forest patches in opposite sides of roads: wildlife overpasses, canopy overpasses, underbridge passes, and underpasses. Asking experts about the resistance of these structures intended on assessing their potential usage by GLT, in the case they are built along roads as a mitigation measure of road widening negative effects.

Forest was the most permeable (less resistant) land use, followed by silviculture, non forest natural areas, agriculture, and pasture (Fig. B1). Urban areas and paved roads were

among the cover types more resistant to GLT movement, according to the experts. Among the crossing structures, overpasses were the most permeable, while underbridge passes and underpasses were among the most resistant. There was a relatively high accordance in the resistance value between experts for the most permeable (forest) and most resistant land uses (urban areas, highways, water, underpasses), but a high variability in expert answer for the other land uses (which show the uncertainty in the assessment of resistance for most land uses).
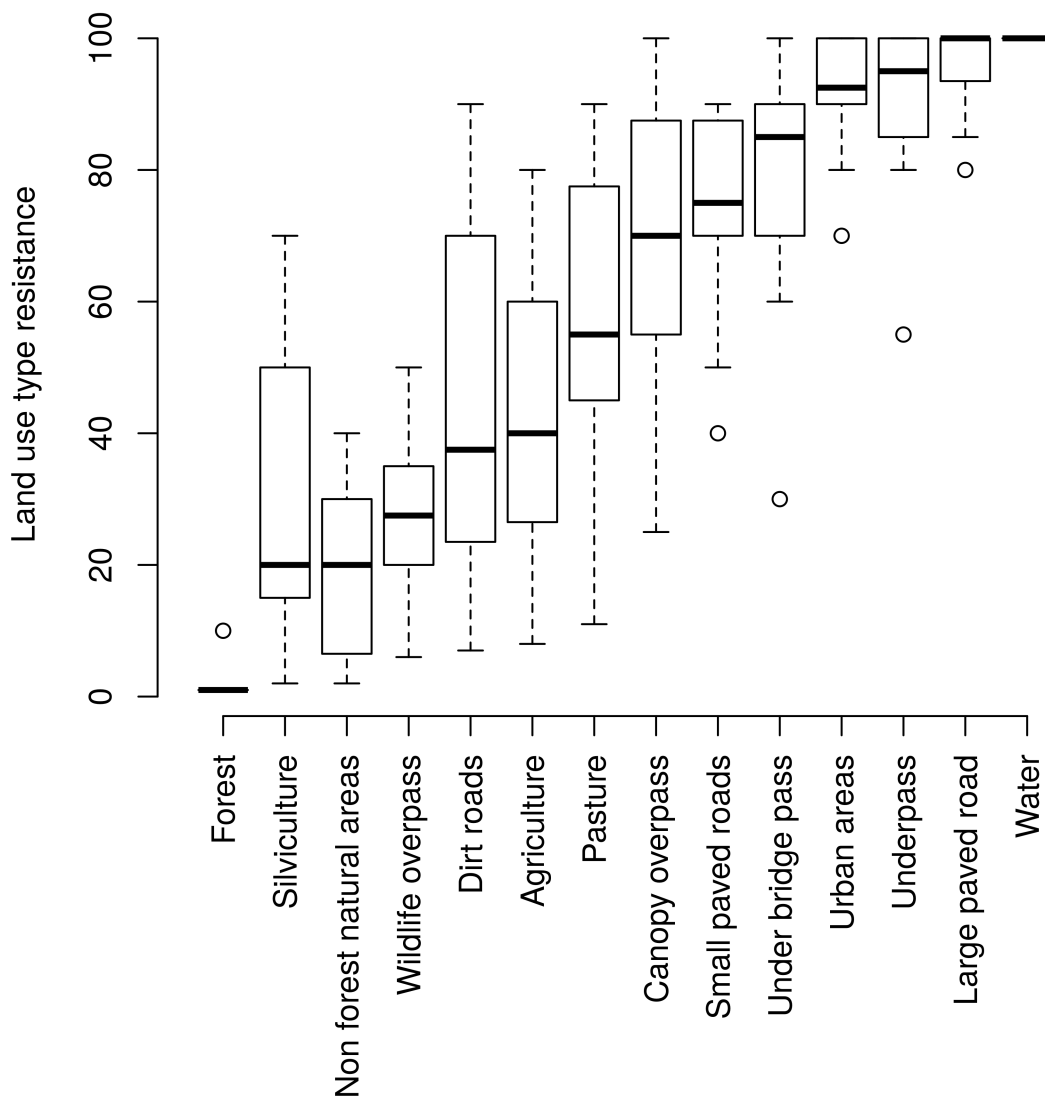
Figure B1. Distribution of resistance values estimated by GLT experts for each land use type and for four road crossing structures.

B2) Resistance surface

To create the final resistance surface used to simulate ecological corridors, first the cells of the land use map were reclassified according to the median resistance value for each land use. As GLT are hardly found in forests with altitude higher than 550 m (Kierulff and Rylands 2003), we assumed the resistance rapidly increases above this level and divided resistance values by a movement likelihood factor, [1 + exp(0.02 * (altitude – 650))], to get the final resistance map (Fig. B2). By doing that, resistance values surpassed 100; we then restrained these values to a maximum of 1000, which represented barriers to the GLT movement. The elevation data (resolution ~30m) was derived from the digital elevation model (DEM) obtained from USGS National Elevation dataset (https://www.usgs.gov/) and resampled to 5m resolution to match the resolution of the land use map.
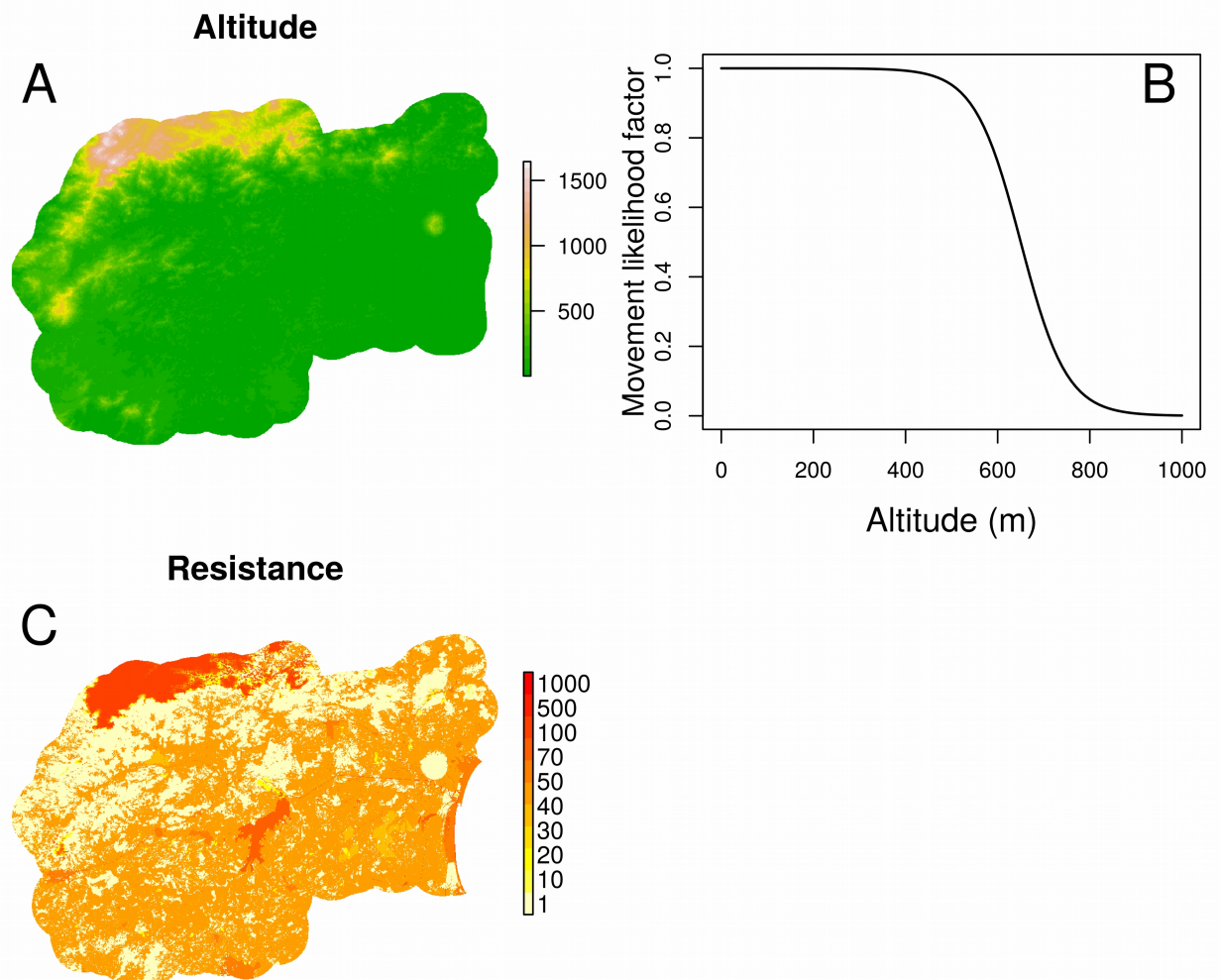
Figure B2. Illustration of the creation of the resistance surface used to simulate ecological corridors for the Golden Lion Tamarin. (A) Altitude map for the study region. (B) Curve

showing a decrease in the land use permeability for GLT; resistance values were divided by this function to generate the final resistance surface (C).

Appendix C – Description of GLT detection and crossing data

Detection data on golden lion tamarins was collected by the Golden Lion Tamarin Association (AMLD) field team in forest patches in the São João River Basin surveyed from March to December 2013. The survey involved playing tamarin long calls and recording their presence by direct observations or vocalizations. Long phee calls were chosen to playback as they are related to territorial defense, being most likely to elicit responses (Ruiz-Miranda et al. 2002). This method has been used prior with success in this species (Kierulff and Rylands 2003). Sampling points were systematically spaced 200m apart from each other within 100-hectare plots randomly superimposed over forest patches in the study region (Fig. C1), and the size of the plots were selected according to the size of the patch. Surveys were carried out from 07h00to 11h00h by two people. The long calls of a male and a female were played in four directions, repeated twice at three-minute intervals. Researchers remained hidden, 20–30 metres apart from each other. The number of individuals and the composition of the sighted tamarin groups were recorded upon its approach; as in some of the sampling points they were detected only through vocalizations, here we consider only detection/non-detection data (and not group size/abundance). Our survey equipment consisted of a portable CD player and a portable field speaker (SME field speaker).

Road crossing data was collected from two sources: sites where tamarins were observed by researchers or field experts on both sides of a road; and sites where they were road killed and collected by the environmental police or by the AMLD personnel.

Figure C1. Illustration of detection and road crossing data for GLT. At the left, we show the
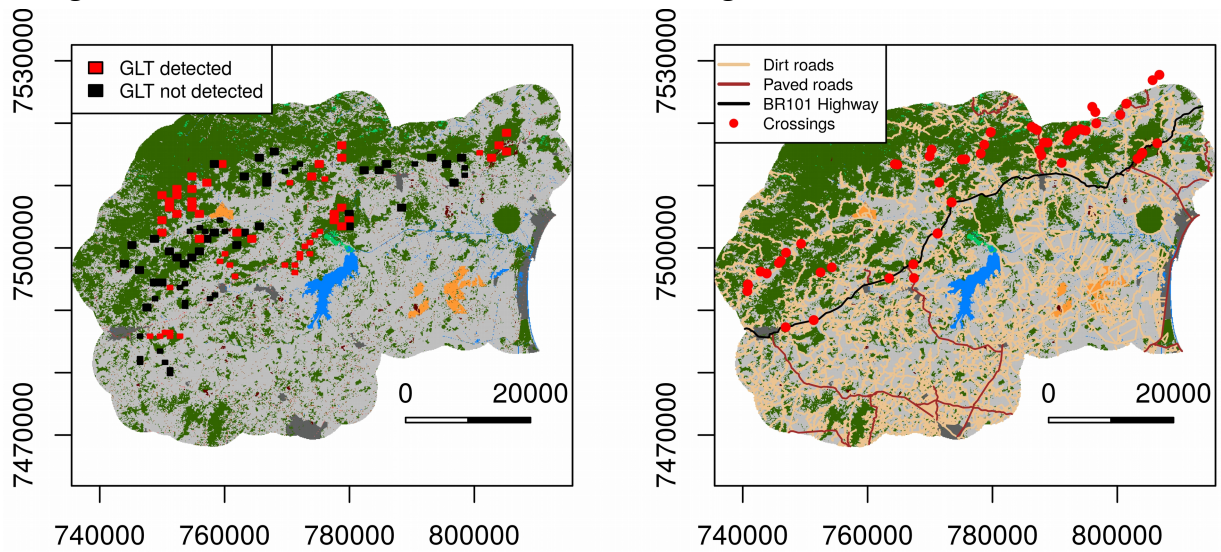
GLT occurrence region with plots where tamarins were or not detected. At the right, we show the three types of roads and places where tamarins were observed crossing roads or where they were road killed.

Appendix D – Threatened species on the Golden Lion Tamarin occurrence area

Table D1. List of species occurring at the São João River Basin that are critically endangered, endangered, vulnerable, or near threatened, according to the IUCN threaten categories.

Fragment	Species	Order	Common name	Method	IUCN category	Endemic (RJ)	Endemic (MA)	Ref.
PDA	*Trinomys eliasi*	Rodentia	Elias's Atlantic spiny-rat	literature	Vulnerable	yes	yes	1
PDA	*Hylaeamys seuanezi*	Rodentia	Large-headed rice rat	trapping	Near threatened	no	yes	1
PDA	*Hylaeamys oniscus*	Rodentia	Sowbug rice rat	literature record	Near threatened	no	yes	1
PDA	*Chrysocyon brachyurus*	Carnivora	Maned worlf	files	Near threatened	no	no	1
PDA	*Panthera onca*	Carnivora	Jaguar	literature record	Near threatened	no	no	1
PDA-União	*Lontra longicaudis*	Carnivora	Neotropical otter	observatio n files	Near threatened	no	no	1, 2
SJRB	*Bradypus torquatus*	Pilosa	Maned sloth	record files	Vulnerable	no	yes	1, 2, 3
PDA	*Claravis godefrida*	Columbiformes	Purple-winged ground dove	Inventory literature	Critically Endangered	no	no	4
SJRB	*Cotinga maculata*	Passeriformes	Banded cotinga	Inventory	Endangered	no	yes	5
União	*Myrmotherula urosticta*	Passeriformes	Band-tailed antwren	Inventory literature	Vulnerable	no	yes	4
PDA	*Myrmotherula minor*	Passeriformes	Salvadori's antwren	Inventory literature	Vulnerable	no	no	4
PDA	*Tangara peruviana*	Passeriformes	Black-backed tanager	Inventory literature	Vulnerable	no	yes	4

Fragment	Species	Order	Common name	Method	Status	Endemic (RJ)	Endemic (MA)	Ref.
SJRB	*Procnias nudicollis*	Passeriformes	Bare-throated bellbird	Inventory	Vulnerable	no	yes	5
PDA	*Phylloscartes paulista*	Passeriformes	Sao Paulo Tyrannulet	Inventory literature	Near threatened	no	no	4
SJRB	*Hemitriccus orbitatus*	Passeriformes	Eye-ringed Tody-Tyrant	Inventory	Near threatened	no	no	5
SJRB	*Laniisoma elegans*	Passeriformes	Shrike-like Cotinga	Inventory	Near threatened	no	yes	5
SJRB	*Ramphastos vitellinus*	Piciformes	Channel-billed toucan	Inventory	Vulnerable	no	no	5
PDA	*Malacoptila striata*	Piciformes	Crescent-chested puffbird	Inventory literature	Near threatened	no	no	4
SJRB	*Ramphodon naevius*	Caprimulgiformes	Saw-billed hermit	Inventory	Near threatened	no	yes	5
União	*Pyrrhura cruentata*	Psittaciformes	Ochre-marked parakeet	Inventory literature	Vulnerable	no	yes	4
União	*Amazona rhodocorytha*	Psittaciformes	Red-browed parrot	literature Inventory	Vulnerable	no	yes	4
SJRB	*Tinamus solitarius*	Struthioniformes	Solitary tinamou	Inventory	Near threatened	no	yes	5
SJRB	***Leontopithecus rosalia***	**Primates**	**Golden Lion Tamarin**	**several**	**Endangered**	**yes**	**yes**	**6**

Fragment: the fragment(s) where animals were detected. PDA: Poço das Antas protected area; União: União protected area; SJRB: different patches at the São João River Basin. Method: source of the sampled record. Endemic (RJ): whether the species is endemic between the species of the state of Rio de Janeiro. Endemic (MA): whether the species is endemic within the Atlantic Forest. Ref.: reference.

