CALEBE PEREIRA MENDES

PATCH SIZE, SHAPE AND EDGE DISTANCE INFLUENCES SEED PREDATION IN A KEYSTONE PALM IN TROPICAL RAINFORESTS

Dissertação apresentada ao Instituto de Biociências do Campus de Rio Claro, Universidade Estadual Paulista Júlio de Mesquita Filho, como parte dos requisitos para obtenção do título de Mestre em Ciências Biológicas (Zoologia).

Orientador: Mauro Galetti
Co-orientador: Milton Ribeiro

Rio Claro
2014

574.5 Mendes, Calebe
M538p Patch size, shape and edge distance influences seed predation in a keystone palm in tropical rainforests / Calebe Mendes. - Rio Claro, 2014
50 f. : il., figs., gráfs., tabs., fots., mapas

Dissertação (mestrado) - Universidade Estadual Paulista, Instituto de Biociências de Rio Claro
Orientador: Mauro Galetti
Coorientador: Milton C. Ribeiro

1. Ecologia. 2. Esquilo. 3. Invertebrados. 4. Jerivá. 5. Roedores. 6. Syagrus romanzoffiana. 7. Ecologia da paisagem. I. Título.

Ficha Catalográfica elaborada pela STATI - Biblioteca da UNESP
Campus de Rio Claro/SP

unesp UNIVERSIDADE ESTADUAL PAULISTA
CAMPUS DE RIO CLARO
INSTITUTO DE BIOCIÊNCIAS DE RIO CLARO

CERTIFICADO DE APROVAÇÃO

TÍTULO: PATH SIZE, SHAPE AND EDGE DISTANCE INFLUENCES SEED PREDATION IN A KEYSTONE PALM IN TROPICAL RAINFORESTS

AUTORA: CALEBE PEREIRA MENDES
ORIENTADOR: Prof. Dr. MAURO GALETTI RODRIGUES
CO-ORIENTADOR: Prof. Dr. MILTON CEZAR RIBEIRO

Aprovada como parte das exigências para obtenção do Título de MESTRE EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA) , pela Comissão Examinadora:

Prof. Dr. MAURO GALETTI RODRIGUES
Departamento de Ecologia / Instituto de Biociências de Rio Claro/UNESP

Prof. Dr. PAULO ROBERTO GUIMARÃES JUNIOR
Depto de Ecologia Geral/Instituto de Biociências/USP

Marco A. Pizo
Prof. Dr. MARCO AURELIO PIZO FERREIRA
Departamento de Zoologia / Instituto de Biociências de Rio Claro/UNESP

Data da realização: 25 de abril de 2014.

DEDICATÓRIA

Dedico este trabalho primeiramente a meu Deus, O Altíssimo, a quem amo e que tem me ajudado e ensinado de forma inacreditavelmente ativa e pessoal. A seu filho Jesus, O Cristo, a quem espero e por quem tenho livre acesso ao Pai.

Dedico também a meus pais, Marcos e Rute que desde pequeno me incentivaram a buscar a justiça, a disciplina e o conhecimento. E a minha irmã Débora a quem amo muito.

AGRADECIMENTOS

Agradeço primeiramente a Deus e a seu filho pelo dom da vida. Vida que nos dá a oportunidade de conhece-Lo, a possibilidade de segui-Lo, e nos permite contemplar a criação. Agradeço pela oportunidade de não apenas contemplar, mas explorar, estudar e buscar entender a criação através da ciência.

Agradeço também a meus pais, Marcos e Rute, a quem amo muito, e que durante toda minha infância me incentivaram a estudar. Lembro-me com carinho dos muitos documentários que gravaram para que eu pudesse assistir quantas vezes quisesse. Eles também me ensinaram a seguir e respeitar os caminhos do Senhor, o que deu início ao meu gosto pela teologia e a minha atual visão sobre a interação entre fé e ciência.

Agradeço a minha irmã Débora, a quem realmente amo. Mesmo que tenhamos brigado muito na infância (o que é normal entre irmãos), o tempo tratou de transformar as discussões em uma relação de intenso respeito e admiração. Realmente, ela faz jus ao nome e ao fato de ter nascido no Dia de Reis.

Agradeço aos professores Mauro Galetti que me ajudou ao longo de todo o mestrado e me ajudou a compreender o complexo sistema com que estávamos lidando, ao ~~Milton Ribeiro~~ Miltinho que me ensinou a ver as coisas sob uma abordagem de paisagem, ao José Flávio Cândido Jr. que me ensinou a pensar de modo cientifico, ao Eliseu Vieira Dias pelas longas e interessantes conversas sobre diversos temas, e a professora Maria Goretti que ainda no colégio me disse: “Acredite em mim, o que você quer é seguir carreira cientifica em ciência biológicas!! Não invente de fazer veterinária ou qualquer outro curso!”. Realmente, ela estava certa...

Agradeço ao pessoal do Laboratório de Ecologia Espacial e Conservação (LEEC) pela enorme contribuição que deram para o desenvolvimento do trabalho. Especialmente a Renata Muylaert e ao Pavel Dodonov que me ajudaram muito com a estatística, e ao Bruno Borges que me ensinou a usar o ArcGIS. Ao pessoal do Laboratório de Ecologia e Conservação (LABIC) que sempre estavam dispostos a debater hipóteses e ideias, ajudando muito no embasamento teórico do trabalho.

Por fim, mas não menos importante, gostaria de agradecer aos técnicos Sérgio Nazareth e Sean Hieda que sempre de bom humor me auxiliaram nos trabalhos de campo, aos membros da Republica Beco (~~Pedro~~ Robinho, ~~Paulo~~ Tocantins, ~~Antônio~~ Tonto, ~~Henrique~~ Americano, ~~Fernando~~

Peruano, ~~Felipe~~ Chapa, ~~Giordano~~ Italiano, Lesley e Fabiano) e ao pessoal da Igreja Batista do Calvário por me acolher quando cheguei em Rio Claro.

"Aquilo a que chamamos acaso não é, não pode deixar de ser, senão a causa ignorada de um efeito conhecido."

Voltaire

RESUMO

A predação de sementes é um importante tipo de processo ecológico, que afeta a abundância, diversidade e distribuição de espécies vegetais. Uma vez que esse processo ecológico depende da presença, abundancia e comportamento dos predadores de sementes, o que é afetado pelas características da paisagem, o processo de predação de sementes também acaba sendo afetado pelas características da paisagem. A maioria dos estudos em paisagens antrópicas não levam em conta as diferentes escalas em que esse processo opera. Aqui, nós avaliamos como a estrutura da paisagem afeta a predação de sementes de uma palmeira espécie-chave (*Syagrus romanzoffiana*) em 13 paisagens que variam em cobertura florestal, número e tamanho de fragmentos na Mata Atlântica brasileira. Nós observamos que a predação total de sementes é explicada pelo tamanho, forma e distância até a borda do fragmento. A predação de sementes pelo principal vertebrado predador de sementes (esquilos) também é relacionada com o tamanho e forma dos fragmentos, e eles interagem com os invertebrados de modo que a predação de sementes por estes é explicada principalmente pela predação por esquilos e pela distância até a borda mais próxima. Por sua vês, roedores não arborícolas são mais correlacionados com a quantidade de habitat na paisagem, predando mais sementes em paisagens com menos de 30% de habitat. Nossos resultados indicam que a predação de sementes de *Syagrus romanzoffiana* é mais afetada por variáveis do fragmento do que por variáveis da paisagem, e que o tamanho, a forma do fragmento e o efeito de borda são melhores preditores da predação de sementes dessa espécie-chave do que a quantidade de habitat na paisagem. Nossos resultados também ressaltam que a geometria do fragmento, uma variável negligenciada na maioria dos estudos, é importante para sistemas ecológicos.

Palavras-chave: Esquilos, Invertebrados, Jerivá, Paisagem, Roedores, *Syagrus romanzoffiana*.

ABSTRACT

Seed predation is an important kind of ecological process that affect the abundance, diversity and distribution of plant species. Since this ecological process depends on the presence, abundance and behavior of seed predators, what it is affected by the landscape characteristics, the process of seed predation becomes also affected by the landscape characteristics. Most of studies on seed predation in human-modified landscapes do not take into account the different scales in which this process operates. Here we evaluate how landscape structure affects seed predation in a palm (*Syagrus romanzoffiana*) that provide a keystone resource to the frugivory community in 13 landscapes that vary in forest cover, fragment number and size in the Brazilian Atlantic forest. We found that the overall seed predation is explained by the fragment size, shape and the distance to the edge. Seed predation by the dominant vertebrate seed predator (squirrels) is also related with the fragment size and shape, and they interact with the invertebrates in such way that the invertebrate seed predation is mainly explained by the squirrel predation and by the distance to the edge. In turn, seed predation by terrestrial rodents is correlated with the habitat amount in the landscape, preying upon more seeds in landscapes with less than 30% of habitat. Our results indicate that the *Syagrus romanzoffiana* seed predation is more affected by the fragment variables than by landscape ones, and that patch size, shape and edge effect are more important predictors of seed predation of this palm than habitat amount in the landscape. Our results also highlights that the fragment geometry, a neglected variable in most of studies, is importance to ecological systems.

Keywords: Invertebrates, Landscape, Queen palm, Rodents, Squirrels, *Syagrus romanzoffiana*.

LISTA DE ILUSTRAÇÕES

Página

ARTIGO

MATERIAL SUPLEMENTAR

LISTA DE TABELAS

Página

ARTIGO

MATERIAL SUPLEMENTAR

SUMÁRIO

INTRODUÇÃO GERAL

A transformação de habitats naturais em áreas antrópicas tem sido considerada uma das maiores ameaças à biodiversidade (FAHRIG, 2003). Biomas como a Mata Atlântica e o Cerrado por exemplo, já tiverem respectivamente 88,3 e 47,84% de sua área original transformada em matrizes antrópicas (MMA et al., 2009; RIBEIRO et al., 2009). Essas modificações na estrutura da paisagem geram inúmeros efeitos sobre a biodiversidade local, afetando a riqueza, abundância e composição das espécies, assim como a rede de interações ecológicas que existe entre elas (TERBORGH et al., 2001; PARDINI, 2004; PARDINI et al., 2005, 2009; DIRZO; MENDOZA, 2007). Em decorrência disso, processos ecológicos fundamentais como a polinização, dispersão e predação de sementes podem ser afetados ou até mesmo extintos, gerando consequências severas sobre a dinâmica e manutenção dos ecossistemas (TERBORGH et al., 2001; DIRZO; MENDOZA, 2007; TYLIANAKIS et al., 2010; ESTES et al., 2011). (TERBORGH et al., 2001; PARDINI, 2004; DIRZO; MENDOZA, 2007; PARDINI et al., 2009)

Nas últimas décadas, diversos estudos vêm demonstrando a profunda influência que a composição e a configuração espacial da paisagem exercem sobre a comunidade animal e vegetal (FAHRIG, 2001; TERBORGH et al., 2001; PARDINI et al., 2005). A quantidade de habitat, por exemplo, quando reduzida tem severos efeitos sobre as redes tróficas, sendo que algumas espécies são beneficiadas em detrimento de várias outras (MICHALSKI; PERES, 2007). Espécies especialistas e de grande porte, por exemplo, tendem a sofrer reduções no tamanho de populações, na diversidade genética, na taxa de recrutamento, aumento da endogamia e das taxas de extinção, enquanto espécies generalistas e de pequeno porte tendem a ser beneficiadas pela perda de habitat devido à redução/extinção de predadores ou competidores, ou pela exploração de recursos novos provenientes da matriz (LUGO, 2001; MICHALSKI; PERES, 2007). Isso gera cascatas tróficas que alteram ainda mais a riqueza, abundância e composição das espécies locais, gerando paisagens com comunidades empobrecidas e com redes de interações mais simples e instáveis (TERBORGH et al., 2001; TYLIANAKIS et al., 2010; ESTES et al., 2011).