1. Brito et al. (2004).

2. MMA/ICMBio (2008a) - União Biological Reserve Management plan.

3. MMA/ICMBio (2008b) - São João River Basin Management plan.

4. Pacheco et al. (2010).

5. Araújo et al. (2008).

6. Holst et al. (2006).

Literature cited

Araújo, R. M. de, M. B. de Souza, and C. R. Ruiz-Miranda. 2008. Densidade e tamanho populacional de mamíferos cinegéticos em duas Unidades de Conservação do Estado do Rio de Janeiro, Brasil. Iheringia, Série Zoologia 98:391–396.

Brito, D., L. C. Oliveira, and M. A. R. Mello. 2004. An overview of mammalian conservation at Poço das Antas Biological Reserve, southeastern Brazil. Journal for Nature Conservation 12:219–228.

Dietz, J. M., C. A. Peres, and L. Pinder. 1997. Foraging ecology and use of space in wild golden lion tamarins (*Leontopithecus rosalia*). American Journal of Primatology 41:289–305.

GRASS Development Team. 2017. Geographic Resources Analysis Support System (GRASS) Software, Version 7.2. Open Source Geospatial Foundation. Electronic document: http://grass.osgeo.org.

Holst, B., P. Medici, O. Marinho-Filho, D. Kleiman, K. Leus, A. Pissinatti, G. Vivekananda, J. D. Ballou, K. Traylor-Holzer, B. Raboy, F. Passos, K. Vleeschouwer, and M. M. Montenegro. 2006. Lion tamarin population and habitat viability assessment workshop: final report. Page UCN/SSC Conservation Breeding Specialist Group. Apple Valley, MN, USA.

Kierulff, M. C. M., and A. B. Rylands. 2003. Census and distribution of the golden lion tamarin (*Leontopithecus rosalia*). American Journal of Primatology 59:29–44.

Martin, T. G., M. A. Burgman, F. Fidler, P. M. Kuhnert, S. Low-Choy, M. Mcbride, and K. Mengersen. 2012. Eliciting expert knowledge in Conservation Science. Conservation Biology 26:29–38.

McBride, M. F., and M. A. Burgman. 2012. What is expert knowledge, how is such knowledge gathered, and how do we use it to address questions in Landscape Ecology? Pages 11–38 *in* A. H. Perera, C. A. Drew, and C. J. Johnson, editors.Expert knowledge and its application in Landscape Ecology. Springer, New York.

McRae, B. H. 2006. Isolation by resistance. Evolution 60:1551–1561.

MMA/ICMBio. 2008a. Plano de Manejo da Reserva Biológica União.

MMA/ICMBio. 2008b. Plano de Manejo da Área de Proteção Ambiental da Bacia do Rio São João/Mico-Leão-Dourado.

Pacheco, J. F., I. Nascimento, D. C. Astor, and C. B. Cesar. 2010. Avifauna da Reserva Biológica de Poço das Antas, Silva Jardim, RJ. Atualidades Ornitológicas 157:55–74.

Paula, V. R. De. 2013. Comportamento de dispersão dos micos-leões-dourados (*Leontopithecus rosalia*, Linnaeus, 1766) reintroduzidos e seus descendentes em vida livre. Universidade Estadual do Norte Fluminense.

Procópio de Oliveira, P., M. C. M. Kieruff, and M. J. Lapenta. 2008. Dieta e área de uso de micos-leões-dourados na Reserva Biológica União, RJ. Pages 40–57*in* P. Procópio de Oliveira, A. D. Grativol, and C. R. Ruiz-Miranda, editors.Conservação do mico-leão-dourado: enfrentando os desafios de uma paisagem fragmentada. Universidade Estadual do Norte Fluminense Darcy Ribeiro, Campos dos Goytacazes.

Ruiz-Miranda, C. R., C. A. Archer, and D. G. Kleiman. 2002. Acousitc Differences Between Spontaneous and Induced Long Calls of Golden Lion Tamarins~1.Pdf. Folia Primatologica 620:124–131.

Seabra, V. da S. 2012. Análise da paisagem em apoio aos estudos de favorabilidade à recuperação florestal na bacia hidrográfica do rio São João Análise da paisagem em apoio aos estudos de favorabilidade à recuperação florestal na bacia hidrográfica do rio São João. Universidade Federal do Rio de Janeiro.

SOS Mata Atlântica, and Instituto Nacional de Pesquisas Espaciais. 2014. Atlas dos remanescentes florestais da Mata Atlântica, 2013-2014. http://www.sosma.org.br.

3 Predicting natural regeneration through landscape structure, movement of frugivore fauna, and seed dispersal

Bernardo Brandão S. Niebuhr[a,b,*], Flavia Santos Pinto[b], John Wesley Ribeiro[b], Karine Machado Costa[c], Ramon Felipe Bicudo da Silva[d], Milton Cezar Ribeiro[a,b]

[a] Universidade Estadual Paulista (UNESP), Instituto de Biociências, Rio Claro, SP, Brazil

[b] Laboratório de Ecologia Espacial e Conservação (LEEC), Departamento de Ecologia, UNESP, Rio Claro, SP, Brazil

[c] Agroicone, São Paulo, SP, Brazil

[d] Núcleo de Estudos e Pesquisas Ambientais, Universidade de Campinas (UNICAMP), Campinas, SP, Brazil

* Corresponding author. E-mail address: bernardo_brandaum@yahoo.com.br

Postal address: Laboratório de Ecologia Espacial e Conservação (LEEC), Departamento de Ecologia, UNESP, Rio Claro, SP, Brazil. Av. 24-A, 1515. CEP 13506-900.

Short title: Landscape regenerability through animal movement

Word count: 3804

Key-words: dispersal kernel; agent-based model (abm); animal-plant interactions; seed rain; landscape restoration

Abstract

Natural regeneration is a fundamental ecological process related to plant population dynamics that depend on seed dispersal. In turn, animal-mediated seed dispersal is highly influenced by the presence of dispersers, their behavior and movement characteristics, which also depend on landscape structure. Landscape revegetation is very costly worldwide, and natural regeneration is a promising perspective to increase the extent of restoration projects. Nonetheless, methods to identify landscapes of higher regenerability are still lacking. We presented two spatially explicit modeling approaches for simulating zoochorous seed dispersal and landscape regenerability from habitat patches into non-habitat matrices, which incorporate both landscape structure and animal movement. The models were exemplified in a case study in the Paraíba Valley, in the Brazilian Atlantic Forest, and their results were compared with regeneration data for two time periods to assess the potential of seed dispersal as a predictor of landscape-level forest regeneration. Landscape regenerability predicted by both models was higher in areas that regenerated than in areas that remained covered by pasture. This is the first approach to produce high resolution maps that identify areas with a high chance of natural regeneration. These maps may be used for planning low cost restoration strategies while enhancing their probability of success.

3.1 Introduction

Seed dispersal is a fundamental ecological process that guarantees plant population dynamics and forest natural regeneration (Holl, 1999; Nathan and Muller-Landau, 2000). It determines the potential area for plant recruitment and, in forest gaps, abandoned pastures and crops, for natural regeneration (Duncan and Chapman, 1999; Howe and Smallwood, 1982; Nathan and Muller-Landau, 2000). Landscape structure and composition strongly influence seed dispersal in fragmented landscapes. Fruit removal rate and seed dispersal distance have been shown to decrease with reduced area of, and increased isolation between, habitat patches in different ecosystems (McConkey et al., 2012), although the effects of habitat reduction may not be strong, depending on the seed dispersal measure (Markl et al., 2012). Regarding the consequences of seed rain for plant recruitment, forest cover (Crouzeilles et al., 2016; Crouzeilles and Curran, 2016) and the proximity to forest and forestry (Silva et al., 2016) influence forest regeneration, and matrix resistance affects genetic differentiation and diversity in plant populations (Carvalho et al., 2015).

Zoochory is the main dispersal syndrome for many plant species worldwide and, in tropical forests, it may be responsible for the dispersal of 90% of species (Howe and

Smallwood, 1982). Animal dispersers' natural history, behavior and movement lead to different patterns of seed dispersal (Morales et al., 2013; Russo et al., 2006). At the same time, landscape structure also affects the structure of animal communities, their interactions with plants and their movement characteristics (McConkey et al., 2012; Niebuhr et al., 2015). Therefore, the interplay between landscape structure and animal movement is key to understand seed dispersal at the landscape-level (Nathan and Muller-Landau, 2000).

Due to the global scenario of natural habitat loss and fragmentation, urban expansion, and intense land use change (Hansen et al., 2013), demands on the identification of areas with high potential for natural regeneration have increased (Lamb et al., 2005; Pinto et al., 2014). However, this demand has seldom been addressed, and the few studies that advanced in this direction did not explicitly account for the ecological processes involved in natural regeneration (e.g. Tambosi et al., 2014). To deal with this gap in the research, we propose the concept of landscape regenerability, the potential of landscapes to maintain fauna and flora, connect their populations, and promote seed dispersal and natural regeneration between habitat patches and beyond them, towards non-habitat areas (Box 1). Since seed dispersal is globally threatened by forest disturbance (Neuschulz et al., 2016), combining phenomenological and mechanistic approaches links patterns and processes (Nathan and Muller-Landau, 2000) to help us understand the factors that influence seed dispersal over large extents and how they affect the natural recovery of landscapes.

We present two spatially explicit modeling approaches, which incorporate both landscape structure and animal movement features, for simulating landscape regenerability based on zoochorous seed dispersal (Holl, 1999). First, we describe these two approaches, one based on landscape seed dispersal patterns and the other focused on the role of individual movement in seed dispersal and natural regeneration. Then, we exemplify and compare these approaches in a case study within the Brazilian Atlantic Forest in the Paraíba Valley, in São Paulo State. Finally, we assess the potential for seed dispersal modeling to predict landscape-level forest regeneration by comparing model outputs and maps of regeneration for two 10-year periods.

Box 1. **Landscape regenerability.** Landscape regenerability is the potential of disturbed environments in a landscape (e.g. pasture, agriculture, and forestry) to regenerate naturally after land abandonment. This may occur particularly when the landscape presents the necessary conditions to maintain fauna and flora at a level that allows connection between populations, promotes seed dispersal, and guarantees natural regeneration between habitat patches and beyond them, towards non-habitat areas. Regenerability is related to the ways the following elements interact to determine landscape-level forest regeneration through seed dispersal: landscape structure and composition; the biodiversity that populates the landscape; the characteristics of seed dispersal vectors; and the environmental, ecological, and social pressures on plant recruitment throughout the landscape. Understanding how these elements influence landscape regenerability may enable the identification of areas and socioecological contexts more prone to natural regeneration after land abandonment, which could potentially increase the extent of recovery achieved by large-scale restoration projects worldwide.

3.2 Material and Methods

We developed two methods to simulate natural regeneration through animal-mediated seed dispersal from habitat patches into non-habitat matrices. Both methods focus on seed dispersal towards matrix areas, since we are interested in forest succession and landscape natural regeneration. One model uses dispersal patterns to simulate seed dispersal and regenerability (phenomenological approach), and the other is based on an agent-based model (ABM) and mechanistically simulates the process of individual animal movement that disperses seeds (mechanistic approach). By comparing them, we seek to simulate and understand seed dispersal in large and fragmented landscapes and fill some knowledge gaps between seed dispersal pattern and process (Nathan and Muller-Landau, 2000). Both models are briefly described here, and a complete description of their details and implementation is found in the Appendices A and B.

To make model outputs easier to interpret and compare, we modeled not the seed deposition probability in space, but rather rescaled seed dispersal values between 0 and 1, and we henceforth call this seed dispersal *chance*. As seed dispersal is used as proxy for landscape regenerability, both terms will be used interchangeably.

3.2.1 Natural regenerability through landscape structure (LS)

The first modeling approach is phenomenological, i.e., it extrapolates seed dispersal patterns estimated from field data or from the literature to a landscape level (Nathan and

Muller-Landau, 2000). Instead of looking at individual adult plants as sources of seeds, it considers habitat patches where adult plants are abundant as sources for seed dispersal. Based on landscape structure, dispersal kernels are applied to simulate the seed rain chance at all positions outside habitat patches; hence, this approach is called *Landscape structure (LS) seed dispersal model.*

By simulating seed dispersal kernels, the LS model only considers the movement of animal dispersers implicitly, through the following assumptions: (i) habitat patch size positively affects the abundance and richness of animal seed dispersers; (ii) in landscapes where habitat patches shelter a higher disperser abundance and richness, the flux of seeds, the chance of seeds being deposited, and the regeneration potential beyond habitat patch edges, towards the matrix interior, are higher; (iii) as a consequence of (i) and (ii), habitat patch size influences seed dispersal kernels—seeds tend to go farther into the matrix around larger patches; (iv) seed rain chance and natural regenerability are higher in places near habitat patch edges and decrease with distance from them. These assumptions (and references supporting them) are shown graphically in Fig. A-1. Under these assumptions, the sum of all seed shadows surrounding the habitat patches in a landscape shows that seed dispersal chance tends to be higher in areas of high landscape connectivity, since animals may use these areas as preferred routes.

A step-by-step description of the model is presented below. A binary (habitat/non-habitat) map is used to produce a map of patch sizes. Then, habitat patches should be divided into ecologically meaningful size classes that represent different abundances, richness, or community compositions of plants and animal dispersers, which will deposit seeds in the surrounding matrix according to a distinct seed dispersal kernel (Figs. 1A and 1B). For each patch size class, a different seed dispersal kernel is applied (Figs. 1C and 1D). In the case study presented here, we modeled dispersal kernels in matrix pixels as negative exponential curves (as the emerging pattern reported by Ramos et al., 2018), with a scale parameter for each patch size class:

$$C(d, S) = 1/\lambda_S \exp(-d/\lambda_S)$$

where $C(d, S)$ is the seed dispersal chance, which depends on the distance from the pixel to the nearest habitat patch edge d and on the class of patch size S; and λ_S is the scale parameter, which varies with patch size and determines how far seeds may be deposited into the matrix. Although considering exponential kernels may not account for long distance seed dispersal events, which are essential for plant population dynamics (Jordano, 2017; Nathan and Muller-Landau, 2000), the variation of the scale parameter with patch size can capture seed dispersal

chance across different spatial extents (approach similar to Clark et al., 1999b).

A final landscape regenerability map considering the matrix around habitat patches is obtained by calculating summary statistics of seed dispersal maps for all patch size classes (Fig. 1E). Here, the final regenerability map was calculated as the maximum chance in each pixel of matrix on the map.

The script for running the LS seed dispersal model is open-source and was developed in Python to run in GRASS GIS—Geographic Resources Analysis Support System. It is freely available at GitHub (https://github.com/LEEClab/seed_dispersal_mapper).
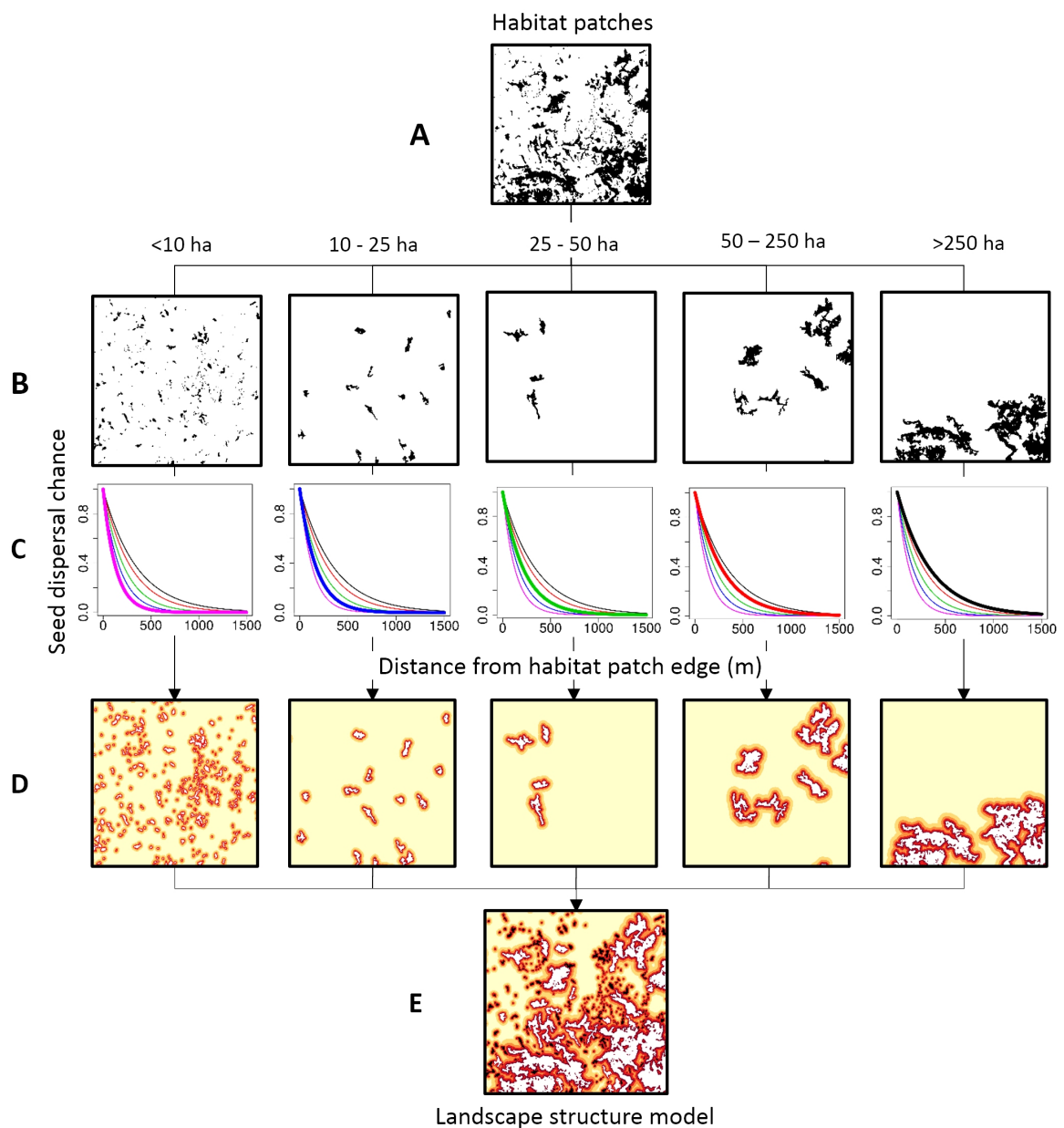
Figure 1. Flowchart of the simulation process for the landscape structure (LS) seed dispersal model. A habitat/non-habitat map (A) is used to produce maps that separate patches in size

classes (B). Around patches of each size class, a dispersal kernel is simulated (C) and a dispersal map is generated (D). In the last step, summary statistics are calculated to generate a final natural regenerability map around habitat patches (E).

3.2.2 Natural regenerability through animal movement (AM)

The mechanistic approach predicts seed dispersal chance and landscape regenerability from the simulation of fine-scale individual dispersal agents as they move, interact with each other and respond to landscape elements. It consists of modeling animal dispersers movement with an agent-based model (ABM) and using simulated animal trajectories to perform an analysis of spatial utilization distribution (Kie et al., 2010). In our ABM, we assume seeds are dispersed as frugivores move throughout the landscape, thus animal space-use patterns estimated from movement are used as a proxy for the seed dispersal pattern (Fig 2). The assumptions of the LS model (Fig. A-1) are still valid in the ABM, but the movement of dispersers is considered explicitly, as a process instead of an emerging pattern. Therefore, this modeling approach is called *Animal movement (AM) seed dispersal model*.

We used the Biologically scaled Dispersal Model (BioDIM), an ABM developed to simulate bird movement and population dynamics in fragmented landscapes and calibrated with data on Brazilian Atlantic Forest understory birds (Ribeiro, 2010). BioDIM simulates the movement of agents that are equally sensitive to landscape structure, and behave and use the landscape in nearly the same way, from habitat specialist to generalist animals.

To represent different bird ecological profiles, a habitat/non-habitat map is reclassified to represent landscape connectivity in the bird agent perspective (Figs. 2A and 2B). To focus the study on seed dispersal beyond habitat edges, we exemplified the model by simulating habitat generalist birds, which can cross 120 m between habitat patches in their routine movements and are more prone to disperse seeds in the matrix than specialist birds (Carlo and Morales, 2016). Agents may present two movement modes (Van Dyck and Baguette, 2005): (i) routine movement, characterized by tortuous trajectories and short displacements inside habitat patches that are functionally connected (here, patches closer than 120 m from each other); and (ii) dispersive/exploratory movement, characterized by faster movements and more rectilinear paths, which animals adopt when they leave a cluster of connected habitat patches to search for and establish their home range in another patch. The switch from routine to dispersive movement patterns is controlled in BioDIM mainly by density-dependent effects —when patches get overcrowded, virtual individuals are more prone to disperse throughout the landscape, aiming to find other habitat patch to establish a new territory.
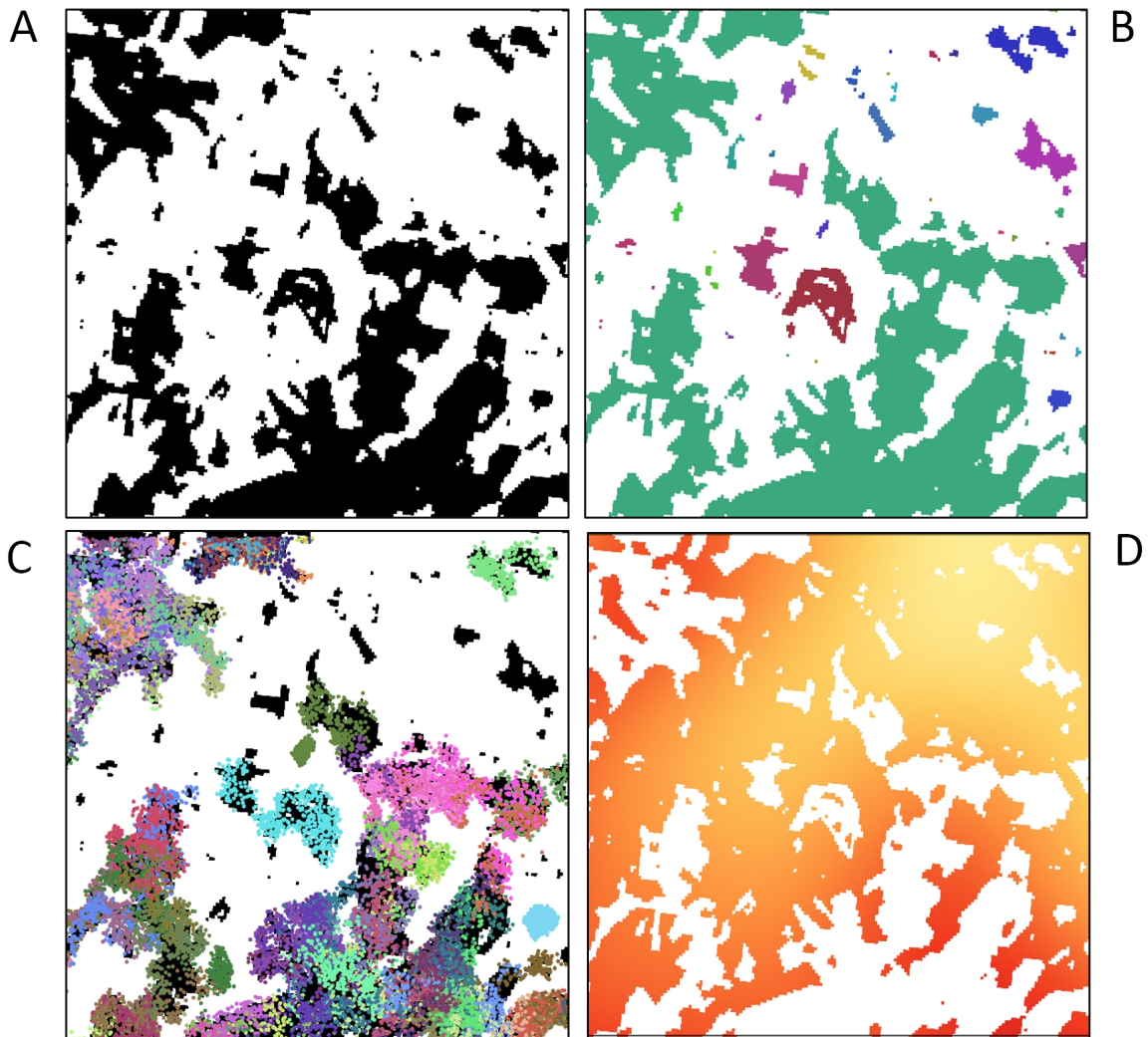
Figure 2. Steps of the animal movement seed dispersal model. A habitat/non-habitat map (A) is reclassified to represent the habitat patches that are functionally connected in the perspective of the seed disperser animal (B; colors represent clusters of functionally connected patches). This functional connectivity map is used as a stage for simulating animal trajectories (C; colors represent different individuals), from which we estimate the animal spatial utilization distribution and the natural regeneration chance in matrix (D; habitat patches are transparent to facilitate visualization).

Three parameters drive animal movement in the AM model: (a) individual space use area, (b) average step length, and (c) dispersal factor. The individual space use area represents the minimum area (in hectares) that an agent needs to live. It determines the carrying capacity of functionally connected habitat patches and controls the probability of individuals switching

from routine to dispersive movement in overcrowded patches. Average step length parameter represents the expected displacement length in routine movement, and the dispersal factor shows how much expected displacements increase in dispersive movement mode compared to the routine movement pattern.

Simulation starts with a number of agents located randomly inside habitat patches. At each time step, their location is updated according to the rules and parameters described above, until the simulation time is reached. The trajectory of all individuals is recorded after each simulation (Fig. 2C). Details on BioDIM implementation may be found in Ribeiro (2010) and Appendix B.

Simulated trajectories were used to generate utilization distributions, i.e., the probability of animals passing through different parts of the landscape, which served as a proxy for seed dispersal chance and natural regeneration occurring throughout the landscape (Fig. 2D). As in the LS model, seed dispersal chance surface was rescaled to the interval [0, 1]. The analyses of utilization distribution were performed in GRASS GIS using a bivariate Gaussian kernel.

3.2.3 Case study: comparing and validating the models

To illustrate and compare the LS and AM models, we conducted a case study in the Paraíba Valley, a region in the southeastern Brazilian Atlantic Forest located in the state of São Paulo (Fig. 3). Paraíba Valley covers 14,500 km² and is characterized by a steep relief, plentiful natural resources, and cities that link the two most important Brazilian industrial centers. Livestock farming transformed nearly 60% of the landscape into pasture during the twentieth century, but pasture abandonment has lead to many cases of natural regeneration in the region (Silva et al., 2017). These reasons make this area ideal for an examination of seed dispersal patterns and their connection to forest regeneration. The region is described in details in Appendix C.

Maps of forest and pasture distribution in the region were obtained from Silva et al. (2017). The authors inferred land use cover through supervised classification of Landsat 5 images, with 30 m spatial resolution, for the years 1985, 1995 and 2005. We defined regeneration areas by comparing the forest cover maps of different years. Forest maps represent all forest formations, including different stages of succession (e.g. shrubland, young forest) and mature forest, while pastures represent both managed and degraded areas. Training and test points of the classifier were carefully selected and evaluated in the field and through high resolution satellite images, guaranteeing classification accuracy between 85 to 88%

(Silva et al., 2017).

LS and AM models were run based on the forest spatial distribution in 1985 and 1995, simulating seed dispersal and natural regeneration patterns for the periods 1985–1995 and 1995–2005, respectively. Since most of the matrix area was covered by pasture, we considered only the simulated natural regenerability in pasture and ignored other land use classes. To compare the regenerability between modeling approaches, 10,000 random points were generated inside the pasture area for each year, and the resulting values from each model were compared via Pearson correlation.

To check whether the models could predict regeneration potential in pasture areas, we compared model outputs to observed forest regeneration in the periods 1985–1995 and 1995–2005. For each period, we identified the areas that were pasture at both the beginning and the end of the period, as well as the areas that had changed from pasture to forest (regenerated areas). For model validation, we first generated a random sample of 1,000 points in areas that remained pasture and 1,000 points in regenerated areas, which we used to test the difference in the predicted natural regenerability between pasture and regeneration areas (Student's t test, significance level 0.01). Then, for regenerated areas we plotted the observed frequency of regenerated pixels at each distance from forest edges and the average (and absolute) regenerability predicted by each model. For ease of comparison, observed frequency of regeneration pixels in each distance class was rescaled to the interval [0, 1].