Interações ecológicas são essenciais para a manutenção dos ecossistemas, e assim como acontece com espécies, interações também podem ser extintas (JANZEN, 1974). As principais causas dessas extinções são a extinção das espécies envolvidas (ESTES et al., 2011), a redução na abundância das espécies a um nível na qual elas não conseguem interagir de forma significativa (chamada extinção ecológica ou funcional) (MCCONKEY; DRAKE, 2006; GALETTI et al., 2013) e mudanças comportamentais nas espécies de modo que elas parem de interagir (BRINKERHOFF et al., 2005; MCCONKEY; DRAKE, 2006). A perda de interações mutualísticas importantes, como a polinização e dispersão de sementes, pode gerar sérios efeitos sobre o recrutamento de populações, sobre a composição de comunidades e até mesmo sobre o curso evolutivo de espécies (DIRZO; MENDOZA, 2007; MULLER-LANDAU, 2007; GALETTI et al., 2013).

A configuração espacial do habitat na paisagem, por sua vês, também possui efeitos sobre os processos ecológicos pois está relacionada com a permeabilidade da paisagem e a quantidade de área sob efeito de borda (FORERO-MEDINA; VIEIRA, 2009). A permeabilidade pode ser definida como o quão livremente um animal pode se deslocar por uma paisagem, e portanto, reduções na permeabilidade podem reduzir a taxa de colonização de manchas de habitat (HARPER et al., 1993; HAMAZAKI, 1996), o fluxo de indivíduos e de genes (ROBINSON et al., 2012), gerando até mesmo problemas como a depressão endogâmica (KELLER; WALLER, 2002).

O efeito de borda, causado pela interação entre dois ecossistemas vizinhos separados por uma transição abrupta, geralmente causa mudanças na dinâmica das áreas de habitat próximas à borda (MURCIA, 1995). O efeito de borda pode se estender por várias centenas de metros habitat a dentro e inclui tanto efeitos abióticos como mudança no microclima, redução na humidade, aumento da temperatura, incidência de luz e fluxos de vento, quanto efeitos bióticos diretos e indiretos como alterações na abundância, riqueza e composição das espécies e alterações nos processos ecológicos, como por exemplo a predação de sementes (LAURANCE; YENSEN, 1991; MURCIA, 1995; LAURANCE et al., 2002).

A predação de sementes, é um exemplo de processo ecológico que depende da presença, abundância e comportamento das espécies predadoras de semente, e portanto é fortemente afetada pelas características da paisagem (ORROCK et al., 2003; BRINKERHOFF et al., 2005; ORROCK; DANIELSON, 2005). Variações na taxa de predação de sementes podem gerar efeitos sobre a distribuição, dominância, regeneração e até mesmo sobre a evolução de espécies vegetais (JANZEN, 1971; SMITH III, 1987; ORROCK et al., 2006; FERREIRA et al., 2011).

Uma vês que mudanças na estrutura da paisagem tem efeito sobre quase toda a rede de interações ecológicas, espécies que participam de um grande número de interações são facilmente afetadas por essas mudanças (ANDREAZZI et al., 2009). E isso é alarmante se considerarmos que parte dessas espécies possuem muitas interações justamente por serem recursos chave para a comunidade. As palmeiras fornecem um ótimo exemplo disso, pois por frutificarem em períodos de menor disponibilidade de recursos para a fauna frugivora acabam sendo um recurso chave para e sendo utilizadas por dezenas de espécies de vertebrados (TERBORGH, 1986; PERES, 1994)

Assim, esse trabalho de dissertação teve como objetivo avaliar como as características da paisagem (quantidade de habitat), do fragmento (tamanho e forma) e locais (produtividade e distância da árvore para a borda mais próxima) afetam a taxa de predação de sementes de uma espécie chave da Mata atlântica, a Palmeira Jerivá *Syagrus romanzoffiana*. Também foi avaliado a contribuição relativa de cada um dos principais grupos de predadores de sementes. O estudo e os resultados obtidos estão descritos na forma de um artigo cientifico, de acordo com as normas editoriais da revista PLOS ONE.

REFERENCIAS

ANDREAZZI, C. S.; PIRES, A. S.; FERNANDEZ, F. A. S. Mamíferos e palmeiras neotropicais: Interações em paisagens fragmentadas. **Oecologia Australis**, v. 13, n. 04, p. 554–574, 2009. Disponível em: <http://www.oecologiaaustralis.org/ojs/index.php/oa/article/view/oeco.2009.1304.02/71>. Acesso em: 3/3/2012.

BRINKERHOFF, R. J.; HADDAD, N. M.; ORROCK, J. L. Corridors and olfactory predator cues affect small mammal behavior. **Journal of Mammalogy**, v. 86, n. 4, p. 662–669, 2005.

DIRZO, R.; MENDOZA, E. Size related differential seed predation in a heavily defaunated neotropical rain forest. **Biotropica**, v. 39, n. 3, p. 355–362, 2007. Disponível em: <http://onlinelibrary.wiley.com/doi/10.1111/j.1744-7429.2007.00274.x/full>. Acesso em: 30/3/2012.

ESTES, J. A; TERBORGH, J.; BRASHARES, J. S.; et al. Trophic downgrading of planet Earth. **Science (New York, N.Y.)**, v. 333, n. 6040, p. 301–6, 2011. Disponível em: <http://www.ncbi.nlm.nih.gov/pubmed/21764740>. Acesso em: 8/3/2012.

FAHRIG, L. How much habitat is enough? **Biological Conservation**, v. 100, n. 1, p. 65–74, 2001. Disponível em: <http://linkinghub.elsevier.com/retrieve/pii/S0006320700002081>. .

FAHRIG, L. Effects of habitat fragmentation on biodiversity. **Annual review of ecology, evolution, and systematics**, v. 34, p. 487–515, 2003. Disponível em: <http://www.jstor.org/stable/10.2307/30033784>. Acesso em: 14/11/2013.

FERREIRA, A. V.; BRUNA, E. M.; VASCONCELOS, H. L. Seed predators limit plant recruitment in Neotropical savannas. **Oikos**, v. 120, n. 7, p. 1013–1022, 2011. Disponível em: <http://doi.wiley.com/10.1111/j.1600-0706.2010.19052.x>. Acesso em: 14/11/2013.

FORERO-MEDINA, G.; VIEIRA, M. Conectividade funcional e a importância da interação organismo paisagem. **Oecologia Australis**, v. 11, n. 4, p. 493–502, 2009. Disponível em: <http://www.oecologiaaustralis.org/ojs/index.php/oa/article/viewArticle/oeco.2007.1104.03>. Acesso em: 10/6/2012.

GALETTI, M.; GUEVARA, R.; CÔRTES, M.; et al. Functional extinction of birds drives rapid evolutionary changes in seed size. **Science**, v. 340, n. May, p. 1086–1090, 2013. Disponível em: <http://www.sciencemag.org/content/340/6136/1086.short>. Acesso em: 17/6/2013.

HAMAZAKI, T. Effects of patch shape on the number of organisms. **Landscape Ecology**, v. 11, n. 5, p. 299–306, 1996. Disponível em: <http://link.springer.com/10.1007/BF02059857>. .

HARPER, S. J.; BOLLINGER, E. K.; BARRETT, G. W. Effects of habitat patch shape on population dynamics of meadow voles (Microtus pennsylvanicus). **Journal of Mammalogy**, v. 74, n. 4, p. 1045–1055, 1993.

JANZEN, D. Seed predation by animals. **Annual review of ecology and systematics**, v. 2, p. 465–492, 1971. Disponível em: <http://www.jstor.org/stable/10.2307/2096937>. Acesso em: 14/11/2013.

JANZEN, D. H. The deflowering of central america. **Natural History**, v. 83, n. 4, p. 48–53, 1974.

KELLER, L. F.; WALLER, D. M. Inbreeding effects in wild populations. **TRENDS in Ecology & Evolution**, v. 17, n. 5, p. 230–241, 2002. Disponível em: <http://www.sciencedirect.com/science/article/pii/S0169534702024898>. Acesso em: 18/3/2014.

LAURANCE, W. F.; LOVEJOY, T. E.; VASCONCELOS, H. L.; et al. Ecosystem decay of Amazonian Forest fragments: A 22-year investigation. **Conservation Biology**, v. 16, n. 3, p. 605–618, 2002.

LAURANCE, W. F.; YENSEN, E. Predicting the impacts of edge effects in fragmented habitats. **Biological Conservation**, v. 55, n. 1, p. 77–92, 1991. Disponível em: <http://linkinghub.elsevier.com/retrieve/pii/000632079190006U>. .

LUGO, A. E. El manejo de la biodiversidad en el siglo XXI. **Interciencia**, v. 26, p. 484–490, 2001.

MCCONKEY, K. R.; DRAKE, D. R. Flying foxes ceace to function as seed dispersers long before they become rare. **Ecology**, v. 87, n. 2, p. 271–276, 2006.

MICHALSKI, F.; PERES, C. A. Disturbance-mediated mammal persistence and abundance-area relationships in Amazonian forest fragments. **Conservation biology**, v. 21, n. 6, p. 1626–40, 2007. Disponível em: <http://www.ncbi.nlm.nih.gov/pubmed/18173486>. Acesso em: 29/6/2011.

MMA; IBAMA; PNUD. Relatório técnico de monitoramento do desmatamento no bioma Cerrado, 2002 a 2008 : Dados Revisados. ,2009. República Federativa do Brasil.

MULLER-LANDAU, H. C. Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. **Biotropica**, v. 39, n. 3, p. 372–384, 2007.

MURCIA, C. Edge effects in fragmented forests: Implications for conservation. **Tree**, v. 10, n. 2, p. 58–62, 1995. Disponível em: <http://www.sciencedirect.com/science/article/pii/S0169534700889776>. Acesso em: 10/6/2012.

ORROCK, J. L.; DANIELSON, B. J. Patch shape , connectivity , and foraging by oldfield mice (Peromyscus polionotus). **Journal of Mammalogy**, v. 86, n. 3, p. 569–575, 2005.

ORROCK, J. L.; DANIELSON, B. J.; BURNS, M. J.; LEVEY, D. J. Spatial ecology of predator-prey interactions: Corridors and patch shape influence seed predation. **Ecology**, v. 84, n. 10, p. 2589–2599, 2003.

ORROCK, J. L.; LEVEY, D. J.; DANIELSON, B. J.; DAMSCHEN, E. I. Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. **Journal of Ecology**, v. 94, n. 4, p. 838–845, 2006. Disponível em: <http://doi.wiley.com/10.1111/j.1365-2745.2006.01125.x>. Acesso em: 6/3/2013.

PARDINI, R. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. **Biodiversity and Conservation**, v. 13, p. 2567–2586, 2004. Disponível em: <http://www.springerlink.com/openurl.asp?id=doi:10.1023/B:BIOC.0000048452.18878.2d>. .

PARDINI, R.; FARIA, D.; ACCACIO, G. M.; et al. The challenge of maintaining Atlantic forest biodiversity : A multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. **Biological Conservation**, v. 142, n. 6, p. 1178–1190, 2009. Elsevier Ltd. Disponível em: <http://dx.doi.org/10.1016/j.biocon.2009.02.010>. .

PARDINI, R.; SOUZA, S. M. DE; BRAGA-NETO, R.; METZGER, J. P. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. **Biological Conservation**, v. 124, n. 2, p. 253–266, 2005. Disponível em: <http://linkinghub.elsevier.com/retrieve/pii/S0006320705000613>. Acesso em: 6/3/2012.

PERES, C. A. Composition, density, and fruiting phenology of arborescent palms in an Amazonian terra firme forest. **Biotropica**, v. 26, n. 3, p. 285–294, 1994. Disponível em: <http://www.jstor.org/stable/10.2307/2388849>. Acesso em: 10/6/2012.