3.3 Results

As expected, the LS model generated homogeneous seed dispersal kernels around forest patches, evident for both large and small patches, and predicted relatively high regenerability levels in the matrix. The anisotropy and high predicted values are the result of ignoring stochasticity in animal population sizes and in individual decisions regarding where and when to move. In turn, the AM model predicted lower regenerability values in general—see Figs. 3 and C-1 for comparisons between the patterns generated by the LS and AM models. Natural regenerability was high only between very close patches and forest branches, but this pattern was highly variable throughout the landscape (Figs. 3 and C-1) due to the effect of randomness in agent movement decisions and their proneness to stay next to patches during most of the simulation time—dispersal events were fast and agents rapidly found and settled in other forest patches. Although the predicted regenerability was higher for the LS than for the AM model, the output values were positively correlated (Appendix C, Fig. C-2).
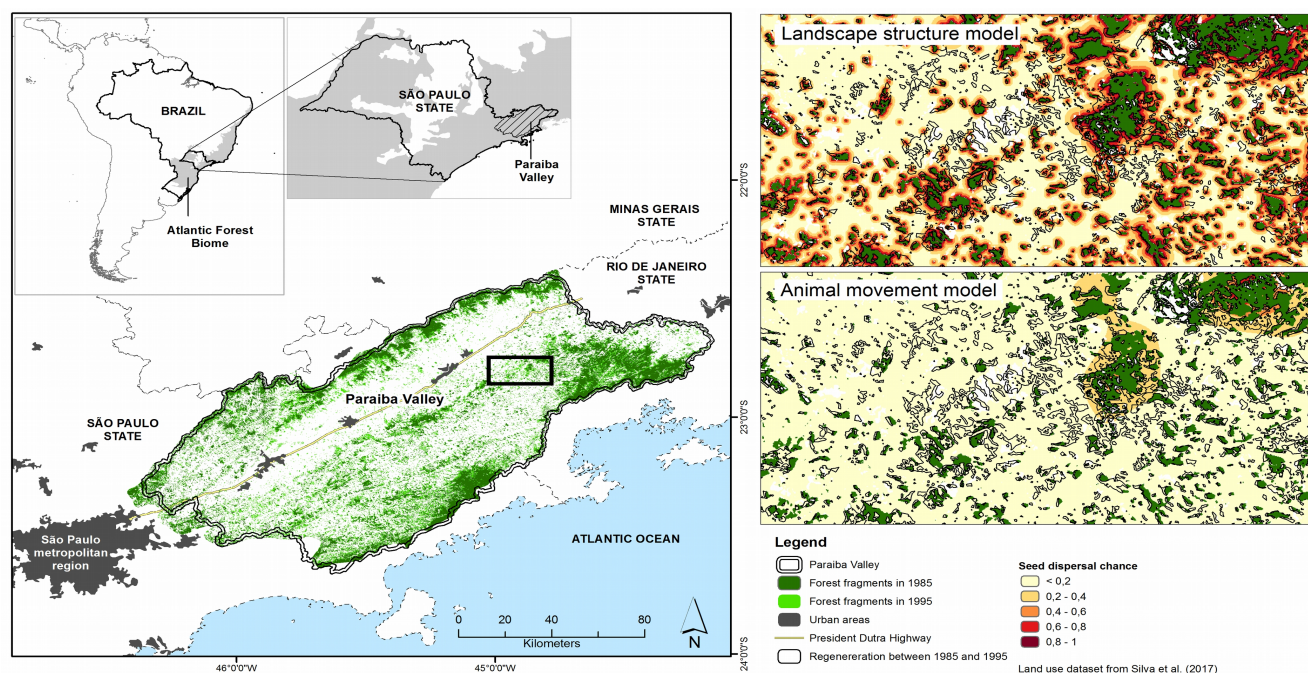
Figure 3. Paraíba Valley within the Brazilian Atlantic Forest, the case study region where we ran the LS and AM models; and forest patches and areas that regenerated in the period 1985–1995, used to compare and validate the models. The insets show a magnification of forest patches in 1985, areas regenerated in the period 1985–1995 and the natural regeneration chance predicted by each model in areas that were pasture in 1985.

When compared to forest regeneration data, both LS and AM models presented higher predicted chances of landscape regenerability for areas that had indeed regenerated than for areas that remained pasture (Fig. 4; LS model in 1985–1995: t = 23.15, d.f. = 1972, p << 0.001; AM model in 1985–1995: t = 14.66, d.f. = 1726, p << 0.001). For 1985–1995, average regenerability of regenerated areas was 0.58 for LS model and 0.16 for AM model, compared to 0.28 and 0.08 for areas that remained pasture. This difference was consistent in the period 1995–2005 (Appendix C, Fig. C-3). Furthermore, the average natural regenerability predicted by the LS model in regeneration pixels matched the observed frequency of regeneration pixels at different distances from habitat edges. However, for the case study, the AM model underestimated landscape-level regeneration (Appendix C, Fig. C-4).
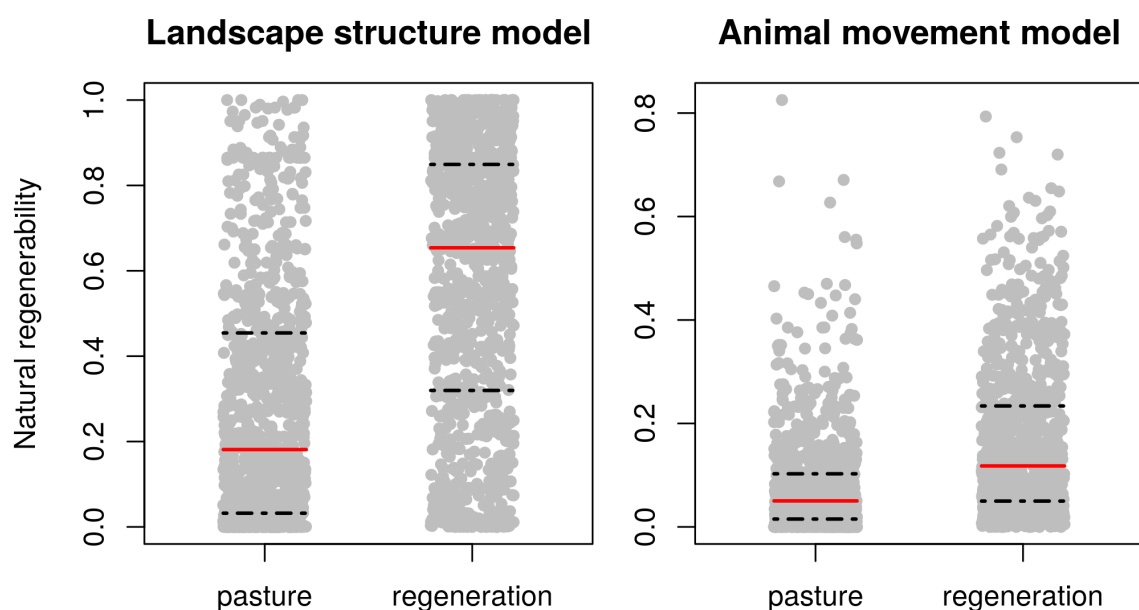
Figure 4. Comparison of natural regenerability, predicted by the LS and AM models, between areas that remained pasture and areas that regenerated in the period 1985–1995, in the Paraíba Valley. Regeneration chance in areas of observed regeneration are higher than in pasture areas for both models. Grey dots correspond to random points, red lines are median values, and dashed lines correspond to 25th and 75th percentiles.

3.4 Discussion

This is the first attempt to develop spatially explicit models of seed dispersal and natural regeneration in a landscape approach and compare the simulated regenerability surfaces with forest regeneration data. By developing a phenomenological and a mechanistic approach, the study has also taken a step further in linking patterns and processes related to plant seed dispersal, plant population dynamics, and natural regeneration.

To our knowledge, the LS model is the first phenomenological seed dispersal model that explicitly includes patch size and landscape connectivity. The inclusion of a seed dispersal-patch size dependence in the structure of the model is supported by the match between the predicted seed dispersal chance and observed regeneration patterns in the Paraíba Valley (Figs. 4, C-3, and C-4). Even predicting high seed dispersal values (Figs. 3 and C-1), the LS model output surface may be filtered by a threshold (e.g., only regenerability values above 0.7) and by different land use classes, as well as crossed with environmental (e.g., relief, temperature, and rainfall) and socioeconomic variables (e.g., urbanization level, farm credit incentives, and management history; Silva et al., 2016), to more accurately predict

landscape regenerability.

In the case study, the LS model was not parameterized with data, because seed dispersal field studies rarely focus on pasture or other matrix areas in large extent landscapes (but see Carlo and Morales, 2016)—researchers either study smaller regions (e.g., Duncan and Chapman, 1999; Martínez-Garza and González-Montagut, 1999) or do not focus on landscape variables (e.g., most studies analyzed by Bullock et al., 2017). Ideally, approaches such as the LS model should be parameterized based on seed dispersal kernels and natural regeneration data estimated from studies with a landscape perspective (Fahrig, 2005). For this purpose, sampling must be designed to detect variation in seed rain thoughtout the landscape, considering the landscape structure and composition as well as the scales at which landscape and local factors matter (Crouzeilles and Curran, 2016).

By incorporating animal movement as a process in the AM model, it was possible to track how animal space-use and seed dispersal patterns change in space and time, which opens avenues to simulate the regeneration process explicitly in time (e.g., see Sasal and Morales, 2013). The AM model predicted higher regenerability values in regenerated areas than in pasture, but presented low overall natural regeneration chance (Figs. 3 and C-1). Two actions may better harmonize the AM model outputs with the LS model outputs and the observed regeneration patterns: (i) summing the seed rain patterns generated by generalist birds with other disperser species profiles (e.g., bats, mammals, and other birds; Jordano et al., 2007); and (ii) averaging ABM track outputs over a large number of simulations to decrease the effects of stochasticity.

We generated seed disperser trajectories using the BioDIM platform, but other ABM (e.g. Morales et al., 2013; Ramos et al., 2018) or reaction-diffusion modeling (e.g. Ovaskainen, 2004) approaches that simulate animal movement in fragmented and heterogeneous landscapes may be equally suitable. Also, we recommend the explicit inclusion of three sets of processes in future modeling studies. First, by considering seed retention times and tracking the movement of seeds (beyond merely the movement of animal dispersers; e.g., Lenz et al., 2011; Ramos et al., 2018; Sasal and Morales, 2013), seed dispersal may be estimated more directly, with animal movement being an intermediate process (instead of a proxy). Second, plant recruitment and other post-dispersal factors may also be incorporated into mechanistic models to predict plant population dynamics and natural regeneration patterns more precisely (e.g. Sasal and Morales, 2013). Third, the models may also incorporate matrix permeability for different ecological groups of dispersers and the regeneration capacity of each type of land use.

The match between the modeling approaches and regeneration data indicates that simulated seed dispersal patterns may be used as a proxy for regeneration potential. However, it was expected that plant population dynamics and natural regeneration depend not only on seed dispersal, but also on ecological (e.g., microhabitat characteristics, competition and predation, temporal variation; Clark et al., 1999a; Nathan and Muller-Landau, 2000), environmental, and socioeconomic factors (Crouzeilles and Curran, 2016; Silva et al., 2016). This explains the great variation in the landscape regenerability modeled across regenerated and pasture areas (Figs. 4, C-3, and C-4), even though the predicted regenerability trends resembled the observed regeneration. Future simulation approaches should take some of these variables into account. Furthermore, by integrating the zoochorous seed dispersal surface generated by the LS or AM models with the results of modeling approaches for other seed dispersal syndromes in the same landscapes (Damschen et al., 2014), one may produce seed rain surfaces that better predict natural regeneration patterns.

Beyond their potential to explore ecological processes such as seed dispersal and plant population dynamics, the modeling approaches presented here, once parameterized, may help us understand how animal movement is related to seed dispersal and how these procesees influence natural regeneration. This understanding would enable the simulation of habitat regeneration potential over large-extent landscapes, which may be useful for planning strategies and policies guiding landscape-level forest restoration and the maintenance of biodiversity and ecosystem services provided by natural habitats. Furthermore, the identification of high regenerability areas may optimize efforts to select areas for natural regeneration and aid in planning low-cost restoration strategies.

3.5 References

Bullock, J.M., Mallada González, L., Tamme, R., Götzenberger, L., White, S.M., Pärtel, M., Hooftman, D.A.P., 2017. A synthesis of empirical plant dispersal kernels. J. Ecol. 105, 6–19. doi:10.1111/1365-2745.12666

Carlo, T.A., Morales, J.M., 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rarebiased seed dispersal. Ecology 97, 1819–1831. doi:10.1890/15-2147.1

Carvalho, C. da S., Ribeiro, M.C., Côrtes, M.C., Galetti, M., Collevatti, R.G., 2015. Contemporary and historic factors influence differently genetic differentiation and diversity in a tropical palm. Heredity (Edinb). 115, 216–224. doi:10.1038/hdy.2015.30

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J., Wyckoff, P., 1999a. Interpreting recruitment limitation in forests. Am. J. Bot. 86, 1–16. doi:10.2307/2656950

Clark, J.S., Silman, M., Kern, R., Macklin, E., HilleRisLambers, J., 1999b. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80, 1475–1494. doi:10.1890/0012-9658(1999)080[1475:SDNAFP]2.0.CO;2

Crouzeilles, R., Curran, M., 2016. Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. J. Appl. Ecol. 53, 440–448. doi:10.1111/1365-2664.12590

Crouzeilles, R., Curran, M., Ferreira, M.S., Lindenmayer, D.B., Grelle, C.E. V., Rey Benayas, J.M., 2016. A global meta-analysis on the ecological drivers of forest restoration success. Nat. Commun. 7, 11666. doi:10.1038/ncomms11666

Damschen, E.I., Baker, D. V., Bohrer, G., Nathan, R., Orrock, J.L., Turner, J.R., Brudvig, L.A., Haddad, N.M., Levey, D.J., Tewksbury, J.J., 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. Proc. Natl. Acad. Sci. U. S. A. 111, 3484–3489. doi:10.1073/pnas.1308968111

Duncan, R.S., Chapman, C.A., 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. Ecol. Appl. doi:10.2307/2641345

Fahrig, L., 2005. When is a landscape perspective important?, in: Wiens, J.A., Moss, M.R. (Eds.), Issues and Perspectives in Landscape Ecology. Cambridge University Press, Cambridge, pp. 3–10.

Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., Patapov, P.V., Moore, R., Hancher, M., Turubanova, S.A. a, Tyukavina, A., Thau, D., Stehman, S.V. V, Goetz, S.J.J., Loveland, T.R.R., Kommaredy, A., Egorov, A., Chini, L., Justice, C.O.O., Townshend, J.R.G.R.G., 2013. High-resolution global maps of 21st-Century forest cover change. Science (80-.). 342, 850–854. doi:10.1126/science.1244693

Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.

Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13, 201–228. doi:10.1146/annurev.es.13.110182.001221

Jordano, P., 2017. What is long-distance dispersal? And a taxonomy of dispersal events. J. Ecol. 105, 75–84. doi:10.1111/1365-2745.12690

Jordano, P., García, C., Godoy, J.A., García-Castaño, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proc. Natl. Acad. Sci. U. S. A. 104, 3278–3282. doi:10.1073/pnas.0606793104

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science (80-.). 310, 1628–1632. doi:10.1126/science.1111773

Lenz, J., Fiedler, W., Caprano, T., Friedrichs, W., Gaese, B.H., Wikelski, M., Böhning-Gaese, K., 2011. Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. Proc. R. Soc. B 278, 2257–2264. doi:10.1098/rspb.2010.2383

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., Böhning-Gaese, K., 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. Conserv. Biol. 26, 1072–1081. doi:10.1111/j.1523-1739.2012.01927.x

Martínez-Garza, C., González-Montagut, R., 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. Plant Ecol. 145, 255–265. doi:10.1023/A: 1009879505765

McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H., Santamaria, L., 2012. Seed dispersal in changing landscapes. Biol. Conserv. 146, 1–13. doi:10.1016/j.biocon.2011.09.018

Morales, J.M., García, D., Martínez, D., Rodriguez-Pérez, J., Herrera, J.M., 2013. Frugivore behavioural details matter for seed dispersal: a multi-species model for cantabrian thrushes and trees. PLoS One 8, e65216.

Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol. Evol. 15, 278–285. doi:10.1016/s0169-5347(00)01874-7

Neuschulz, E.L., Mueller, T., Schleuning, M., Böhning-Gaese, K., 2016. Pollination and seed dispersal are the most threatened processes of plant regeneration. Sci. Rep. 6, 29839. doi:10.1038/srep29839

Niebuhr, B.B.S., Wosniack, M.E., Santos, M.C., Raposo, E.P., Viswanathan, G.M., da Luz, M.G.E., Pie, M.R., 2015. Survival in patchy landscapes: the interplay between dispersal, habitat loss and fragmentation. Sci. Rep. 5, 11898. doi:10.1038/srep11898

Ovaskainen, O., 2004. Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. Ecology 85, 242–257. doi:10.1890/02-0706

Pinto, S.R., Melo, F., Tabarelli, M., Mesquita, C.A., Scaramuzza, C.A. de M., Castro, P., Carrascosa, H., Calmon, M., Rodrigues, R., César, R.G., Brancalion, P.H.S., 2014.
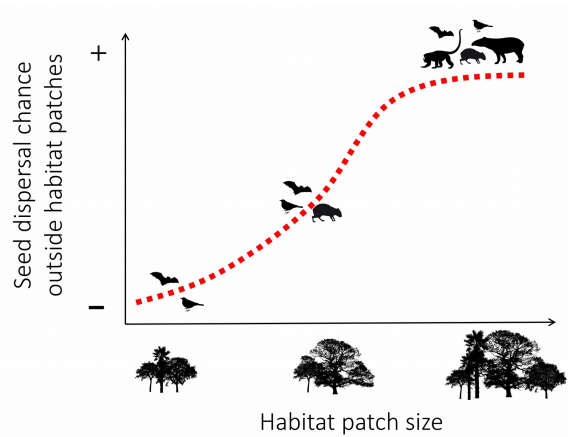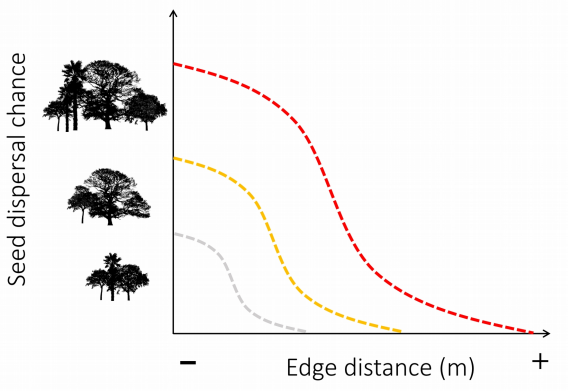
Governing and delivering a biome-wide eestoration initiative: the case of Atlantic Forest Restoration Pact in Brazil. Forests' 5, 2212–2229. doi:10.3390/f5092212

Ramos, D.C.T.L., Morales, J.M., Ribeiro, M.C., Alves, R.S.C., Pizo, M.A., 2018. Effects of bird movements on seed dispersal patterns in degraded areas: insights from simulation experiment. Submitted to Natureza & Conservação, special issue on "Applying movement ecology to biodiversity conservation and policy".

Ribeiro, M.C., 2010. Simulation models applied to the conservation of fragmented landscapes in the Brazilian Atlantic Forest. Universidade de São Paulo.

Russo, S.E., Portnoy, S., Augspurger, C.K., 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecology 87, 3160–3174.

Sasal, Y., Morales, J.M., 2013. Linking frugivore behavior to plant population dynamics. Oikos 122, 95–103. doi:10.1111/j.1600-0706.2012.20669.x

Silva, R.F.B. da, Batistella, M., Moran, E.F., 2016. Drivers of land change: Human-environment interactions and the Atlantic forest transition in the Paraíba Valley, Brazil. Land use policy 58, 133–144. doi:10.1016/j.landusepol.2016.07.021

Silva, R.F.B. da, Batistella, M., Moran, E.F., Lu, D., 2017. Land changes fostering Atlantic Forest transition in Brazil: Evidence from the Paraíba Valley. Prof. Geogr. 69, 80–93. doi:10.1080/00330124.2016.1178151

Tambosi, L.R., Martensen, A.C., Ribeiro, M.C., Metzger, J.P., 2014. A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. Restor. Ecol. 22, 169–177. doi:10.1111/rec.12049

Van Dyck, H., Baguette, M., 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? Basic Appl. Ecol. 6, 535–545.

SUPPLEMENTARY MATERIAL

APPENDIX A – DETAILS ON THE LANDSCAPE STRUCTURE (LS) MODEL

APPENDIX B – DETAILS ON THE ANIMAL MOVEMENT (AM) MODEL

APPENDIX C – CASE STUDY: COMPARISON BETWEEN MODELING APPROACHES AND VALIDATION

APPENDIX A – DETAILS ON THE LANDSCAPE STRUCTURE (LS) MODEL

Here we present the detailed version of the Landscape structure (LS) seed dispersal model, presented in the main text. The LS model is a phenomenological model, i.e., it extrapolates seed dispersal patterns estimated from field data or from the literature to a landscape level (Nathan and Muller-Landau, 2000). Instead of looking at individual plant adults as sources of seeds, it considers habitat patches where adult plants are abundant as sources for seed dispersal. Based on the landscape structure, dispersal kernels are applied to simulate the seed rain chance and landscape regenerability at all positions outside habitat patches.

By simulating seed dispersal kernels, the LS model only considers the movement of animal dispersers implicitly, through the following assumptions: (i) habitat patch size positively affects the abudance and richness of animal seed dispersers; (ii) in landscapes where habitat patches shelter a higher disperser abundance and richness, the flux of seeds, the chance of seeds being deposited, and the regeneration potential beyond habitat patch edges, towards the matrix interior, are higher; (iii) as a consequence of (i) and (ii), habitat patch size influences seed dispersal kernels—seeds tend to go farther into the matrix around larger patches; (iv) the seed rain chance and natural regenerability are higher in places near habitat patch edges and decrease with distance from them. These assumptions (and references supporting them) are shown in Fig. A-1. As a consequence of them, when the seed shadow around each habitat patch in a landscape is summed, seed dispersal chance is higher between habitat patches next to each other, as animals may move between them often and use these areas as preferred routes.

Graphical description	Textual description	References
	(i) Habitat patch size positively affects the abudance and richness of animal seed dispersers.	Arroyo-Rodríguez and Dias, 2010; Boyle and Smith, 2010; Breitbach et al., 2010; Cordeiro and Howe, 2003; Farwig et al., 2006; Kirika et al., 2008; Luck and Daly, 2003; Magioli et al., 2015; Pizo, 1997
	(ii) In landscapes where habitat patches shelter a higher disperser abundance and richness, the flux of seeds, the chance of seeds being deposited, and the regeneration potential beyond habitat patch edges, towards the matrix interior, are higher.	Bleher and Böhning-Gaese, 2001; Cordeiro and Howe, 2003; Galetti et al., 2013; García et al., 2010; Markl et al., 2012; McConkey et al., 2012; Ramos et al., 2018; Stevenson, 2011; Uriarte et al., 2015
	(iii) As a consequence of (i) and (ii), habitat patch size influences the seed dispersal kernels—seeds tend to go farther into the matrix around larger patches.	Markl et al., 2012; McConkey et al., 2012; Ramos et al., 2018; Uriarte et al., 2015
	(iv) Seed rain chance and natural regenerability are	Breitbach et al., 2012;

higher in places near habitat patch edges and decreases with distance from them.	Bullock et al., 2017; Clark et al., 1999; Holl, 1999; Martínez-Garza and González-Montagut, 1999; Nathan and Muller-Landau, 2000; Ramos et al., 2018; Silva et al., 2016

Figure A-1. Graphical and textual description of the landscape structure seed dispersal model assumptions, and references supporting each of them.

A step-by-step description of the model is presented below. First a binary (habitat/non-habitat) map is used to produce a map of patch sizes. Then, one should look at dividing habitat patches into ecologically meaningful size classes that represent patches with different abundances and richness of animal dispersers, which will deposit seeds in the surrounding matrix according to a distinct seed dispersal kernel (Figs. 1A and B of the main text). For instance, Magioli et al. (2015) found two thresholds in the relation between functional diversity and patch size of mammals in the Brazilian Atlantic Forest, i.e., they verified that patches in each of the three size classes (smaller than 60 ha, between 60 and 2050 ha, larger than 2050 ha) present different mammal functional diversity indices. A similar approach may be applied to identify patch size classes with different disperser abundances and compositions or different seed dispersal related functional diversities, so that these classes may be used to simulate the seed dispersal chance in the landscape.

In the case study presented here, we divided patches in 5 classes: (i) 0-10 ha, (ii) 10-25 ha, (iii) 25-50 ha, (iv) 50-250 ha, and (v) greater than 250 ha. Although these values were defined quite arbitrarily, these classes aim at representing the variation of patch sizes observed in the Atlantic Forest (Ribeiro et al., 2009), where the study is located. Since forest patches of less than 50 ha correspond to nearly 83.4% of all fragments of the Atlantic Forest (Ribeiro et al., 2009), they were divided into three size classes (instead of a single class). Patches with 50-250 ha correspond to 13.8% of all patches, and those with more than 250 ha, although important in terms of biodiversity and as sources of seed dispersal, represent only 2.8% of Atlantic Forest patches (Ribeiro et al., 2009).

For each patch size class, a different seed dispersal kernel is applied (Fig. 1C of the main text). In the case study presented here, we modeled dispersal kernels in matrix pixels as negative exponential curves (as the emerging pattern reported by Ramos et al., 2018), with a scale parameter for each patch size class:

$$C(d, S) = 1/\lambda_S \exp(-d/\lambda_S)$$

where $C(d, S)$ is the seed dispersal chance, which depends on the distance from the pixel to the nearest habitat patch edge d and on the class of patch size S; and λ_S is the scale parameter, which depends on the patch size and determines how far the seeds may be deposited into the matrix. Before starting the simulations, we multiplied the curves $C(d, S)$ by λ_S to keep the simulated seed dispersal chance between 0 and 1 (and for this reason we call it a dispersal chance instead of a probability). This operation makes the interpretation of the seed dispersal pattern easier and allows one to compare seed rain chance across different regions and landscapes with different extents. Although considering exponential kernels may not account for long distance seed dispersal events, which are essential for plant population dynamics (Jordano, 2017; Nathan and Muller-Landau, 2000), the variation of the scale parameter with patch size can capture the seed dispersal chance across different spatial extents (approach similar to Clark et al., 1999).

In the case study presented here, for each habitat patch size class the scale parameter of the exponential curve was chosen so that the chance of seeds being deposited over a certain limit distance (which may be related to the dispersers' movement scale) decreased to 0.05. The chosen parameters and corresponding kernels are shown in Table A-1 and Fig. A-2.

Table A-1. Parameters used for generating seed dispersal kernels for the case study presented here, for each habitat patch size class.

Habitat patch size (ha)	Limit distance/movement scale (m)	Scale parameter λ_S
< 10	350	130
10 − 25	500	170
25 − 50	650	220
50 − 250	850	290
> 250	1000	350
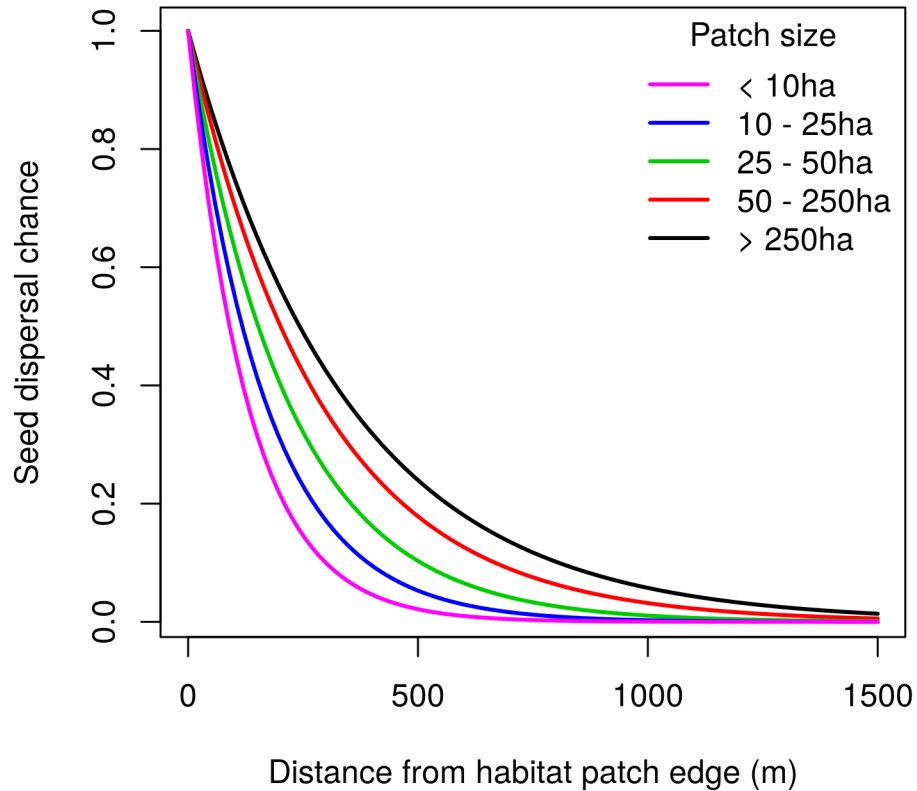
Figure A-2. Exponential seed dispersal kernel in matrices for each habitat patch size class, used in the case study (see Fig. 1 of the main text).

Applying each curve to the correspondent patch size class map results in patch size dependent regenerability maps. A final landscape regenerability map considering the matrix around habitat patches is then obtained by calculating summary statistics of this set of maps, such as the maximum value or the sum of the contributions of the dispersal process by dispersers in patches of each size class (Figs. 1D and 1E of the main text). In the case study presented here, we calculated the final regenerability map as the maximum chance in each pixel of matrix on the map; however, other measures may be taken, as the average, median, or sum of the pixel values.

The script for running the Landscape structure seed dispersal model is free and open-source and was developed in Python, that functions coupled with the free geographic information system GRASS GIS—Geographic Resources Analysis Support System (GRASS Development Team, 2015). It is freely available at GitHub (https://github.com/LEEClab/seed_dispersal_mapper) with instructions for running it.

The input map is a patch size raster map in which each pixel of the map represents the size (in hectares) of the habitat patch it is part of, and non-habitat pixels are represented by NoData (NA). This map may be generated, for instance, from binary (habitat/non-habitat) maps in softwares like FRAGSTATS (McGarigal et al., 2012) or LSMetrics (Ribeiro et al., 2017, in review). The final natural regenerability map is a raster with the same extent and resolution of the input map, with a regeneration chance value in each matrix pixel. The model can also filter the regenerability values by a land use class mask of interest (such as pasture, for example). The script also presents the option to export from GRASS GIS the raster maps generated along the simulation process (patch size and seed dispersal maps for each patch size class). As the dispersal kernels are parameterized based on distances measured in meters and areas measured in hectares, we encourage users of the model to use projections such as UTM, Polyconic, Lambert and Albers and avoid using geographic projections.

Although in our case study we simulated exponential dispersal kernels, the script is already prepared to simulate both Weibull (from which the exponential is a special case) and logistic kernels (Fig. A-3). Furthermore, as the tool is free and open-source, it is easy to change the dispersal kernel characteristics, so that it is possible to simulate more flexible and fat-tailed kernels (such as 2Dt, inverse-power law, or other probability distributions; Bullock et al., 2017; Clark et al., 1999; Jordano, 2017; Nathan and Muller-Landau, 2000). In the GitHub repository we have also shared an R script in which the users may explore and check the behavior of the kernels already implemented, before choosing parameters and simulating seed dispersal.