RIBEIRO, M. C.; METZGER, J. P.; MARTENSEN, A. C.; PONZONI, F. J.; HIROTA, M. M. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation**, v. 142, n. 6, p. 1141–1153, 2009. Elsevier Ltd. Disponível em: <http://linkinghub.elsevier.com/retrieve/pii/S0006320709000974>. Acesso em: 28/2/2013.

ROBINSON, S. J.; SAMUEL, M. D.; LOPEZ, D. L.; SHELTON, P. The walk is never random: subtle landscape effects shape gene flow in a continuous white-tailed deer population in the Midwestern United States. **Molecular ecology**, v. 21, n. 17, p. 4190–205, 2012. Disponível em: <http://www.ncbi.nlm.nih.gov/pubmed/22882236>. Acesso em: 30/1/2014.

SMITH III, T. J. Seed predation in relation to tree dominance and distribution in mangrove forests. **Ecology**, v. 68, n. 2, p. 266–273, 1987. Disponível em: <http://www.jstor.org/stable/10.2307/1939257>. Acesso em: 22/12/2013.

TERBORGH, J. Keystone plant resources in the tropical forest. In: M. Soule (Ed.); **Conservation biology**, 1986. Sinauer, Sunderland, Massachussets.

TERBORGH, J.; LOPEZ, L.; NUÑEZ, P.; et al. Ecological meltdown in predator-free forest fragments. **Science**, v. 294, p. 1923–1926, 2001. Disponível em: <http://www.ncbi.nlm.nih.gov/pubmed/11729317>. Acesso em: 18/7/2011.

TYLIANAKIS, J. M.; LALIBERTÉ, E.; NIELSEN, A.; BASCOMPTE, J. Conservation of species interaction networks. **Biological Conservation**, v. 143, n. 10, p. 2270–2279, 2010. Elsevier Ltd. Disponível em: <http://linkinghub.elsevier.com/retrieve/pii/S0006320709005126>. Acesso em: 21/1/2014.

PATCH SIZE, SHAPE AND EDGE DISTANCE INFLUENCES SEED PREDATION ON A KEYSTONE PALM IN TROPICAL RAINFORESTS

Calebe P. Mendes[1*], Milton C. Ribeiro[1,] Mauro Galetti[1]

1 Departamento de Ecologia, Instituto de Biociências, Universidade Estadual Paulista, 13506-900 Rio Claro, São Paulo, Brasil

* Address for correspondence: calebepm3@hotmail.com

ABSTRACT

Background: Seed predation is an important ecological process that affect the abundance, diversity and distribution of plant species. This ecological process has been affected by defaunation and forest fragmentation, yet most of studies on seed predation in human-modified landscapes do not take into account the different scales in which this process operates.

Principal findings: Here we evaluate how landscape structure affects seed predation in a palm (*Syagrus romanzoffiana*) that provide a keystone resource to the frugivory community in 13 landscapes that vary in forest cover, fragment number and size in the Brazilian Atlantic forest. We found that the overall seed predation is explained by the fragment size, shape and the distance to the edge. Seed predation by the dominant vertebrate seed predator (squirrels) is also related with the fragment size and shape, and they interact with the invertebrates in such way that the invertebrate seed predation is mainly explained by the squirrel predation and by the distance to the edge. In turn, seed predation by terrestrial rodents is correlated with the habitat amount in the landscape, preying upon more seeds in landscapes with less than 30% of habitat.

Conclusions and significance*:* Our results indicate that the *Syagrus romanzoffiana* seed predation is more affected by the fragment variables than by landscape ones, and that patch size, shape and edge effect are important predictors of seed predation of this palm. Our results also highlights the fragment geometry importance to ecological systems.

INTRODUCTION

Habitat loss and fragmentation are considered the dominant threats to the biodiversity with potential effects on ecosystems processes [1]. However, most of the studies have focused on evaluating how the patch size and isolation affects population size, abundance or species persistence [2,3]. The landscape structure influence several key ecological aspects such as gap crossing ability [4], connectivity [5,6], gene flow [7] , edge effect [8], microclimate [9–11], influences on isolation [12], time lagged responses to habitat loss or regeneration [13,14], matrix effects [15]. Nevertheless, much less attention has focused on the trophic consequences of landscape changes on important ecological processes, such as seed dispersal, herbivory and seed predation [12].

The habitat amount and its spatial configuration strongly influences the local communities and species interactions [17–20]. The habitat loss, when reach critical habitat amount (i.e. <20%) for instance, have severe effects on the trophic web, with some species being benefited in detriment of others, leading to trophic cascades, changing the species richness, abundance and composition of plants and animals [19,21–23]. It can create landscapes with impoverished communities with simpler and unstable interaction networks [1,21,24]. This loss of ecological interactions can occur because of the extinction of the involved species [25], by reductions in the specie abundances to a level where it cannot interact significantly with other species, also called ecological extinction [26,27], and as a response to changes in the behavior of the involved species [26,28]. The loss of important mutualistic interactions such seed dispersal and pollination can influences species recruitment, composition and even on evolution [23,27,29].

The spatial configuration of the habitat, on the other hand, affects both the landscape permeability to the species flow, what have consequences on the species genetics [7], and the amount of edges in the landscape [30]. The edge can be defined as the interaction between two different environments and can lead, in some cases, to dramatic biotic and abiotic changes in the habitat area near the transitional zones, with consequences on some ecological interactions [9,10]. The seed predation, herbivory and seed dispersal, for instance, can act together with abiotic changes such as low air moisture and wind damage, and this combination lead to fast changes in the dynamics of habitat near the edge [2,3,10].

Seed predation is an important kind of ecological interaction, because it has direct consequences for plant recruitment [31], regeneration [32], species abundance[33], spatial distribution [33] and evolution [34]. Considering that seed predation rates depends on the seed predator's abundance and behavior, which vary with the microhabitat and landscape characteristics [28,35–38], it is paramount to understand how habitat amount and configuration affects the seed predators and its relative importance to the overall seed predation. This is particularly important for plants who provide keystone resources to the animal community, because although tropical forests hold a high diversity of plant species, few species are able to maintain the population of resident frugivores [39,40].

Here, we investigate how changes in the landscape structure (e.g. habitat amount, fragment size, shape and distance from the edge) affects the seed predation of the Queen Palm (*Syagrus romanzoffiana*), an important resource to the frugivore community in the Atlantic rainforest. We also estimate the relative contribution of the main groups of seed predators (the squirrels, the invertebrates and the terrestrial rodents) and tested 4 hypotheses about how the seed predation should respond to the this changes in the landscape structure.

The Rodentization hypothesis (Figure 1), proposes that in more degraded landscapes (here defined as landscapes with a lower amount of habitat, with smaller fragments and with higher amount of edges) the density of rodents should be higher due to the absence of more sensible predators or competitors [39], and/or due to the higher productivity of the edges [9], causing a higher seed predation in this areas. The Intermediate hypothesis proposes that in very degraded landscapes the squirrel seed predation should be low due to the lack of habitat to maintain an strictly arboreal species [41,42], while in landscapes with intermediate levels of degradation the seed predation should be high because the squirrels should have habitat enough to live and should be benefited by the higher productivity of the edge areas [9,25,41,43]. In very preserved landscapes, the squirrel seed predation should be lower due to the presence of mesopredators than control the squirrel population [43,44].

The Predator Turnover hypothesis proposes that the seed predation should be high in landscapes with high and intermediate levels of degradation due to the rodents and squirrels, respectively (as predicted by the Rodentization and Intermediate hypothesis), but in very preserved areas the seed predation should be high due to the invertebrates, which should become abundant due to the reduction in the predation of larvae by rodents [45,46]. This way, the landscape degradation should have nearly no effect in the overall seed predation due to this turnover in the main groups of seed predators.

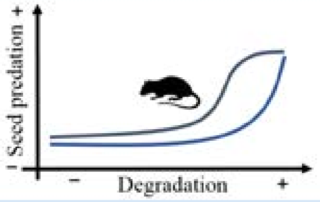
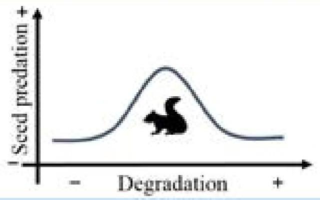
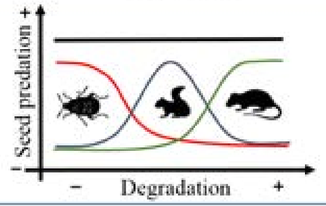
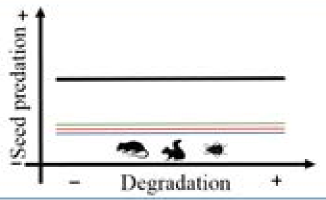
Hypothesis	Description of the expected responses	Sketch of expected responses
H1: Rodentization Hypothesis	There are a relation between the degradation and seed predation, due to the higher presence of terrestrial rodents in more degraded areas.	
H2: Intermediate Hypothesis	The seed predation is higher in areas with intermediate levels of degradation, because the squirrels are benefited in these areas.	
H3: Predator Turnover Hypothesis	The overall seed predation is not affected by none of the tested variables, but there is a turnover between the groups of seed predators.	
H0: Null Hypothesis	The predation of *S. romanzoffiana* seeds is not affected by habitat degradation, as well as the main groups of seed predators.	

Figure 1 shows the list of tested hypotheses with the respective description and sketches of expected responses. Note that not all hypothesis are mutually exclusive, and some of them can be true at the same time (i.e. Hypotheses H1, H2 and H3).

MATERIAL AND METHODS

ETHICS STATEMENT

All the work was conducted in accordance with relevant national and international guidelines, and conforms to the legal requirements of the Brazilian Minister of Environment (Instituto Chico Mendes). SISBIO and Instituto Florestal of São Paulo gave us permission to conduct the study in the protected areas.

QUEEN PALM (*SYAGRUS ROMANZOFFIANA*) AS A MODEL SPECIES

We chose the Queen Palm (*Syagrus romanzoffiana*) as the study model because it is a common species in the semideciduous Atlantic Forest, with a large distribution in South America [47]. Queen palm is 7 to 15 m high, it produce fruits throughout the entire year, sometimes with flowers and fruit bunches in different ripeness at the same time [42]. The fruits are yellow-orange round drupes with 2 to 3 centimeters in diameter, containing a sweet and fibrous mesocarp, and one seed with a lipid rich endosperm wrapped in a stony endocarp [47,48]. Their fruits are consumed by at least 60 vertebrate species, including primates, ungulates, rodents, birds (Table S1), and by several invertebrates [49], but few species can prey upon the seeds. The seed predators of *S. romanzoffiana* can be divided into three main groups: Squirrels (*Sciurus (Guerlinguetus) ingrami*), which predate upon ripe and unripe fruits collecting them both on the ground and directly from the bunch [50–52]; Agoutis (*Dasyprocta* spp.) and other small rodents (here and after terrestrial rodents) that prey only upon seeds in the ground [53]; And the invertebrates, mainly the curculionid *Revena rubiginosa* and the bruchid *Pachymerus cardo*, oviposit on the fruit so that the larvae can grow eating the endosperm and killing the seed [49,54].

STUDY AREA

We performed our study in one of the most fragmented landscapes of the interior of São Paulo State, Brazil. The region is part of the Atlantic Forest domain, originally with 150 million ha and now reduced to less than 12% of it, where about 83% of the remaining fragments have less than 50 ha [55]. The chosen landscapes were spread between the latitudes 21º50´ S and 22 º 43´ S, and the longitudes 47 º 05´ W and 49 º 45´ W (Figure 2 and Supplemental material Table S2). All forest fragments are surrounded mainly by sugar cane plantation, with only 2 fragments in some contact with orange or coffee plantation.

LANDSCAPE SELECTION

We chose 13 landscapes with a 1500 meters radius (~707 ha) in a gradient of forest cover amount ranging from 2 to 70 % (Table S2). We define one of the landscapes as control area, which was established in the Estação Ecológica dos Caetetus, a 2,100 ha forest with the complete fauna that could eat and prey upon the *S. romanzoffiana* seeds [56,57]. In order to minimize the spatial correlation between our sampling landscapes, we define that each landscape were placed with minimal distance of three kilometers from another landscape [58]. To aid the process of landscape selection we use a set of CBERS 2B (spatial resolution of 20 m and 3 m) and Landsat 7 (spatial resolution of 30 m) imagery. Forest and non-forest (i.e. matrix) classes were used on our analyses. All the images were freely obtained from the Brazilian National Institute for Space Research (INPE) website.

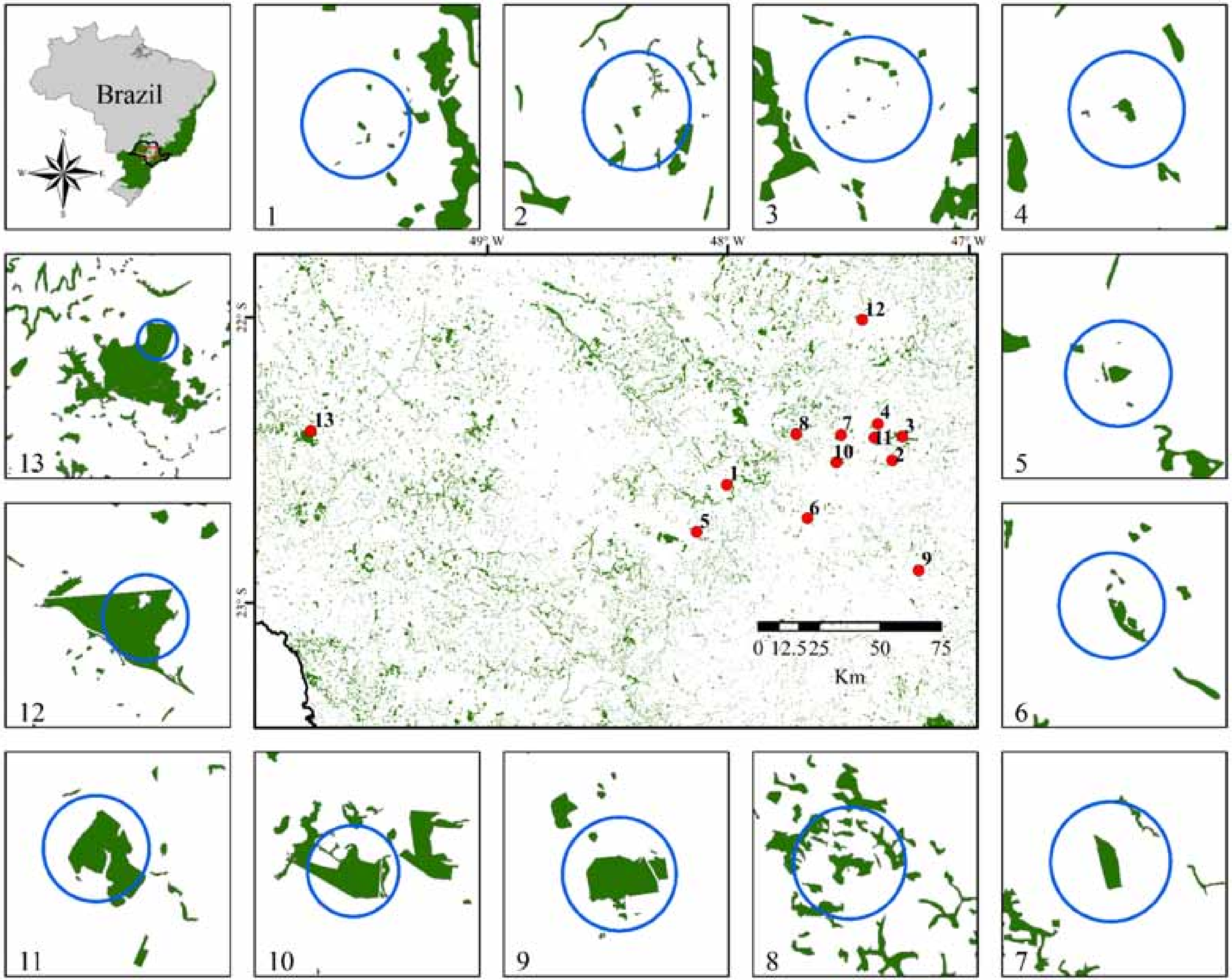


Figure 2: Location of 13 landscapes (red dots) in Atlantic forest remnants, São Paulo, Brazil. Around, in clockwise, the landscapes are shown in ascending order of habitat amount. The blue circles have 1500 m radius and show the biggest scale tested in our variables.

LANDSCAPE METRICS AND EXPLANATORY VARIABLES

The percentage of habitat in the landscape was calculated in three different scales, from the geographical centroid of the sampled palms tree (called local forest cover). We used three scales: 1- area up to 500 m from the centroids; 2- up to 1000 m; 3- up to 1500 m (Supplementary material Figure S2 - A). The habitat percentage in a ring shaped buffer, encompassing the area between 1000 and 1500 m from the centroids was also calculated to isolate the effect of the habitat amount in the landscape from the habitat amount immediate around the palms (Figure S2 - B). This last metric was called regional forest cover. To each fragment we also calculated a fragment shape variable by dividing the fragment area in a grid with cells of 5x5 meters and calculating the average Euclidean distance of the grid cells to the nearest edge (average edge distance). Then, to extract the effect of the fragment area from the fragment shape, we created a Generalized Addictive Model (GAM) with the average edge distance as a function of fragment area, and we used the model residuals as our fragment shape variable (Figure S2 - C). We did not calculate any connectivity variable because the connectivity can be also expressed as the inverse of the amount of habitat in a landscape [1,59,60], all the explanatory variables are in the Table 1.

Table 1: List of predictor variables, with the respective descriptions. For more details about the Fragment Shape, Local and Regional Forest Cover variables, see the Figure S2.

Variable	Level	Description and unit
Edge Distance	Plant	Euclidean distance in meters of the palm tree to the edge of fragment
Number of fruits	Plant	Mean of the number of fruits collected using four 1x1 meters squares under the palm tree
Fragment Area	Fragment	Area in ha of the fragment where the palm is located
Fragment Shape	Fragment	Residual of the mean Euclidean distance of the fragment area to the nearest edge as a function of fragment Area. Unitless variable.
Local Forest Cover	Landscape	Percentage of habitat inside a buffer around the geographic centroid of the palms. Calculated in 3 scales: 500, 1000 and 1500 meters.
Regional Forest Cover	Landscape	Percentage of habitat inside a doughnut shaped buffer of 1000 to 1500 meters radius, centered in the geographic centroid of the palms.

SEED PREDATION

To evaluate the proportion of predated seeds in each landscape, we selected from 1 to 9 palms within each landscape. The sampled palm number in each fragment range according to the fragment size. Each palm was mapped and the distance from palm to nearest edge was estimated. Beneath each palm, we delimited four 1m² squares, each one 30 centimeters apart from the plant trunk in each cardinal direction, and all fruits on the leaf-litter within the squares were collected, washed and peeled to expose the endocarp, that were separated and counted according with the seed fate. We excluded from analyzes the endocarps decomposed enough to be crushed by hand because it could obscure the predators marks.

The identification of the seed predator of each seed was possible due to the patterns leaved by these in the fruit endocarp (Figure S1). The squirrels leave thin and deep cuts, usually with a triangular shape or less frequently using other patterns as described in Bordignon *et al.* [52]. Terrestrial rodents gnaw the fruit endocarp in a way that all teeth marks have the same direction, making a concave mark. The invertebrates create a small and perfectly round hole when the larvae bore the endocarps. The endocarps with no marks were opened to confirm whether there was a larva inside it, because the larvae only bore it to leave the seed at the least stages of its development [61]. Then the endocarps with larvae were counted as predated by invertebrates, while the ones without larvae were counted as non-predated. We also measured the diameter at breast height (D.B.H.) of each palm.

DATA ANALYSIS

We used a multiple competing hypothesis approach [62], where several biologically coherent ecological models were defined *a priori*. To fit the relationship between response and explanatory variables we used both generalized linear models (GLM) and generalized addictive models (GAM) model types. The main difference between these model types is that GLM is good to fit linear relationships, and GAM fit well non-linear responses. As explanatory variables we used both plant, fragment and landscape independent variables. The models were compared using the Akaike Information Criterion corrected for small sample sizes (AICc). For each model we calculated the Akaike weights (wAICc), the AIC difference (ΔAICc), which are a parameter of relative likelihood and relative difference between models, respectively. The model with higher wAICc have a better weight of evidence in its favor and is considered the best model of the set and models with ΔAICc < 2 were considered equally plausible [62]. We also calculated a bootstrap model selection frequency (πi), which is the frequency that each model *i* receive the lowest AICc value in 10000 random resamples of the data [62].

Preliminary tests were performed to find the best model type (GLM or GAM) to each set of variables, and the best scale to each model that uses the local habitat amount variable. The models with both variables local and regional forest cover were tested only in the 500 meters scale, because the objective of these models were separate the local and regional forest cover. Because is documented in the literature that squirrels prey upon invertebrate larvae [45], in the tests to evaluate the seed predation by invertebrates, we added four models that consider the squirrels as an independent variable. For this, we used the squirrel seed predation as a proxy of the effect inflicted on the larvae.

We did a model validation by plotting the model prediction against the residuals of the model independent variables and looking for patterns in the scatterplots. We also run the Moran's I spatial autocorrelation test with 10000x permutation, using the residuals of the winner models, and we found no spatial autocorrelation except two distance classes with marginal autocorrelation, one for invertebrate and one for rodent (P=0.048 and 0.05 respectively). The analyses were performed using the statistic softwares SAM v4.0 and R [63], using bbmle and gam packages. The model list is showed in the Supplementary material Table S3.

RESULTS

We sampled 76 palms, from 15 fragments, summing 107,869 endocarps. Each palm produced a mean of 1449.3 ± 1441.9 endocarps, ranging from 21 to 8170, and at each landscape we collected a mean of 8297.6 ± 6459.2 endocarps, ranging from 692 to 25139. We found that 50% of the seeds were preyed upon invertebrates (*Pachymerus cardo*, *Revena rubiginosa* and *Scotylidae* beetles), 15.37% by squirrels and only 5.38% by terrestrial rodents (Supplementary material Table S4).

Two GAMs obtained equally plausible results in describing the overall seed predation, and the landscape characteristics with best effect on it were the fragment size, the fragment shape and the palm distance from the edge. The first model used the interaction between the fragment area and the palm distance from the edge as explanatory variables, and the second model used the interaction between the fragment area and fragment shape (Table 3). These models have a similar wAICc (0.431 and 0.368, respectively), πi values (0.25 and 0.4 respectively) and a ΔAICc smaller than 2 (0.0 and 0.3 respectively). The first model predict a higher seed predation in fragments between 250 and 400 ha, and in very large fragments (> 1000 ha), with a reduction in the seed predation in areas between 100 and 400 meters from the edge (Figure 3A), while the model second model predict a higher seed predation in fragments with a more irregular shape, mainly in fragments between 100 and 400 ha (Figure 3B). The overall seed predation were not correlated with the palm's D.B.H. (r=0.03, df=72, p=0.78).