Also, despite the modeled seed dispersal and landscape regenerability was based mainly on assumptions related to the effects of habitat patch size on disperser abundance and seed deposition chance, other landscape (e.g. habitat cover, landscape heterogeneity, and the type of matrix surrounding habitat patches; Böhning-Gaese, 1997; García et al., 2010; McConkey et al., 2012) and local (e.g. fruit abundance, soil quality, land cover type and other seed deposition microsite characteristics; Breitbach et al., 2012; García et al., 2010; Nathan and Muller-Landau, 2000) variables may be used to define these amounts and predict seed dispersal patterns, and post-dispersal processes such as predation, competition, and secondary

dispersal can also be included to define the natural regeneration potential. Once one have fitted and studied these patterns explicitly in space, this aspects are easily modifiable in the LS seed dispersal code.
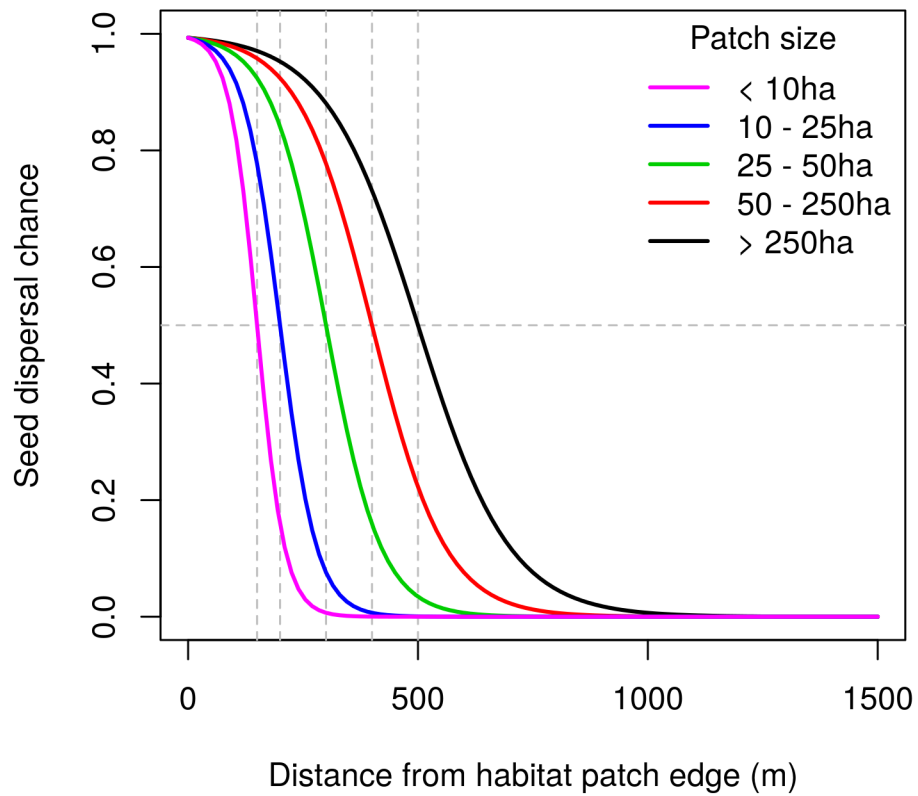
Figure A-3. Examples of logistic curves already implemented to simulate seed dispersal kernels in the Landscape structure model.

APPENDIX B – DETAILS ON THE ANIMAL MOVEMENT (AM) MODEL

Here we present the detailed version of the description of the Animal movement (AM) seed dispersal model, presented in the main text. Also, we give details on the definition of model parameters.

Description of the model

The Animal movement model is mechanistic and uses the simulation of fine-scale individual dispersal agents as they move, interact with each other and respond to landscape elements, in order to predict seed dispersal chance. The approach consists of modeling the movement of animal dispersers with an agent-based model (ABM) and using the simulated animal trajectories to perform an analysis of spatial utilization distribution (Kie et al., 2010). We then assume that animal frugivores disperse seeds as they move throughout the landscape, so one may use animal space-use patterns estimated from movement as a proxy for the seed dispersal pattern and the potential of natural regeneration thourhgout the landscape (Fig. 2 of the main text).

The aim of the ABM here is to represent a typical frugivory and seed dispersal scenario, rather than to reproduce exactly trajectories and dynamics as they are observed in nature. The rules that drive animal movement in the ABM were built so that the assumptions of the LS model (Fig. A-1) are still valid, but the movement of dispersers is considered explicitly, as a process instead of as an emerging pattern.

We used the Biologically scaled Dispersal Model (BioDIM), an ABM developed to simulate bird movement and population dynamics in fragmented landscapes and calibrated with data on Brazilian Atlantic Forest understory birds (Ribeiro, 2010). The model simulates the movement of agents with similar ecological characteristics, i.e., that are equally sensitive to landscape structure, and behave and use the landscape in nearly the same way. It is able to simulate from habitat specialist individuals, that prefer habitat patch interior and avoid edges and habitat corridors, to generalist animals that although using predominantly habitat can use the matrix and cross large gaps between habitat patches.

To represent different bird ecological profiles, a binary (habitat/non-habitat) map is reclassified to represent landscape connectivity in the bird agent perspective (Figs. 2A and 2B of the main text). To focus the study on seed dispersal and natural regeneration beyond habitat edges, we exemplified the model by simulating habitat generalist birds, which can cross 120 m between habitat patches in their routine movements, and then are more prone to disperse

seeds in the matrix than specialist birds (Carlo and Morales, 2016). Agents may present two movement modes (Van Dyck and Baguette, 2005): (i) routine movement, characterized by tortuous trajectories and short displacements inside habitat patches that are functionally connected for a given ecological profile (here, all patches closer than 120 m from each other); and (ii) dispersive/exploratory movement, characterized by faster movements and more rectilinear paths, which animals adopt when they leave a cluster of connected habitat patches to search for and establish their home range in another patch. The switch from routine to dispersive movement patterns is controlled in BioDIM mainly by density-dependent effects – when patches get overcrowded, virtual individuals are more prone to disperse throughout the landscape, aiming to find other habitat patch to establish a new territory.

Once the time step unit of simulations is defined, three main parameters drive animal movement in the model: (a) the individual space use area, (b) the average step length, and (c) the dispersal factor. The individual space use area represents the minimum area (in hectares) that an agent needs to live. It determines the carrying capacity of clusters of functionally connected habitat patches and controls the probability of individuals switching from routine to dispersive movement in case the patches are overcrowded. The routine movement mode is determined by a Brownian walk (Viswanathan et al., 2011), without directional preference and an expected displacement per time step defined by the average step length parameter (in meters). In turn, the dispersive movement mode is represented by a correlated random walk with a correlation parameter varying uniformly between 0.6 and 0.95 and an expected displacement length equals the multiplication between the step length and dispersal factor parameters (Bartumeus et al., 2008; Viswanathan et al., 2011). Because of this, the average step length parameter represents the expected displacement length in routine movement, and the dispersal factor shows how much expected displacements increase in the dispersive movement mode compared to the routine movement pattern.

In the beginning of each simulation, a starting number of bird agents is located randomly inside habitat patches. At each time step, their location is updated according to the rules and parameters described above, until the simulation time is reached. After each simulation, the trajectory of all animal individuals is recorded (Fig. 2C of the main text). More details on the BioDIM implementation may be found in Ribeiro (2010).

After trajectories were simulated, they were used to generate utilization distributions, that represent the probability of animals passing through different parts of the landscape. This utlization distributions served as a proxy for seed dispersal chance and natural regenerability throughout the landscape (Fig. 2D of the main text). As in the LS model, this seed dispersal

chance surface was rescaled to present seed dispersal values between 0 and 1; however, for a given study region, one may normalize the values to obtain a seed dispersal or natural regeneration *probability* surface.

The analyses of utilization distribution for generating natural regeneration chance surfaces were performed in GRASS GIS using a bivariate Gaussian kernel with the module *v.kernel* (Okabe et al., 2009). For illustration, the smoothing parameters were calculated as the optimal (reference) value for large sample sizes (Worton, 1989) and calculated over all the study area using the simulated bird disperser trajectories. This calculation resulted in the values h = 3300 and h = 3100 for the two simulated periods, 1985–1995 and 1995–2005. However, the value of the smoothing parameter may be decided based on other criteria, related to the scale of animal mobility or the scale in which landscape elements influence the species presence and movement, for example (Boscolo and Metzger, 2009; Jackson and Fahrig, 2015).

Here we used kernel density estimation (KDE) with the *v.kernel* module, which is able to quickly generate utilization distributions for very large datasets (in the order of billions of points) without losing map resolution. However, the UDs generated by it does not consider the inherent characteristics of movement data. Therefore, if it is computationally feasible, Brownian bridges (Horne et al., 2007), autocorrelated kernel density estimators (Fleming et al., 2015) or other estimators that consider animal trajectories should be used (Calabrese et al., 2016; Kie et al., 2010).

Parameter settings for simulations

The simulations we run to illustrate the AM model were performed considering generalist bird individuals that are able to cross 120 m matrix gaps between habitat patches. Besides being mainly frugivorous and some of the most important seed dispersers in tropical and temperate forests (Galetti et al., 2013; Jordano et al., 2007), birds are important in dispersing seeds from forest patches to pastures and open matrices (Carlo and Morales, 2016; Duncan and Chapman, 1999; Ramos et al., 2018).

Simulations considered each time step as 1 week and were run for an extension of 500 time steps, equivalent to nearly 10 years. Initial population size was considered as the maximum carrying capacity of the landscape, i.e., the ratio between the total habitat area in the landscape and the average individual space use area. As we aimed at simulating a general scenario rather than the population dynamics, we did not consider either mortality or stochastic variation in population size along time.

The parameters defined for the simulated individuals were:

(a) Individual space use area: random value defined in the beginning of each simulation, drawn from an uniform distribution between 5 and 30 ha. These values cover a range of home range areas estimated for many understory Atlantic Forest bird species (Hansbauer et al., 2008), as well as other tropical generalist birds (Cohen and Lindell, 2005).

(b) Average step length: 100 m (see, e.g., Da Silveira et al., 2016 and Ramos et al., 2018).

(c) Dispersal factor: 5.0. The dispersal factor (or, in turn, the average step length while dispersing) is a parameter of difficult empirical estimation, since it differs for distinct matrices and needs fine scale records of bird movement. For simplicity, here we consider a single dispersal factor for all individuals and matrices.

As the initial population size was considered at the landscape carrying capacity and the individual starting position is random in habitat areas, larger local populations tend to dwell larger habitat patches, which is in accordance with the assumption (i) of the LS model (Fig. A-1). Besides, as a result of the rules driving individual movement and the functional connectivity of nearby habitat patches (120 m in this case), the AM model also agrees with the assumptions (ii – iv) of the LS model, at least to the extent at which bird individuals can move between habitat patches. By considering these rules, the AM model aims to simulate as a process a typical emergent situation represented by the LS model.

APPENDIX C – CASE STUDY: COMPARISON BETWEEN MODELING APPROACHES AND VALIDATION

Description of the case study area

The case study to illustrate the application of the seed dispersal models was developed in the Paraíba Valley, in state of São Paulo, in Brazil. The Paraíba Valley region is delimited by the Paraíba do Sul river basin, which extends through the states of São Paulo, Rio de Janeiro and Minas Gerais. The portion of the basin located in the state of São Paulo covers about 14,500 km² (Instituto Florestal, 2010) and is composed by a landscape characterized by a steep relief with altitudes between 20 and 1,800 meters above sea level (Itani et al., 2011). The region's climate is classified as high-altitude tropical (Cwa), with rainy summer and dry winter, and precipitation between 50 and 250 mm/month (Itani et al., 2011). The region is mainly rural (55.4% of region area; SÃO PAULO (Estado), 2008) and have a high supply of natural resources, what ensures the hydric and energetic provision to more than 2 million inhabitants. However, the region also concentrates a relevant industrial center located around the President Dutra highway which connects two big metropolises, São Paulo and Rio de Janeiro. This contrasting context is a reason why the region demands a strategic environmental planning (Itani et al., 2011).

In the past, successive agricultural cycles have been responsible for native forest deforestation. The remaining native vegetation, located in Atlantic Forest biome, computed 370 thousand hectares in 2008, covering 26% of the basin area (Instituto Florestal, 2010). The native vegetation is highly fragmented: 70.4% of the vegetation pathces have less than 10 hectares and only 2.2% have more than 100 hectares (Instituto Florestal, 2010). Another consequence of these agricultural cycles is the soil degradation due to inappropriate soil management (Itani et al., 2011). After the coffee plantation decline, in the beginning of the twentieth century, one of the few viable activities in this degraded soil was livestock farming, which became to the main activity in the region (Itani et al., 2011), occupying around 60% of the basin rural area (Instituto Florestal, 2010). Livestock farming still remains as a substantial driver of deforestation; although, due to its low profitability, lots of pasture areas are currently been replaced by other activities. Forestry, for instance, in 2008, was already covering 10% (Instituto Florestal, 2010) of the rural area and continued to expand every year up to date (Arguello et al., 2010). Additionally, many of these pastures areas, which are underused or abandoned, already showed evidences of natural regeneration, as observed by Silva et al. (2017). In the context of the Brazilian Forest Code (Law 12,651/2012, Brazilian

Government), these specific areas can be strategic opportunities for environmental compliance. They may be used as a low cost restoration alternative to the comply of the property's own environmental liabilities, and also as a way to generate a new source of income for the land owners. For instance, this may be accomplished through the compensation mechanism, by which these pasture areas can compensate the Legal Reserve liabilities of other proprieties.

For the case study we run in the Paraíba Valley region, the forest fragments and regenerated areas (extracted from Silva et al., 2017), and model outputs in the period 1985–1995 are shown in Fig. 3 of the main text. For comparison, we present here the same data and simulation outputs for the period 1995–2005 (Fig. C-1). The results were consistent in both periods.
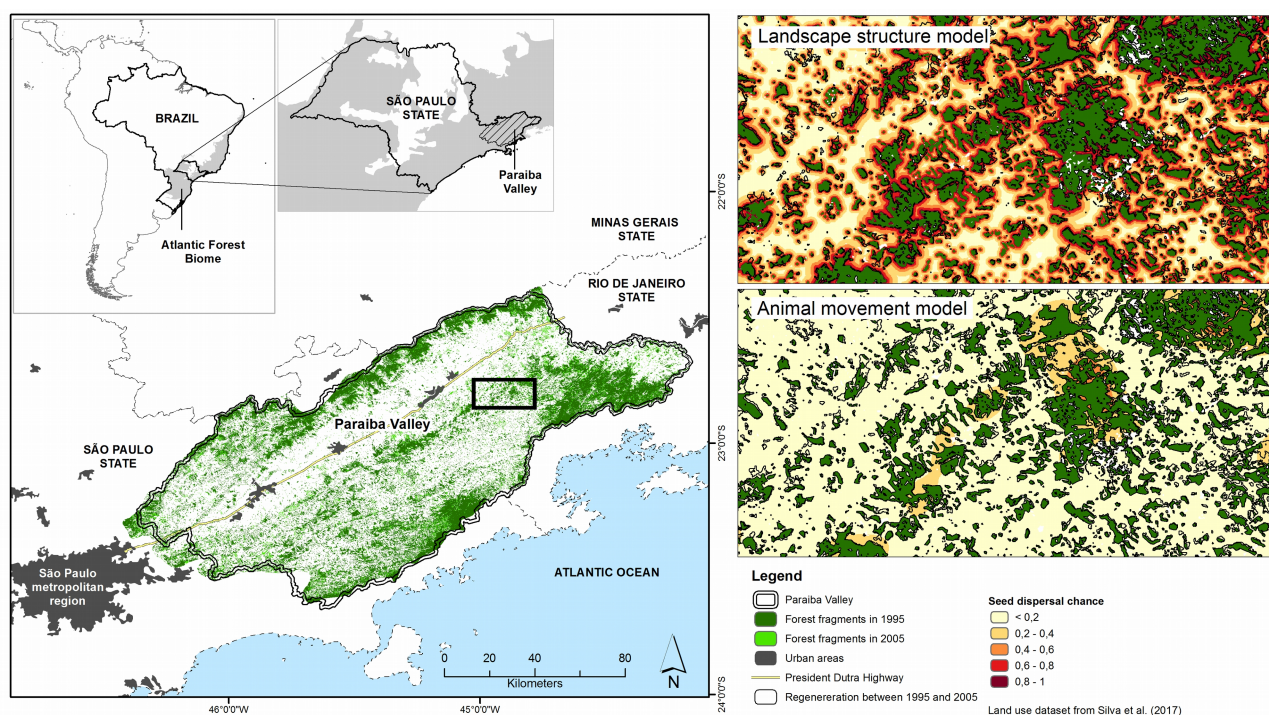
Figure C-1. Paraíba Valley within the Brazilian Atlantic Forest, the case study region where we ran the LS and AM models; and forest patches and areas regenerated in the period 1995–2005, used to compare and validate the models. The insets show a magnification of forest patches in 1995, areas regenerated in the period 1995–2005 and the natural regeneration chance predicted by each model in areas that were pasture in 1995. The figure is similar to Fig. 3 of the main text, but for the period 1995–2005.