The squirrel seed predation were also better explained by a GAM that used the interaction between the fragment area and fragment as explanatory variables, with a wAICc = 0.96 and a πi value = 0.94 (Table 3). Similar to the overall seed predation, the model predict a higher squirrel seed predation in fragments between 100 and 400 ha with a more irregular shape (Figure 4A). It is also similar to the predicted by our the Intermediate hypothesis. The second best model to explain the squirrel seed predation used the local forest cover (in a 500 m scale) and the distance from edge as explanatory variables, but was not a good plausible model, because it obtained a ΔAICc = 2.3 and a wAICc < 0.01. We also observed a strong negative correlation between the squirrel and the invertebrate seed predation (r=-0.72, df=72, p<0.01), and a negative correlation between the squirrel and terrestrial rodent seed predation (r=-0.25, df=72, p=0.03).

The best model to explain the invertebrate seed predation was a GAM that considers the distance from the nearest edge and the seed predation by squirrels as explanatory variables, and obtained a wAICc = 0.79 and a πi value = 0.68 (Table 3). The model predict a higher invertebrate seed predation in areas where the squirrel seed predation is low, and a light reduction in the invertebrate seed predation in areas between 100 and 400 meters from the nearest edge (Figure 4B). The second best model to explain the invertebrate seed predation used the local forest cover (in a 1000 m scale) and the squirrel seed predation as predictors, but it obtained a ΔAICc of 4.1 and is not considered a plausible model. The invertebrate seed predation was not correlated with the terrestrial rodent predation (r=0.03, df=72, p=0.77).

The terrestrial rodent seed predation were best explained by a GAM that used only the local forest cover in the 500 m scale as explanatory variable, with a wAICc = 0.81 and a πi value = 0.91 (Table 3). As described by the Rodentization hypothesis, it predict a higher seed predation in landscapes with forest cover amount lower than 30% (Figure

Table 3: Results of the model selection for overall seed predation of *Syagrus romanzoffiana* and for each group of seed predators. The best models are in bold. (*Only the best scale for each predator group were used).

Models	**Overall seed predation**				**Squirrel**				**Invertebrate**				**Terrestrial rodents**			
	Type	**ΔAICc**	**wAICc**	***π*i**	**Type**	**ΔAICc**	**wAICc**	***π*i**	**Type**	**ΔAICc**	**wAICc**	***π*i**	**Type**	**ΔAICc**	**wAICc**	***π*i**
GLM0: VD ~ Mean (Null Model)	GLM	15.1	<0.001	0	GLM	7.4	<0.01	<0.01	GLM	58.8	<0.01	0	GLM	22.3	<0.01	0
GAM0: VD ~ Mean (Null Model)	GAM	15.5	<0.01	<0.01	GAM	9.9	<0.01	<0.01	GAM	58.5	<0.01	0	GAM	20.6	<0.01	<0.01
M01: VD ~ Edge Distance	GAM	5.1	0.03	0.05	GAM	8	<0.01	<0.01	GLM	58.3	<0.01	0	GLM	19.1	<0.01	<0.01
M02: VD ~ Fruit Number	GLM	15.2	<0.01	<0.01	GLM	8.9	<0.01	<0.01	GAM	60	<0.01	0	GLM	19.2	<0.01	0.05
M03: VD ~ Fragment Area	GAM	7	0.01	<0.01	GAM	2.4	<0.01	<0.01	GAM	50.3	<0.01	0	GAM	19	<0.01	<0.01
M04: VD ~ Fragment Shape	GAM	4.8	0.03	0.08	GAM	6.9	0.03	0.03	GAM	55.8	<0.01	0	GLM	22.9	<0.01	0
M05: VD ~ Local Forest Cover*	GAM	9.2	<0.01	0.05	GAM	8.4	<0.01	0	GAM	52.5	<0.01	0	**GAM**	**0**	**0.812**	**0.91**
M06: VD ~ Regional Forest Cover	GAM	8.4	<0.01	0.03	GAM	3.5	<0.01	0	GAM	55.4	<0.01	0	GLM	21.4	<0.01	<0.01
M07: VD ~ Fruit Number + Edge Distance	GAM	8.5	<0.01	<0.01	GLM	11	<0.01	0	GAM	61.5	<0.01	0	GLM	18.5	<0.01	<0.01
M08: VD ~ Fragment Area + Edge Distance	**GAM**	**0**	**0.431**	**0.25**	GAM	10.5	<0.01	0.01	GAM	52.8	<0.01	0	GLM	21.2	<0.01	0
M09: VD ~ Fragment Area + Fragment Shape	**GAM**	**0.3**	**0.368**	**0.4**	**GAM**	**0**	**0.96**	**0.94**	GAM	49.7	<0.01	0	GLM	22.3	<0.01	0.01
M10: VD ~ Local Forest Cover* + Edge Distance	GAM	3.4	0.07	0.07	GAM	8.8	<0.01	<0.01	GAM	53.3	<0.01	0	GAM	3.9	0.114	<0.01
M11: VD ~ Regional + Local Forest Cover (500 m)	GAM	6.4	0.01	0.06	GAM	2.3	<0.01	<0.01	GLM	59.1	<0.01	0	GAM	4.8	<0.07	0
M12: VD ~ Squirrel predation									GLM	6.7	0.02	0.12				
M13: VD ~ Edge distance + Squirrel predation									**GAM**	**0**	**0.79**	**0.68**				
M14: VD ~ Fragment area + Squirrel predation									GAM	4.8	0.07	0.05				
M15: VD ~ Local forest cover* + Squirrel predation									GAM	4.1	0.1	0.14				

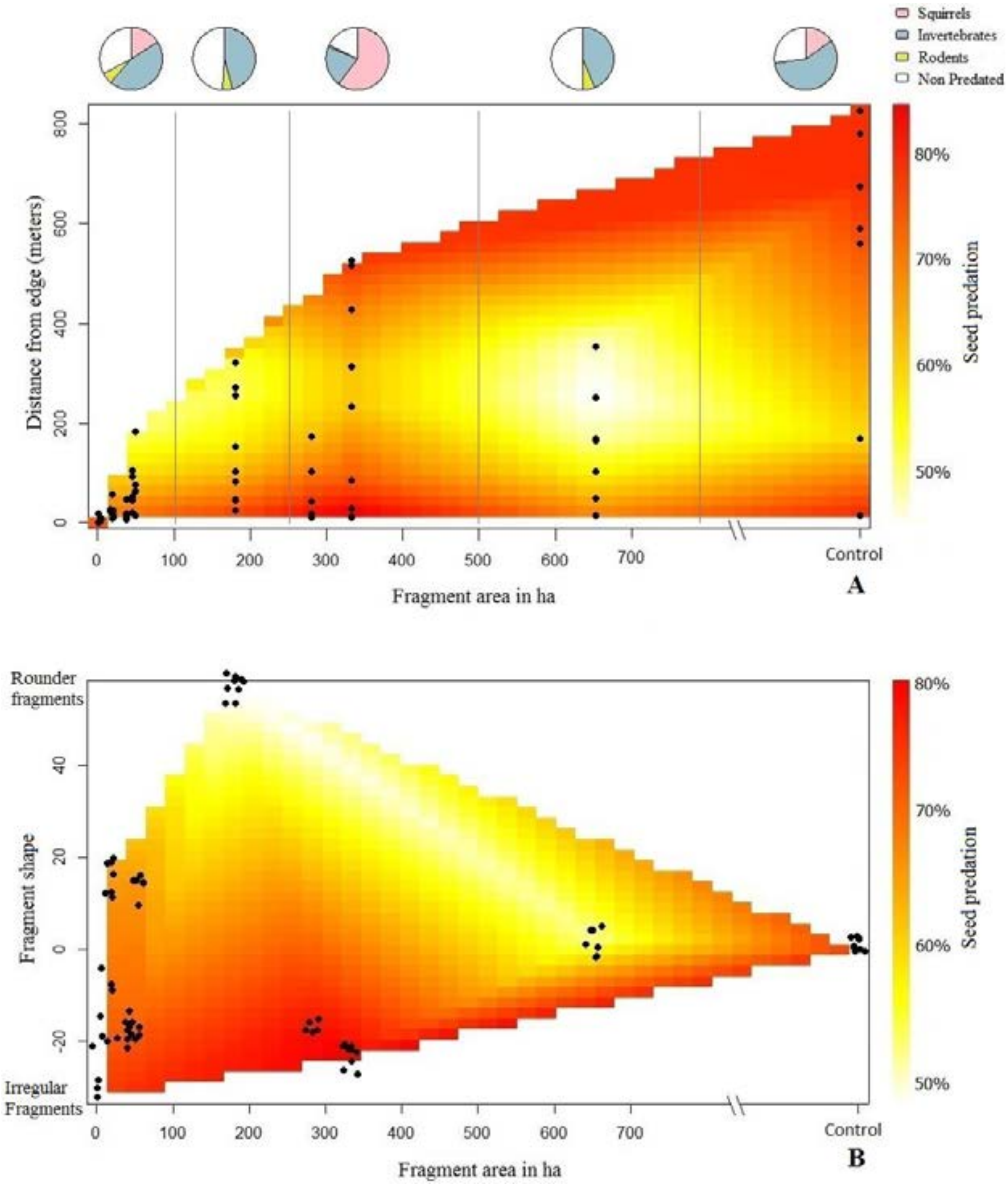


Figure 3: Distribution of S. romanzoffiana seed predation. Predicted distribution of the overall predation of *Syagrus romanzoffiana* seeds along a gradient of: A- Fragment area and distance to the nearest edge; B- Fragment area and shape, where the smaller numbers represent more irregular shapes. The black points represent sampled palms and darker colors represent areas with a higher seed predation.