Comparing model outputs

The comparison between the LS and AM model's predicted regeneration chance in the

Paraíba Valley presented a positive correlation for both periods analyzed [1985–1995: Pearson's r = 0.66 (95% CI 0.65-0.67), t = 87.48, d.f. = 9998, p << 0.001; 1995–2005: Pearson's r = 0.63 (95% CI 0.62-0.64), t = 80.52, d.f. = 9998, p << 0.001]. However, the LS model presented a regenerability higher than the AM model for most of the random points generated (Fig. C-2). This is also evident by visual comparison in Figs. 1E, 2D, 3 (of the main text), and C-1.
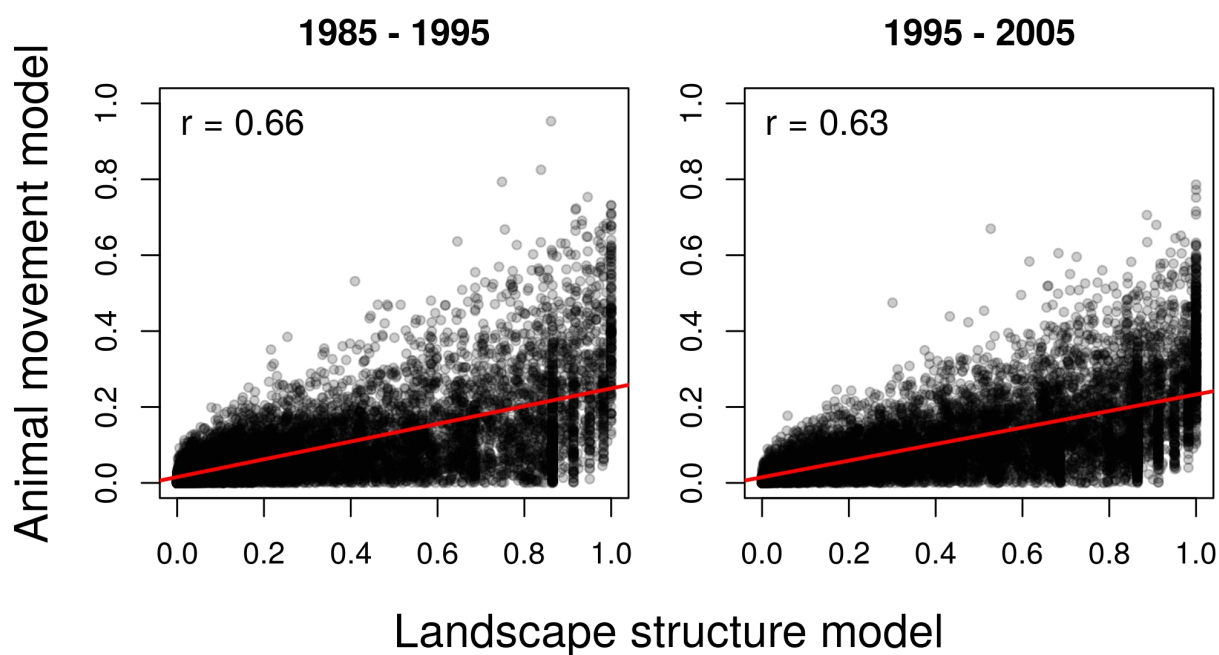
Figure C-2. Comparison between the natural regeneration chance predicted by each modeling approach, for 10,000 random locations generated in the Paraíba Valley region, in areas the were pasture in the beginning year for each period. The red line shows the tendency of a regression between models. The Pearson correlation coefficient estimated is shown in the upper left part of each plot.

Comparing models with regeneration data

The comparison between the natural regeneration chance predicted by the LS and AM models in areas that regenerated and areas that kept as pasture was shown in the main text for the period 1985–1995 (Fig. 4). The same pattern was observed for the period 1995-2005 (Fig. C-3; LS model in 1995–2005: t = 25.79, d.f. = 1936, p << 0.001; AM model in 1995-2005: t = 18.03, d.f. = 1762, p << 0.001). For this period, average dispersal chance on regenerated locations was 0.75 for the LS model and 0.21 for the AM model, values higher than in locations that kept being covered by pasture (average regenerability equals 0.43 and 0.11,

respectively).
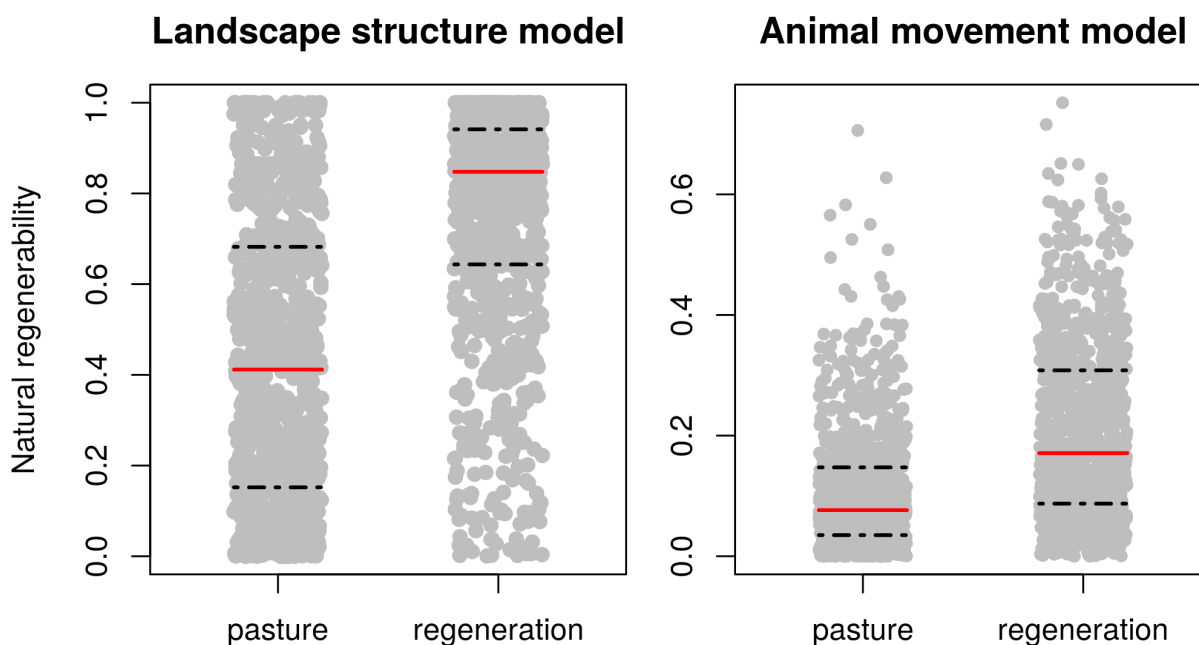
Figure C-3. Comparison of natural regenerability, predicted by the LS and AM models, between areas that remained pasture and areas that regenerated in the period 1995–2005, in the Paraíba Valley region. Regeneration chance in areas of observed regeneration are higher than in pasture areas for both models. Grey dots correspond to 1000 random points, red lines are median values, and dashed lines correspond to 25th and 75th percentiles.

When looking at the natural regenerability only in regeneration pixels and their variation with the distance from these pixels to the nearest habitat edge, the LS model presented a good match between the predicted values, averaged over the classes of distance from habitat edge, and the observed frequency of pixels that regenerated at these classes. This is clear for the period 1985–1995, but in the period 1995–2005 the average values overestimated the observed regeneration (Fig. C-4, upper plots). In turn, average regenerability predicted by the AM model was much lower than the observed frequency of regeneration (Fig. C-4, lower plots).

Landscape structure model
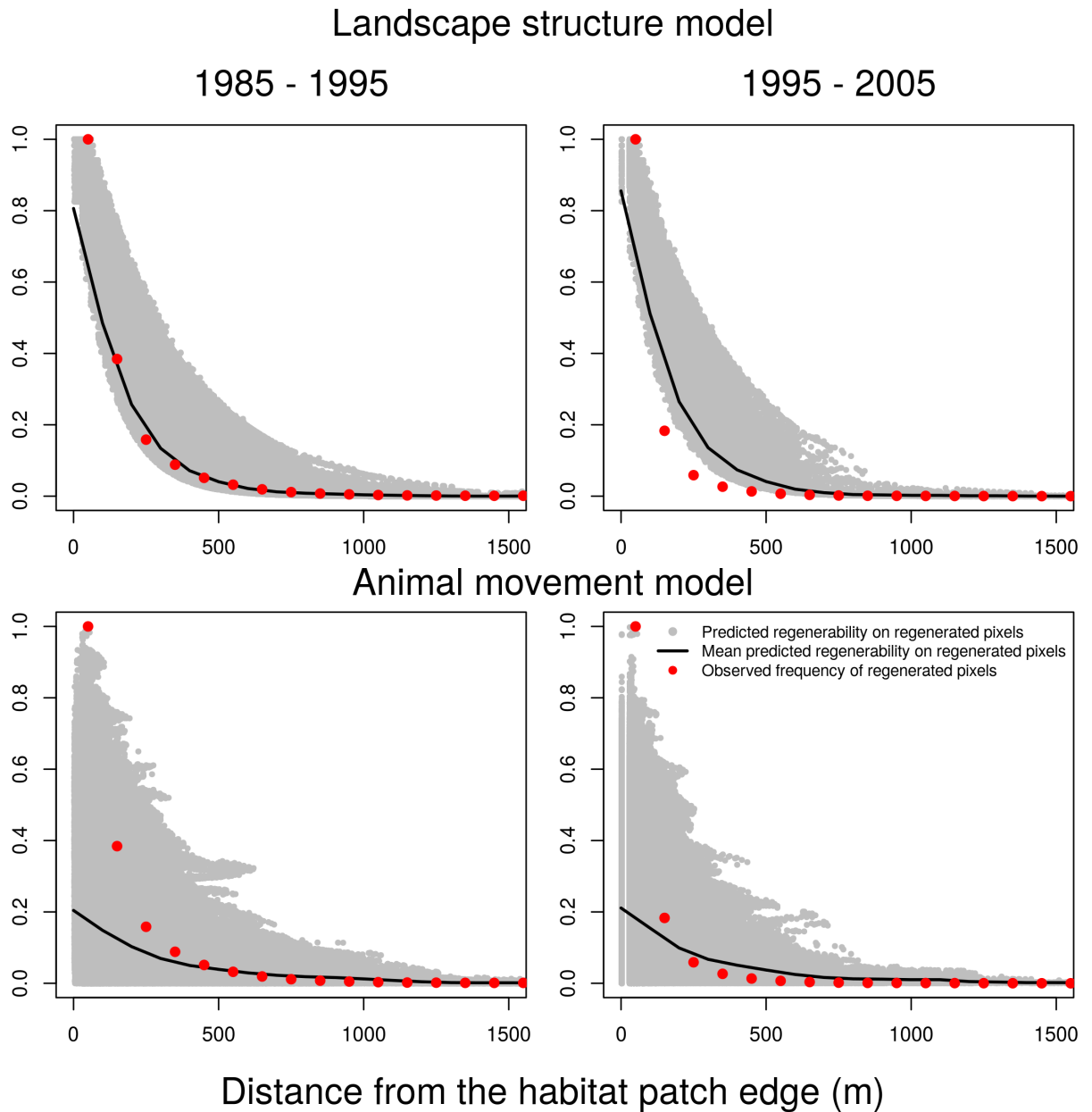
Figure C-4. Comparison between the natural regenerability pattern predicted by each model (above: LS model; below: AM model) and the observed regeneration, considering only pixels that regenerated in each period (left: 1985–1995; right: 1995–2005). The frequency of pixels that regenerated (red dots) at different distances form the habitat patch edges was rescaled to present values between 0 and 1 and facilitate the comparison with model outputs. Grey dots correspond to regenerability values in the whole set of pixels that regenerated in the landscape and black lines are the average predicted regeneration potential on pixels that regenerated at each class of distance from habitat edges.

LITERATURE CITED

Arguello, F.V.P., Batista, G.T., Ponzoni, F.J., Dias, N.W., 2010. Distribuição espacial de plantios de Eucalipto no trecho paulista da bacia hidrográfica Rio Paraíba do Sul, SP, Brasil [Spatial distribution of eucalyptus plantations in São Paulo stretch of Rio Paraiba do Sul watershed, SP, Brazil]. Ambi-Água 5, 133–146. doi:10.4136/ambi-agua.158

Arroyo-Rodríguez, V., Dias, P.A.D., 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. Am. J. Primatol. 72, 1–16. doi:10.1002/ajp.20753

Bartumeus, F., Catalan, J., Viswanathan, G.M., Raposo, E.P., da Luz, M.G.E., 2008. The influence of turning angles on the success of non-oriented animal searches. J. Theor. Biol. 252, 43–55.

Bleher, B., Böhning-Gaese, K., 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. Oecologia 129, 385–394. doi:10.1007/s004420100747

Böhning-Gaese, K., 1997. Determinant of avian species richness at different spatial scales. J. Biogeogr. 24, 49–60. doi:10.1111/j.1365-2699.1997.tb00049.x

Boscolo, D., Metzger, J.P., 2009. Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? Landsc. Ecol. 24, 907–918. doi:10.1007/s10980-009-9370-8

Boyle, S.A., Smith, A.T., 2010. Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? Biol. Conserv. 143, 1134–1143. doi:10.1016/j.biocon.2010.02.008

Breitbach, N., Böhning-Gaese, K., Laube, I., Schleuning, M., 2012. Short seed-dispersal distances and low seedling recruitment in farmland populations of bird-dispersed cherry trees. J. Ecol. 100, 1349–1358. doi:10.1111/1365-2745.12001

Breitbach, N., Laube, I., Steffan-dewenter, I., Böhning-Gaese, K., 2010. Bird diversity and seed dispersal along a human land-use gradient: high seed removal in structurally simple farmland. Oecologia 162, 965–976. doi:10.1007/s00442-009-1547-y

Bullock, J.M., Mallada González, L., Tamme, R., Götzenberger, L., White, S.M., Pärtel, M., Hooftman, D.A.P., 2017. A synthesis of empirical plant dispersal kernels. J. Ecol. 105, 6–19. doi:10.1111/1365-2745.12666

Calabrese, J.M., Fleming, C.H., Gurarie, E., Freckleton, R., 2016. Ctmm: an R Package for Analyzing Animal Relocation Data As a Continuous-Time Stochastic Process. Methods Ecol. Evol. 7, 1124–1132. doi:10.1111/2041-210X.12559

Carlo, T.A., Morales, J.M., 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rarebiased seed dispersal. Ecology 97, 1819–1831. doi:10.1890/15-2147.1

Clark, J.S., Silman, M., Kern, R., Macklin, E., HilleRisLambers, J., 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80, 1475–1494. doi:10.1890/0012-9658(1999)080[1475:SDNAFP]2.0.CO;2

Cohen, E.B., Lindell, C.A., 2005. Habitat use of adult White-throated Robins during the breeding season in a mosaic landscape in Costa Rica. J. F. Ornithol. 76, 279–286.

Cordeiro, N.J., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proc. Natl. Acad. Sci. U. S. A. 100, 14052–14056. doi:10.1073/pnas.2331023100

Da Silveira, N.S., Niebuhr, B.B.S., Muylaert, R. de L., Ribeiro, M.C., Pizo, M.A., 2016. Effects of land cover on the movement of frugivorous birds in a heterogeneous landscape. PLoS One 11, e0156688. doi:10.1371/journal.pone.0156688

Duncan, R.S., Chapman, C.A., 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. Ecol. Appl. doi:10.2307/2641345

Farwig, N., Böhning-Gaese, K., Bleher, B., 2006. Enhanced seed dispersal of Prunus africana in fragmented and disturbed forests? Oecologia 147, 238–252. doi:10.1007/s00442-005-0288-9

Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., Calabrese, J.M., Cooch, E.G., 2015. Rigorous home range estimation with movement data: A new autocorrelated kernel density estimator. Ecology 96, 1182–1188. doi:10.1890/14-2010.1.sm

Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C. da S., Collevatti, R.G., Pires, M.M., Guimarães Jr., P.R., Brancalion, P.H., Ribeiro, M.C., Jordano, P., 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. Science (80-.). 340, 1086–1091. doi:10.1126/science.1233774

García, D., Zamora, R., Amico, G.C., 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. Conserv. Biol. 24, 1070–1079. doi:10.1111/j.1523-1739.2009.01440.x

GRASS Development Team, 2015. Geographic Resources Analysis Support System (GRASS) Software, Version 7.0.