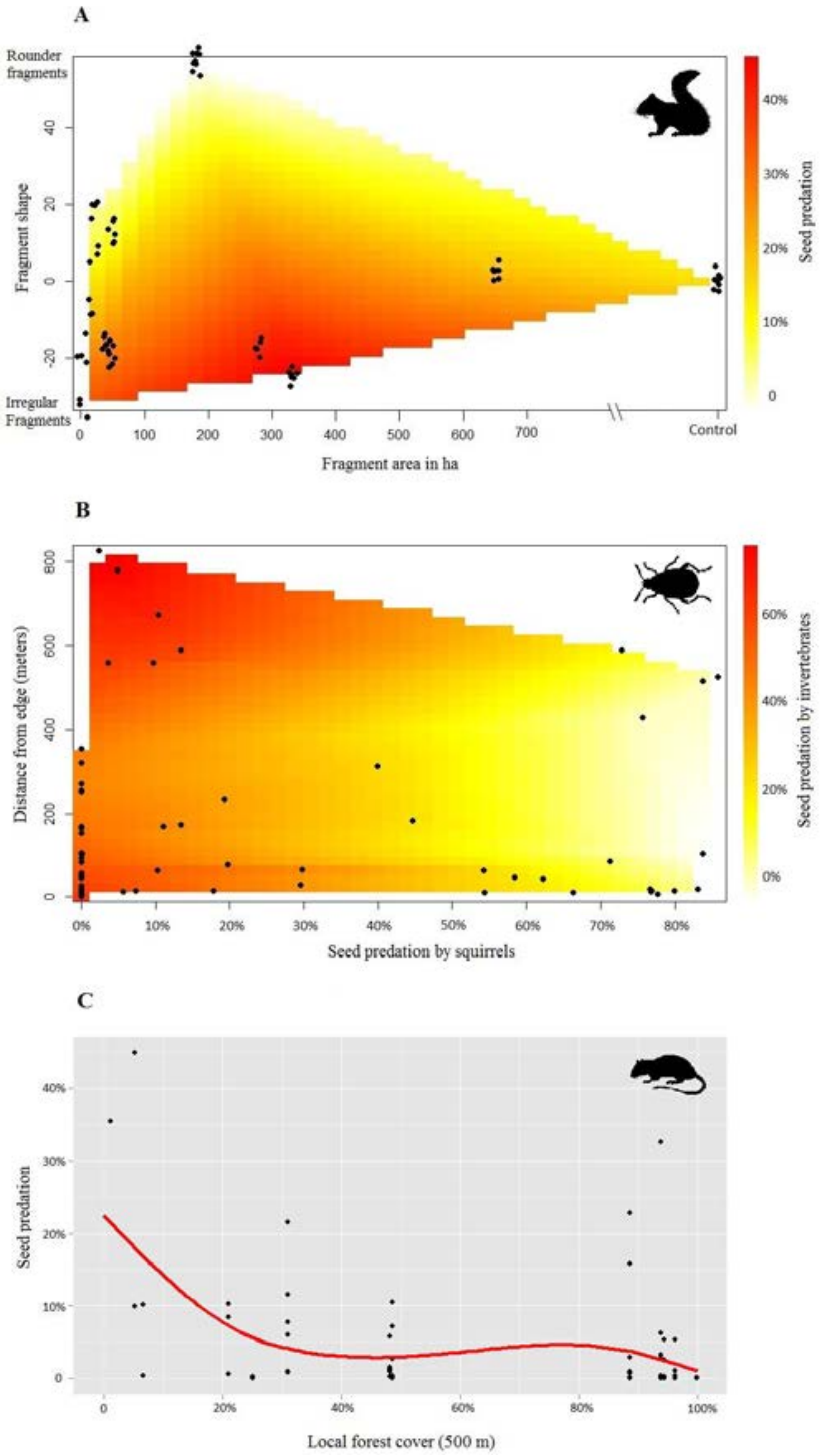


Figure 4: Distribution of S. romanzoffiana seed predation. Predicted distribution of the predation of *Syagrus romanzoffiana* seeds by each predator group: A- Squirrels; B- Invertebrates; C- terrestrial rodents. The black points represent sampled palms and darker colors represent areas with a higher seed predation.

4C). At last, we observed a marginal correlation between the palm's D.B.H. and the distance from the nearest edge (r=-0.22, df=72, p=0.05), but not with the number of fruits (r=0.05, df=72, p=0.64).

DISCUSSION

Our results indicate that the overall seed predation of the queen palm seeds is affected mainly by the fragment size, shape and the distance to the edge, which are the same variables that affect the two main groups of seed predators. The seeds predation by squirrels are affected by the fragment size and shape, and although they prey upon only 15% of the seeds, they also indirectly affect the overall seed predation by affect the invertebrates, which prey upon 50% of the seeds and are also affected by the edge distance. This arrangement of prey-predators interaction is called tri-trophic interaction [45]. Terrestrial rodents, in turn, have only a small effect on the overall seed predation, preferring areas with low forest cover. Thus, although there are turnover between the seed predators, as predicted by the Predator Turnover hypothesis, it is not a completely turnover and the overall seed predation fluctuate according mainly to these three variables that affect the squirrels and invertebrates.

The squirrels' response to the fragment size (a fragment-level variable), and not to the landscape forest cover (a landscape-level variable), probably happen because they are strictly forest-dwelling animals [41], with small home ranges [64], and rarely use the matrix areas [41]. Moreover, the capacity of small forest mammals to move in the matrix tend to be reduced by the absence of corridors and in croplands (as the sugar cane, present in all sampled landscapes), which blocks the vision and reduce the animals' perceptual range [65,66]. With such low use of areas outside the fragment, the *S. ingrami* may not be significantly affected by changes in these areas, as observed in strictly forest-dwelling birds [67]

As predicted by our Intermediate hypothesis, at least to the fragment area variable, the squirrel seed predation were higher in fragments between 100 and 500 ha, with a peak in the fragments about 300 ha. It agree with the results observed by Fleury e Galetti [25] to the same species. The way in which the fragment size affect the squirrel seed predation is not clear, but it is possible that the fragments about 300 ha have an ideal balance between resource availability and mesopredator amount, such ocelots and margays, and thereupon a higher squirrel density [25,41,44]. Some north hemisphere squirrel species are also more abundant in fragmented than in continuous areas [41,43,68]. Small fragments may also be not able to support viable populations in long-term due to genetic complications and/or due to the patch hyperdynamism, which facilitate local extinctions [3,10,46,69]. A second possibility is that fragments about 300 ha should have and ideal balance between core areas (absent in smaller areas) and areas under the edge effect, which are apparently favorable to the squirrels [25,41]. In this situation, the fragment shape become important due to its relationship with the perimeter-area ratio of the fragment, and our data agree with this hypothesis, indicating that the squirrel seed predation in fragments about 300 ha is intense only when the fragment have an irregular shape.

The effect of the fragment shape in biological process is usually related with its influence in the edge amount and connectivity of the fragment [70,71]. Anyway, the connectivity may not have an important effect in the squirrel seed predation, because it is strongly inversely related to the amount of habitat in the landscape [1,59,60], and none of the habitat amount variables were a good predictor of the squirrel seed predation. Other North American squirrels also didn’t respond very well to the landscape connectivity [68]. Due to geometrical reasons, fragments with more irregular shape have a higher perimeter-area ratio, thus, they are relatively more affected by the edge effect [72]. It is known that the area and perimeter-area ratio of grassland patches are together better predictors of species richness, abundance and probability of occurrence than patch area alone [71,73]. The amount of edges have also an effect in the behavior of rodents with consequences in the proportion of predated seeds [36,38]. Thus, it is plausible that the amount of core and edge area can be affecting the squirrels, and consequently they seed predation, but the way in which it occur still unclear.

Invertebrates are the main predators of palm seeds in the neotropics [46,74–76]. We observed peaks of invertebrate seed predation up to 96% in some palms, what is similar with the observed to other palm species. For instance, proportions of seed predation above 90% were also observed to the palms *Attalea tessmannii* and *Attalea phalerata* [74] and 80% for *Astrocaryum aculeatissimum* [75]. The consequences of this high proportions of seed predation to the *S. romanzoffiana* population still not clear [46], however, similar proportions registered in other species are enough to deeply affect the species abundance [31,33]. The seed predation by invertebrates can also act as a selective filter, with effects on plant species evolution [76].

The negative effect created by squirrels on the invertebrate seed predation may occur mainly due to the predation of the larvae that grow inside the palm fruits. Squirrels are avid predators of bruchid larvae, sometimes preferring infested fruits than uninfected ones [45], probably due to the higher nitrogen contend [76]. Moreover, larvae predation by vertebrates is a significant mortality factor that affect the abundance of several invertebrate species [45,74,76,77], and have indirect effects on the species that are predated by these invertebrates [45]. Indeed, the trophic cascades tend to be stronger in systems where the herbivorous species are invertebrates without an effective defense against the predation [78,79]. Thus, in this tri-trophic interaction, when the squirrel predation is high they reduce the invertebrate abundance, what is reflected in the overall seed predation as predicted by the Predator Turnover hypothesis.

The observed response of the invertebrates to the edge distance may be related with the microhabitat changes caused by the fragment edge. The lower humidity, higher temperature and light incidence of the areas near the fragment edges have direct effects on the invertebrate community [10]. Indeed, if the landscapes with squirrels were excluded from the analyses, the distance to the nearest edge alone (model GAM01) become the best variable to explain the invertebrate seed predation with a wAICc = 0.51 and a πi = 0.58, followed by the fruits amount and the edge distance (model GAM07) with a wAICc = 0.51, a πi = 0.21 and a ΔAICc = 1. Anyway, our results indicate that the invertebrate seed predation is lower between 100 and 500 meters from the edge, and the cause of the increase in the seed predation at less than 100 m and beyond 500 m from the edge is not clear.

The seed predation by terrestrial rodents responded exactly as we predicted in the Rodentization hypothesis, being more intense in the landscapes with less that 30% of forest cover. However, even in extremely degraded landscapes, terrestrial rodents predate only a small amount of seeds when compared with other predators, and only 10 palms in the study had more than 10% of seeds predated by the group. A relatively small predation of *S. romanzoffiana* seed by terrestrial rodents was also observed by Fleuri e Galetti [25]. Since the best scale in which a specie respond is usually related with its habitat requirements and mobility [80,81], the fact that the terrestrial rodent response were better explained in the 500 m scale may happen due to the small home range of these animals. The agouties, for instance, are probably the biggest species in the group, have a home range between 3 and 8.5 ha [82]. At least, how the landscapes with less than 30% of habitat are composed mainly by habitats under intense edge effect, the increase in the terrestrial rodent seed predation may be caused by the increase in the rodent abundance in these areas [21,22,83], probably due to the higher productivity or heterogeneity of the edge habitats [9].

Our findings show that the overall predation of *Syagrus romanzoffiana* seeds is more affected by the fragment characteristics than by landscape ones, with a turnover between the seed predation by squirrels and invertebrates. But it is not like the predicted by the Predator Turnover hypothesis because the terrestrial rodents that have nearly no effect on the overall seed predation. Anyway, it is not a complete turnover and both the fragment size and shape, by affecting the squirrels, and the distance from the nearest edge, by affecting the invertebrates, have effects on the overall seed predation. Our work also highlights the effect of the fragment shape in biological systems, something usually neglected in most of studies. In our study system, the fragment shape have a clear effect in the intensity of seed predation, especially in the fragments about 300 ha.

At least, if the observed pattern is present in the entire Atlantic forest, it is possible that the *S. romanzoffiana* populations are suffering high levels of seed predation in most of its distribution, with possible effects on its recruitment and persistence. It should occur because 83% of the Atlantic forest fragments have less than 50 ha (Ribeiro), and in these fragments, the predicted seed predation is between 60 and 75%. Moreover, near 50% of the Atlantic forest area are at less than 100 meters away of an edge (Ribeiro), and in these areas the seed predation should be between 65 and 85%. Studies evaluating the germination success and seedling survival should get more data about the final fate of the seeds who escaped this intense seed predation.

ACKNOWLEDGEMENTS

We thank to S. Nazareth and S. Hieda for the assistance in the field, and to the people from the Laboratório de Biologia da Conservação (LABIC) and Laboratório de Ecologia Espacial e Conservação (LEEC) for the advices and fruitful discussions. P. Jordano, B. Loiselle, M. A. Pizo, R. L. Muylaert and P. Dodonov for useful suggestions in the analyses. CM, MG and MCR receive a fellowship from CNPq. To FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo) for financial support.

REFERENCES

1. Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34: 487–515. Available: http://www.jstor.org/stable/10.2307/30033784. Accessed 14 November 2013.

2. Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ribeiro JELS, et al. (2006) Rapid decay of tree-community composition in Amazonian forest fragments. PNAS 103: 19010–19014. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1682011&tool=pmcentrez&rendertype=abstract.

3. Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, et al. (2011) The fate of Amazonian forest fragments: A 32-year investigation. Biol Conserv 144: 56–67. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320710004209. Accessed 7 November 2013.

4. Awade M, Metzger JP (2008) Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. Austral Ecol 33: 863–871. Available: http://doi.wiley.com/10.1111/j.1442-9993.2008.01857.x. Accessed 28 January 2014.

5. 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. Biol Conserv 141: 2184–2192. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320708002140. Accessed 21 January 2014.

6. 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. Conserv Biol 26: 1100–1111. Available: http://www.ncbi.nlm.nih.gov/pubmed/23003666. Accessed 28 January 2014.

7. Robinson SJ, Samuel MD, Lopez DL, Shelton P (2012) The walk is never random: subtle landscape effects shape gene flow in a continuous white-tailed deer population in the Midwestern United States. Mol Ecol 21: 4190–4205. Available: http://www.ncbi.nlm.nih.gov/pubmed/22882236. Accessed 30 January 2014.

8. Dodonov P, Harper KA, Silva-matos DM (2013) The role of edge contrast and forest structure in edge influence : vegetation and microclimate at edges in the Brazilian cerrado. Plant Ecol 214: 1345–1359. doi:10.1007/s11258-013-0256-0.