Hansbauer, M.M., Storch, I., Leu, S., Nieto-Holguin, J.P., Pimentel, R.G., Knauer, F., Metzger, J.P.W., 2008. Movements of neotropical understory passerines affected by

anthropogenic forest edges in the Brazilian Atlantic rainforest. Biol. Conserv. 141, 782–791. doi:10.1016/j.biocon.2008.01.002

Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.

Horne, J.S., Garton, E.O., Krone, S.M., Lewis, J.S., 2007. Analyzing animal movements using Brownian bridges. Ecology 88, 2354–2363.

Instituto Florestal, 2010. Inventário florestal da vegetação natural do Estado de São Paulo 2008/2009. São Paulo.

Itani, M.R., Barros, C.M., Figueiredo, F.E.L., Andrade, M.R.N., Mansor, M.T.C., Mangabeira, R.L., Carvalho, V.S. (Eds.), 2011. Subsídios ao planejamento ambiental: Unidade de Gerenciamento de Recursos hídricos Paraíba do Sul – UGRHI 02 [Environmental planning: Unit of water management of Paraíba do Sul]. SMA, São Paulo, Brazil.

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63. doi:10.1111/geb.12233

Jordano, P., 2017. What is long-distance dispersal? And a taxonomy of dispersal events. J. Ecol. 105, 75–84. doi:10.1111/1365-2745.12690

Jordano, P., García, C., Godoy, J.A., García-Castaño, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proc. Natl. Acad. Sci. U. S. A. 104, 3278–3282. doi:10.1073/pnas.0606793104

Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S., Gaillard, J.-M., Moorcroft, P.R., 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philos. Trans. R. Soc. B 365, 2221–2231.

Kirika, J.M., Bleher, B., Böhning-Gaese, K., Chira, R., Farwig, N., 2008. Fragmentation and local disturbance of forests reduce frugivore diversity and fruit removal in *Ficus thonningii* trees. Basic Appl. Ecol. 9, 663–672. doi:10.1016/j.baae.2007.07.002

Luck, G.W., Daly, G.C., 2003. Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. Ecol. Appl. 13, 235–247. doi:10.1890/1051-0761(2003)013[0235:TCBARC]2.0.CO;2

Magioli, M., Ribeiro, M.C., Ferraz, K.M.P.M.B., Rodrigues, M.G., 2015. Thresholds in the relationship between functional diversity and patch size for mammals in the Brazilian Atlantic Forest. Anim. Conserv. 18, 499–511. doi:10.1111/acv.12201

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., Böhning-Gaese, K., 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. Conserv. Biol. 26, 1072–1081. doi:10.1111/j.1523-

1739.2012.01927.x

Martínez-Garza, C., González-Montagut, R., 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. Plant Ecol. 145, 255–265. doi:10.1023/A: 1009879505765

McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H., Santamaria, L., 2012. Seed dispersal in changing landscapes. Biol. Conserv. 146, 1–13. doi:10.1016/j.biocon.2011.09.018

McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst.

Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol. Evol. 15, 278–285. doi:10.1016/s0169-5347(00)01874-7

Okabe, A., Satoh, T., Sugihara, K., 2009. A kernel density estimation method for networks, its computational method and a GIS-based tool. Int. J. Geogr. Inf. Sci. 23, 7–32. doi:10.1080/13658810802475491

Pizo, M.A., 1997. Seed dispersal and predation in two populations of Cabralea canjerana (Meliaceae) in the Atlantic Forest of southeastern Brazil. J. Trop. Ecol. 13, 559–578. doi:10.1017/S0266467400010713

Ramos, D.C.T.L., Morales, J.M., Ribeiro, M.C., Alves, R.S.C., Pizo, M.A., 2018. Effects of bird movements on seed dispersal patterns in degraded areas: insights from simulation experiment. Submitted to Natureza & Conservação, special issue on "Applying movement ecology to biodiversity conservation and policy".

Ribeiro, M.C., 2010. Simulation models applied to the conservation of fragmented landscapes in the Brazilian Atlantic Forest. Universidade de São Paulo.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153.

Ribeiro, M.C., Ribeiro, J.W., dos Santos, J.S., Niebuhr, B.B.S., Dodonov, P., Tonetti, V.R., Ribeiro, F.M., 2017. Landscape Metrics (LSMetrics): a tool for calculating landscape connectivity and other ecologically-scaled landscape metrics. Submitted to Natureza & Conservação, special issue on Connectivity.

SÃO PAULO (Estado), 2008. Secretaria de Agricultura e Abastecimento – SAA. Coordenadoria de Assistência Técnica Integral – CATI. Instituto de Economia Agrícola –

IEA. Levantamento censitário de unidades de produção agropecuária do Estado de São Paulo – 2007/2008. São Paulo.

Silva, R.F.B. da, Batistella, M., Moran, E.F., 2016. Drivers of land change: Human-environment interactions and the Atlantic forest transition in the Paraíba Valley, Brazil. Land use policy 58, 133–144. doi:10.1016/j.landusepol.2016.07.021

Silva, R.F.B. da, Batistella, M., Moran, E.F., Lu, D., 2017. Land changes fostering Atlantic Forest transition in Brazil: Evidence from the Paraíba Valley. Prof. Geogr. 69, 80–93. doi:10.1080/00330124.2016.1178151

Stevenson, P.R., 2011. The abundance of large Ateline monkeys is positively associated with the diversity of plants regenerating in Neotropical forests. Biotropica 43, 512–519.

Uriarte, M., Anciães, M., Silva, M.T.B. da, Rubim, P., Johnson, E., Bruna, E.M., 2015. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. Ecology 92, 924–937. doi:10.1890/10-0709.1

Van Dyck, H., Baguette, M., 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? Basic Appl. Ecol. 6, 535–545.

Viswanathan, G.M., da Luz, M.G.E., Raposo, E.P., Stanley, H.E., 2011. The Physics of Foraging: an Introduction to Random Searches and Biological Encounters. Cambridge University Press, Cambridge.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168.

Considerações finais

Na presente tese buscamos nos aprofundar no conceito de conectividade de paisagens, nas suas causas e consequências, bem como modelar como ela está relacionada à dinâmica de populações e ao processo ecológico de dispersão de sementes, à luz de elementos de ecologia de paisagens e de ecologia do movimento. Para isso, utilizamos sistemas de informação geográfica, ferramentas estatísticas e de computação a as combinamos a dados de diferentes naturezas, desde mapeamentos produzidos em diferentes escalas e contextos, para identificar as características e mudanças no usos da terra nos biomas Mata Atlântica e Amazônia, até dados da literatura sobre a movimentação de várias espécies, e dados brutos a respeito da genética, ocorrência, e uso do espaço para os micos leões dourados. Um primeiro olhar descuidado pode passar sem notar a conexão entre as diferentes abordagens. Como ressaltado anteriormente, nosso foco não caiu sobre organismos ou ecossistemas específico, mas em como o espaço e o movimento dos organismos afetam a conectividade e diferentes processos ecológicos, em diferentes contextos, e como eles podem nos auxiliar a entender os processos por trás dos padrões ecológicos. Aqui retomamos as três abordagens, os principais resultados, e suas consequências potenciais para conservação e restauração da biodiversidade, levantando seus pontos fortes e limitações.

Primeiramente, desenvolvemos um pacote de acesso livre e código aberto, o LSMetrics, que tem o intuito de calcular a conectividade e gerar métricas de paisagem de maneira ecologicamente calibrada, levando em conta a percepção e o comportamento das espécies. Utilizamos ferramentas de SIG, que avaliam aspectos da estrutura da paisagem, e construímos um sistema em que a conectividade e outras métricas podem ser mensuradas para espécies distintas, com diferentes capacidades de movimentação na matriz, considerando múltiplas escalas e ambientes. Seu potencial uso foi ilustrado em duas aplicações. Na primeira, avaliamos o status de fragmentação da Amazônia brasileira: calculamos o tamanho dos fragmentos, a área funcionalmente conectada e a área de bordas para descrever estatisticamente e espacialmente quanto há de cada tipo de cobertura da terra na Amazônia, onde está concentrada a floresta e quais áreas estão sofrendo mais mudanças. Os cálculos e estatísticas são simples, mas representam um uso importante de métricas da paisagem e da conectividade para entender o processo de fragmentação e planejar esforços de conservação (veja, p. ex., Ribeiro et al. 2009).

A segunda aplicação exemplifica a utilização de métricas de conectividade e heterogeneidade da paisagem para o desenho experimental em ecologia de paisagens. Para

além desses usos, as métricas geradas podem ser úteis desde o planejamento de pesquisas e a realização de suas análises estatísticas para compreender dinâmicas ecológicas até o planejamento para conservação e restauração, buscando conexões entre manchas de habitat e espacializando a maneira como diferentes organismos enxergam as mesmas paisagens. Apesar de apresentar somente algumas métricas simples, o LSMetrics consegue integrar em seu cálculo a estrutura da paisagem e as características das espécies, de forma a a complementar outras ferramentas existentes na literatura (FRAGSTATS: McGarigal et al. 2012; Guidos: Vogt & Riitters 2017; r.pi: Wegmann et al. 2018). Além disso, o fato de ser livre e ter seu código aberto à contribuição de qualquer um faz a ferramenta em constante construção, sempre aberta à implementação de novas métricas e maneiras de calcular a conectividade. Por exemplo, diversas outras métricas foram e estão sendo desenvolvidas pelos membros do Laboratório de Ecologia Espacial e Conservação, da UNESP, na realização de diferentes pesquisas de em ecologia espacial, e em breve serão incorporadas ao pacote LSMetrics para utilização do público em geral nos mais diversos contexos.

Na segunda abordagem, partimos desse contexto mais geral para um caso específico – a avaliação da conectividade da paisagem habitat pelos micos leões dourado, uma espécie de primata ameaçada da Mata Atlântica. Essa avaliação foi feita considerando as duas componentes da conectividade – a estrutural e a funcional. A conectividade estrutural foi avaliada ao calcularmos os tamanhos de fragmentos e as proporções de floresta que se encontram a diferentes distâncias da borda. A conectividade funcional, por sua vez, foi avaliada de três formas: considerando a capacidade de cruzamento na matriz por micos leões e outros organismos que ocorrem na região, numa abordagem multi-espécie, utilizando o LSMetrics; por meio de marcadores genéticos, considerando que o relacionamento genético entre indivíduos é um dos indicadores diretos da conectividade funcional da paisagem; pela simulação de corredores e fluxos de corrente, que consideram a estrutura da paisagem e a resistência dos organismos à se movimentarem por diferentes usos da terra. Unindo essas abordagens, pudemos compreender as dimensões da conectividade dessa paisagem, levando em conta essa espécie bandeira, o mico leão dourado, bem como outros organismos que ocorrem na região, e pensar em alternativas para a recuperação da conectividade entre fragmentos florestais.

Em específico, avaliamos o papel que diferentes tipos de estradas têm sobre a conectividade da paisagem. Observamos que tanto estradas pavimentadas quanto estradas de terra afetam a dispersão e reprodução de micos leões, o que nos indica que medidas que visem a recuperação da conectividade devem focar em ambos os tipos de estradas, e não somente

naquelas maiores e maior tráfego de veículos, como é o caso da BR-101. A simulação de corredores permitiu indicar locais ao longo da rodovia onde passagens de fauna e outras medidas mitigatórias podem ser mais úteis e eficientes, o que pode ser ampliado para outras estradas e desconexões entre fragmentos florestais na paisagem. Uma passagem de fauna florestada já está em planejamento ao longo da BR-101, fruto do diálogo entre a Associação do Mico Leão Dourado, o IBAMA, o ICMBio, a ANTT, a concessionaria Arteris, e outras organizações. No entanto, essa passagem ainda precisa ser implantada, e monitorada ao longo do tempo. Esperamos que nossa contribuição seja útil para propor a multiplicação de medidas eficientes que conectem às populações, não somente ao longo da BR101 como em outros locais importante para manter o fluxo gênico e a viabilidade de populações de micos leões e de outras espécies da região.

Estudos futuros, a fim de entender mais pormenorizadamente como a estrutura da paisagem e as estradas afetam a conectividade das populações de micos leões e outras espécies deve considerar, pelo menos: (i) um desenho amostral que não seja simplesmente baseado nas oportunidade de observação, mas que avalie e amostre de maneira sistemática indivíduos dos dois lados de BR101 e das outras estradas da região; (ii) a aplicação de modelos baseados em indivíduos, como aqueles utilizados no terceiro capítulo, para simular a dinâmica populacional dos micos leões e modelar explicitamente a movimentação e a dispersão dos indivíduos, considerando a estrutura da paisagem e o comportamento dos dispersores, além de aspectos de mortalidade e reprodução. Esse segundo ponto já está em desenvolvimento, mas não pôde ser incluído nessa tese.

Por fim, como a conectividade afeta a movimentação da fauna, e por sua vez como a movimentação da fauna pode levar à dispersão de sementes e à regeneração natural – que em última análise tende a aumentar a área de habitat e a conectividade das paisagens. Buscamos compreender como a estrutura da paisagem e a movimentação da fauna frugívora afetam o padrão de dispersão de sementes dos fragmentos florestais para matrizes não florestais, e como esse processo está relacionado ao potencial de regeneração natural. Desenvolvemos um modelo fenomenológico e um modelo baseado em indivíduos, ambos considerando o espaço e a movimentação, para prever a dispersão de sementes. Esses modelos foram contrastados com dados de regeneração natural de pastagens do Vale do Paraíba, na Mata Atlântica, e os padrões gerais de dispersão de sementes e regeneração natural foram coincidentes. Diversos outros fatores influenciam a regeneração natural, que precisam ser considerados conjuntamente em modelos de simulação futuros. No entanto, nossa abordagem dá um passo nessa direção ao simular a dispersão potencial de sementes e olhar processualmente como ela afeta a

regeneração.

A identificação de áreas com alto potencial de regeneração natural é de extrema importância para ações que visem a recuperação de ambientes degradados e a restauração de habitats, ainda mais em contextos de extrema fragmentação como na Mata Atlântica brasileira (Rodrigues et al. 2009). Nossos modelos vem a somar nessa empreitada, e podem servir como ferramenta para a identificação de tais áreas em diferentes ecossistemas – os códigos para sua aplicação também são livre e de acesso aberto. Os modelos já foram aplicados para toda a Mata Atlântica, e estão agora sendo re-ajustados e validados, e suas consequências para a biodiversidade avaliadas. Uma vez isso pronto, esse pode ser um importante instrumento que contribua para a priorização de áreas para restauração passiva e para o planejamento da restauração da conectividade da Mata Atlântica.

Referêcias

McGarigal K, Cushman SA, Ene E. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available from http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation **142**:1141–1153.

Rodrigues RR, Brancalion PHS, Isenhagen I, editors. 2009. Pacto pela restauração da Mata Atlântica: Referencial dos conceitos e ações de restauração florestal. LERF/ESALQ/Instituto BioAtlântica, São Paulo.

Vogt P, Riitters K. 2017. GuidosToolbox: universal digital image object analysis. European Journal of Remote Sensing **50**:352–361. Taylor & Francis. Available from https://www.tandfonline.com/doi/full/10.1080/22797254.2017.1330650.

Wegmann M, Leutner BF, Metz M, Neteler M, Dech S, Rocchini D. 2018. r.pi: A GRASS GIS package for semi-automatic spatial pattern analysis of remotely sensed land cover data. Methods in Ecology and Evolution **9**:191–199.