9. Murcia C (1995) Edge effects in fragmented forests: Implications for conservation. Tree 10: 58–62. Available: http://www.sciencedirect.com/science/article/pii/S0169534700889776. Accessed 10 June 2012.

10. Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, et al. (2002) Ecosystem decay of Amazonian Forest fragments: A 22-year investigation. Conserv Biol 16: 605–618.

11. Ewers RM, Thorpe S, Didham RK (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. Ecology 88: 96–106. Available: http://www.esajournals.org/doi/abs/10.1890/0012-9658(2007)88%5B96:SIBEAA%5D2.0.CO%3B2. Accessed 18 March 2014.

12. Boscolo D, Paul Metzger J (2011) Isolation determines patterns of species presence in highly fragmented landscapes. Ecography (Cop) 34: 1018–1029. Available: http://doi.wiley.com/10.1111/j.1600-0587.2011.06763.x. Accessed 22 January 2014.

13. Lira PK, Ewers RM, Banks-leite C, Pardini R, Metzger JP (2012) Evaluating the legacy of landscape history: extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic forest. J Appl Ecol 49: 1325–1333. doi:10.1111/j.1365-2664.2012.02214.x.

14. Metzger JP, Martensen AC, Dixo M, Bernacci LC, Ribeiro MC, et al. (2009) Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biol Conserv 142: 1166–1177. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320709000780. Accessed 22 January 2014.

15. Umetsu F, Metzger JP, Pardini R (2008) Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: a test with Atlantic forest small mammals. Ecography (Cop) 31: 359–370. doi:10.1111/j.2008.0906-7590.05302.x.

16. Hulme PE (1998) Post-dispersal seed predation: consequences for plant demography and evolution. Perspect Plant Ecol Evol Syst 1: 32–46. Available: http://linkinghub.elsevier.com/retrieve/pii/S1433831904700037.

17. Tewksbury JJ, Levey DJ, Haddad NM, Sargent S, Orrock JL, et al. (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. PNAS 99: 12923–12926. Available: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=130561&tool=pmcentrez&rendertype=abstract.

18. Pardini R, Souza SM de, Braga-Neto R, Metzger JP (2005) The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biol Conserv 124: 253–266. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320705000613. Accessed 6 March 2012.

19. Pardini R, Faria D, Accacio GM, Laps RR, Mariano-neto E, et al. (2009) The challenge of maintaining Atlantic forest biodiversity : A multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in

southern Bahia. Biol Conserv 142: 1178–1190. Available: http://dx.doi.org/10.1016/j.biocon.2009.02.010.

20. Mortelliti A, Amori G, Capizzi D, Cervone C, Fagiani S, et al. (2011) Independent effects of habitat loss, habitat fragmentation and structural connectivity on the distribution of two arboreal rodents. J Appl Ecol 48: 153–162. Available: http://doi.wiley.com/10.1111/j.1365-2664.2010.01918.x. Accessed 11 August 2011.

21. Terborgh J, Lopez L, Nuñez P, Rao M, Shahabuddin G, et al. (2001) Ecological meltdown in predator-free forest fragments. Science (80-) 294: 1923–1926. Available: http://www.ncbi.nlm.nih.gov/pubmed/11729317. Accessed 18 July 2011.

22. Pardini R (2004) Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. Biodivers Conserv 13: 2567–2586. Available: http://www.springerlink.com/openurl.asp?id=doi:10.1023/B:BIOC.0000048452.18878.2d.

23. Dirzo R, Mendoza E (2007) Size related differential seed predation in a heavily defaunated neotropical rain forest. Biotropica 39: 355–362. Available: http://onlinelibrary.wiley.com/doi/10.1111/j.1744-7429.2007.00274.x/full. Accessed 30 March 2012.

24. Tylianakis JM, Laliberté E, Nielsen A, Bascompte J (2010) Conservation of species interaction networks. Biol Conserv 143: 2270–2279. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320709005126. Accessed 21 January 2014.

25. Fleury M, Galetti M (2006) Forest fragment size and microhabitat effects on palm seed predation. Biol Conserv 131: 1–13. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320706000504. Accessed 3 March 2012.

26. McConkey KR, Drake DR (2006) Flying foxes ceace to function as seed dispersers long before they become rare. Ecology 87: 271–276.

27. Galetti M, Guevara R, Côrtes M, Fadini R, Matter S, et al. (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. Science (80-) 340: 1086–1090. Available: http://www.sciencemag.org/content/340/6136/1086.short. Accessed 17 June 2013.

28. Brinkerhoff RJ, Haddad NM, Orrock JL (2005) Corridors and olfactory predator cues affect small mammal behavior. J Mammal 86: 662–669.

29. Muller-landau HC (2007) Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. Biotropica 39: 372–384.

30. Forero-Medina G, Vieira M (2009) Conectividade funcional e a importância da interação organismo paisagem. Oecologia Aust 11: 493–502. Available: http://www.oecologiaaustralis.org/ojs/index.php/oa/article/viewArticle/oeco.2007.1104.03. Accessed 10 June 2012.

31. Orrock JL, Levey DJ, Danielson BJ, Damschen EI (2006) Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. J Ecol 94: 838–845. Available: http://doi.wiley.com/10.1111/j.1365-2745.2006.01125.x. Accessed 6 March 2013.

32. Wright SJ, Hernandéz A, Condit R (2007) The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. Biotropica 39: 363–371. Available: http://onlinelibrary.wiley.com/doi/10.1111/j.1744-7429.2007.00289.x/full. Accessed 30 April 2012.

33. Smith III TJ (1987) Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68: 266–273. Available: http://www.jstor.org/stable/10.2307/1939257. Accessed 22 December 2013.

34. Talluto M V., Benkman CW (2013) Landscape-scale eco-evolutionary dynamics: selection by seed predators and fire determine a major reproductive strategy. Ecology 94: 1307–1316. Available: http://www.ncbi.nlm.nih.gov/pubmed/23923494.

35. Pinto SRR, Santos AMM, Tabarelli M (2009) Seed predation by rodents and safe sites for large-seeded trees in a fragment of the Brazilian Atlantic forest. Rev brasleira Biol 69: 763–771. Available: http://www.ncbi.nlm.nih.gov/pubmed/19802435.

36. Orrock JL, Danielson BJ (2005) Patch shape , connectivity , and foraging by oldfield mice (Peromyscus polionotus). J Mammal 86: 569–575.

37. Bowers MA, Dooley Jr. JL (1993) Predation hazard and seed removal by small mammals: Microhabitat versus patch scale effects. Oecologia 94: 247–254. Available: http://link.springer.com/10.1007/BF00341324.

38. Orrock JL, Damschen EI (2005) Corridors Cause Differential Seed Predation. Ecol Appl 15: 793–798. Available: http://www.esajournals.org/doi/abs/10.1890/04-1129.

39. Terborgh J (1986) Keystone plant resources in the tropical forest. In: Soule M, editor. Conservation biology. Sinauer, Sunderland, Massachussets.

40. Peres CA (2000) Identifying keystone plant resources in tropical forests: the case of gums from Parkia pods. J Trop Ecol 16: 287–317. Available: http://www.journals.cambridge.org/abstract_S0266467400001413.

41. Koprowski JL (2005) The response of tree squirrels to fragmentation: a review and synthesis. Anim Conserv 8: 369–376. Available: http://doi.wiley.com/10.1017/S1367943005002416. Accessed 11 June 2012.

42. Freire CC, Closel MB, Hasui E, Ramos FN (2013) Reproductive phenology, seed dispersal and seed predation in Syagrus romanzoffiana in a highly fragmented landscape. Ann Bot Fenn 50: 220–228.

43. Bayne E, Hobson K (2000) Relative use of contiguous and fragmented boreal forest by red squirrels (Tamiasciurus hudsonicus). Can J Zool 78: 359–365. Available: http://www.nrcresearchpress.com/doi/abs/10.1139/z99-219.

44. Solórzano-Filho JA (2006) Mobbing of Leopardus wiedii while hunting by a group of Sciurus ingrami in an Araucaria forest of Southeast Brazil. Mammalia 70: 156–157. Available: http://www.degruyter.com/view/j/mamm.2006.70.issue-1_2/mamm.2006.031/mamm.2006.031.xml. Accessed 28 May 2013.

45. Visser MD, Muller-Landau HC, Rutten G, Jansen PA (2011) Tri-trophic interactions affect density dependence of seed fate in a tropical forest palm. Ecol Lett 14: 1093–1100. doi:10.1111/j.1461-0248.2011.01677.x.

46. Andreazzi CS, Pires AS, Fernandez FAS (2009) Mamíferos e palmeiras neotropicais: Interações em paisagens fragmentadas. Oecologia Aust 13: 554–574. Available: http://www.oecologiaaustralis.org/ojs/index.php/oa/article/view/oeco.2009.1304.02/71. Accessed 3 March 2012.

47. Henderson A, Galeano G, Bernal R (1995) Palms of the Americas. Princeton: Princeton University Press. doi:10.1007/s13744-011-0002-z.

48. Lorenzi H (1998) Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil. 2nd ed. Nova Odessa: Editora Plantarum.

49. Silva FR da, Begnini RM, Scherer KZ, Lopes BC, Castellani TT (2008) Predação de Sementes de Syagrus romanzoffiana (Cham.) Glassman (Arecaceae) por Insetos na Ilha de Santa Catarina, SC. Rev Bras Biocienccias 5: 681–683. Available: http://www6.ufrgs.br/seerbio/ojs/index.php/rbb/article/viewArticle/693. Accessed 30 April 2012.

50. Galetti M, Paschoal M, Pedroni F (1992) Predation on palm nuts (Syagrus romanzoffiana) by squirrel (Siurus ingrami) in south-east Brazil. J Trop Ecol 8: 121 – 123.

51. Paschoal M, Galetti M (1995) Seasonal foof used by the neotropica squirrel Sciurus ingrami in southeastern Brazil. Biotropica 27: 268–273.

52. Bordignon M, Margarido TCC, Lange RR (1996) Formas de abertura dos frutos de Syagrus romanzoffiana (Chamisso) Glassman efetuadas por Sciurus ingrami Thomas (Rodentia, Sciuridae). Rev Bras Zool 13: 821–828.

53. Guimarães PR, Lopes PFM, Lyra ML, Muriel AP (2005) Fleshy pulp enhances the location of Syagrus romanzoffiana (Arecaceae) fruits by seed-dispersing rodents in an Atlantic forest in south-eastern Brazil. J Trop Ecol 21: 109–112. doi:10.1017/S0266467404001932.

54. Alves-Costa CP, Knogge C (2005) Larval competition in weevils Revena rubiginosa (Coleoptera: Curculionidae) preying on seeds of the palm Syagrus romanzoffiana (Arecaceae). Naturwissenschaften 92: 265–268. Available: http://www.ncbi.nlm.nih.gov/pubmed/15871001. Accessed 3 March 2012.

55. 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. Biol Conserv 142: 1141–1153. Available: http://linkinghub.elsevier.com/retrieve/pii/S0006320709000974. Accessed 28 February 2013.

56. Keuroghlian A, Eaton DP (2009) Removal of palm fruits and ecosystem engineering in palm stands by white-lipped peccaries (Tayassu pecari) and other frugivores in an isolated Atlantic Forest fragment. Biodivers Conserv 18: 1733–1750. doi:10.1007/s10531-008-9554-6.

57. Galetti M, Giacomini HC, Bueno RS, Bernardo CSS, Marques RM, et al. (2009) Priority areas for the conservation of Atlantic forest large mammals. Biol Conserv 142: 1229–1241. Available: http://dx.doi.org/10.1016/j.biocon.2009.01.023.

58. Fortin MJ, Dale MRT (2005) Spatial Analysis: A Guide for Ecologists. Cambridge University Press.

59. Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40: 1649–1663. Available: http://doi.wiley.com/10.1111/jbi.12130. Accessed 20 January 2014.

60. Bender D, Tischendorf L, Fahrig L (2003) Using patch isolation metrics to predict animal movement in binary landscapes. Landsc Ecol 18: 17–40. Available: http://link.springer.com/article/10.1023/A:1022937226820. Accessed 18 March 2014.

61. Brancalion PHS, Rodrigues RR, Novembre ADLC, Gómez JM (2011) Are we misinterpreting seed predation in palms ? Oecologia 43: 12–14.

62. Burnham KP, Anderson DR (2010) Model selection and multi-model inference: A practical information-theoretic approach. 2nd ed. Springer.

63. R Core Team (2012) R: A language and environment for statiscal computing. Available: http://www.r-project.org.

64. Bordignon M, Monteiro-Filho ELA (2000) Behaviour and daily activity of the squirrel Sciurus ingrami in a secondary araucaria forest in southern Brazil. Can J Zool 78: 1732–1739.

65. Prevedello JA, Forero-Medina G, Vieira MV (2010) Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. J Anim Ecol 79: 1315–1323. doi:10.1111/j.1365-2656.2010.01736.x.

66. Zollner PA, Lima SL (1997) Landscape-level perception abilities in whited-footed mice: perceptual range and the detection of forest habitat. Oikos 80: 51–60.

67. Grahan CH, Blake JG (2001) Influence of patch- and landscape-level factors on bird assemblages in a fragmented tropical landscape. Ecol Appl 11: 1709–1721.

68. Walpole A a., Bowman J (2011) Patch occupancy by squirrels in fragmented deciduous forest: effects of behavior. Acta Theriol (Warsz) 56: 63–72. Available: http://link.springer.com/10.1007/s13364-010-0010-0. Accessed 18 March 2014.

69. Keller LF, Waller DM (2002) Inbreeding effects in wild populations. TRENDS Ecol Evol 17: 230–241. Available: http://www.sciencedirect.com/science/article/pii/S0169534702024898. Accessed 18 March 2014.

70. Harper SJ, Bollinger EK, Barrett GW (1993) Effects of habitat patch shape on population dynamics of meadow voles (Microtus pennsylvanicus). J Mammal 74: 1045–1055.

71. Davis SK (2004) Area sensitivity in grassland passerines: Effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. Auk 121: 1130–1145.

72. Benitez-Malvido J (2008) Impact of Forest Fragmentation on Seedling Abundance in a Tropical Forest. Conserv Biol 12: 380–389.

73. Helzer CJ, Jelinski DE (1999) The Relative Importance of Patch Area and Perimeter-Area Ratio to Grassland Breeding Birds. Ecol Appl 9: 1448. Available: http://www.jstor.org/stable/2641409?origin=crossref.

74. Delobel A, Couturier G, Kahn F, Nilsson JA (1995) Trophic relationships between palms and bruchids (Coleoptera: Bruquidae: Pachymerini) in Peruvian Amazonia. Amazoniana 13: 209–219.

75. Dracxler CM, Pires AS, Fernandez F a. S (2011) Invertebrate Seed Predators are not all the Same: Seed Predation by Bruchine and Scolytine Beetles Affects Palm Recruitment in Different Ways. Biotropica 43: 8–11. Available: http://doi.wiley.com/10.1111/j.1744-7429.2010.00723.x.

76. Sallabanks R, Courtney SP (1992) Frugivory, seed predation, and insect-vertebrate interactions. Annu Rev Entomol 37: 377–400. Available: http://www.ncbi.nlm.nih.gov/pubmed/1539939.

77. Peguero G, Espelta JM (2013) Evidence for insect seed predator dynamics mediated by vertebrate frugivores. Rev Chil Hist Nat 86: 161–167. Available: http://www.scielo.cl/pdf/rchnat/v86n2/art05.pdf. Accessed 18 March 2014.

78. Borer ET, Seabloom EW, Shurin JB, Anderson KE, Blanchette CA, et al. (2005) What determines the strength of a trophic cascade? Ecology 86: 528–537.

79. Polis GA, Strong DR (1996) Food web complexity and community dynamics. Am Nat 147: 813–846.

80. Boscolo D, Metzger JP (2009) Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? Landsc Ecol 24: 907–918. Available: http://link.springer.com/10.1007/s10980-009-9370-8. Accessed 19 February 2014.

81. Lyra-Jorge MC, Ribeiro MC, Ciocheti G, Tambosi LR, Pivello VR (2010) Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. Eur J Wildl Res 56: 359–368. Available: http://link.springer.com/10.1007/s10344-009-0324-x. Accessed 25 February 2014.

82. Silvius KM, Fragoso JM V (2003) Red-rumped Agouti (Dasyprocta leporina) home range use in an Amazonian Forest: Implications for the aggregated distribution of forest trees. Biotropica 35: 74–83.

83. Fleury M, Galetti M (2004) Effects of microhabitat on palm seed predation in two forest fragments in southeast Brazil. Acta Oecologica 26: 179–184. Available: http://linkinghub.elsevier.com/retrieve/pii/S1146609X04000384. Accessed 3 March 2012.

MATERIAL SUPLEMENTAR

TABLE S1: Vertebrate species that eat the fruits of *Syagrus romanzoffiana* in the Atlantic forest

SPECIES	BEHAVIOR	REFERENCES
MAMMALIA		
Artiodactyla		
Pecari tajacu	Disperser	Keuroghlian e Eaton, 2008
Tayassu pecari	Disperser	Keuroghlian e Eaton, 2008
Sus scrofa	Disperser	F. Pedrosa, unp. data
Carnivora		
Cerdocyon thous	Disperser	Guix e Ruiz, 2000; Messias e Alves, 2009
Chrysocyon brachyurus	Disperser	Bueno e Motta-Junior, 2009
Eira barbara	Disperser	Klier e Castellani, 2009
Lycalopex vetulus	Disperser	Dalponte e Lima, 1999
Nasua nasua	Disperser	Klier e Castellani, 2009
Procyon cancrivorus	Disperser	Messias e Alves, 2009
Puma concolor	Disperser	M. Ribeiro, unp. data
Chiroptera		
Artibeus fimbriatus	Disperser	Guix e Ruiz, 2000
Artibeus lituratus	Disperser	Galetti e Morellato, 2004; Guix e Ruiz, 2000
Didelphimorphia		
Didelphis aurita	Pulp thief	M. Galetti unpubl. data
Didelphis albiventris	Pulp thief	Cáceres, 2002
Perissodactyla		
Tapirus terretris	Disperser	Galetti *et al.* 2001; Giombini*et al.* 2009
Primates		
Alouatta caraya	Disperser	Guix e Ruiz, 2000
Alouatta guariba	Disperser	Galetti et al. 2004; Guix e Ruiz, 2000
Callithrix jacchus	Pulp thief	Messias e Alves, 2009
Callithrix penicillata	Pulp thief	Messias e Alves, 2009
Leontopithecus chrysopygus	Pulp thief	Passos, 2012
Sapajus nigritus	Pulp thief	Galetti e Pedroni, 2004; Klier e Castellani, 2009
Rodentia		
Agouti paca	Predator, Disperser	Messias e Alves, 2009
Dasyprocta agouti	Predator, Disperser	Guimarães et al. 2005.
Dasyprocta azarae	Predator, Disperser	Guix e Ruiz, 2000
Euryoryzomys russatus	Predator, Pulp thief	Silva et al. 2011
Sciurus ingrami	Predator, Disperser	Guix e Ruiz, 2000; Paschoal e Galetti, 1995

AVES		
Galliforme		
Penelope obscura	Disperser	Guix e Ruiz, 2000
Penelope superciliaris	Disperser	Guix e Ruiz, 2000
Passeriformes		
Coereba flaveola	Pulp thief	M. Galetti unpubl. data
Cyanocorax caeruleus	Disperser	Guix e Ruiz, 2000
Cyanocorax chrysops	Disperser	Guix e Ruiz, 2000
Cyanocorax cristatellus	Disperser	Guix e Ruiz, 2000
Cyanocorax cyanomelas	Pulp thief, Disperser	Guix e Ruiz, 2000
Euphonia violacea	Pulp thief	Athiê e Dias, 2012
Platycichla flavipes	Pulp thief	Guix e Ruiz, 2000
Procnias nudicollis	Disperser	Guix e Ruiz, 2000
Ramphocelus bresilius	Pulp thief	Silva et al. 2011
Tachyphonus coronatus	Pulp thief	Messias e Alves, 2009
Thraupis sayaca	Pulp thief	Messias e Alves, 2009
Turdus amaurochalinus	Pulp thief	Guix e Ruiz, 2000
Turdus leucomelas	Pulp thief	Guix e Ruiz, 2000
Turdus rufiventris	Pulp thief	Guix e Ruiz, 2000
Piciformes		
Pteroglossus aracari	Disperser	Guix e Ruiz, 2000
Pteroglossus castanotis	Disperser	Guix e Ruiz, 2000
Ramphastos dicolorus	Disperser	Guix e Ruiz, 2000
Ramphastos toco	Disperser	Guix e Ruiz, 2000
Ramphastos vitellinus	Disperser	Guix e Ruiz, 2000
Psittaciformes		
Amazona brasiliensis	Pulp thief	Serafini*et al.* 2011; Martuscelli, 1995
Anodorhinchus hyacinthinus	Predator	Kuniy*et al.* 2007
Anodorhinchus leari	Predator	Kuniy*et al.* 2007
Ara ararauna	Predator	Kuniy*et al.* 2007
Ara chloroptera	Predator	Scherer-Neto e Terto, 2011
Aratinga leucophthalmus	Pulp thief	Messias e Alves, 2009
Brotogeris chiriri	Pulp thief	Paranhos *et al.* 2007
Brotogeris tirica	Pulp thief? Disperser?	Sazima, 2008
Pyrrhura frontalis	Pulp thief	Luccas *et al.* 2009
Struthioniformes		
Rhea americana	Disperser	Guix e Ruiz, 2000
REPTILIA		
Squamata		
Tupinambis merianae	Disperser	Castro e Galetti, 2004

TABLE S2: List of sampled areas, showing their localization, percentage of forest cover, size of the sampled patches and type of surrounding matrix.

Landscape	**Coordinates (UTM)**	**Municipality**	**Forest Cover (%)**	**Patch Sizes (ha)**	**Matrix**
1	-22.4647, -47.9280	São Pedro	2.02	3.07	Sugar cane
2	-22.2480, -47.2139	Araras	6.89	0.64	Sugar cane
3	-22.3351, -47.2473	Martinho Prado	2.05	4.13	Sugar cane and orange
4	-22.2123, -47.3203	Leme	2.87	16.49	Sugar cane
5	-22.6363, -48.0412	São Pedro	4.81	20.68 and 3.73	Sugar cane
6	-22.5586, -47.5806	Piracicaba	7.02	37.39	Sugar cane
7	-22.2600, -47.4684	Leme	8.46	49.62	Sugar cane
8	-22.2691, -47.6573	Corumbataí	22.1	44.91	Sugar cane
9	-22.7111, -47.0962	Cosmópolis	29.26	179.93 and 19.46	Sugar cane
10	-22.3586, -47.4771	Rio Claro	34.09	332.62	Sugar cane
11	-22.2630, -47.3304	Araras	36.36	280.64	Sugar cane
12	-21.8519, -47.4212	Porto Ferreira	61.65	652.52	Sugar cane
13 - Control	-22.3878, -49.6847	Gália	71.5	1200	Sugar cane, coffee and pasture

FIGURE S1: Seeds of Syag*rus romanzoffiana* with predation marks by: A- squirrels (*Sciurus ingrami*); B- terrestrial rodents; C- Invertebrate larvae (*Revena rubiginosa*).

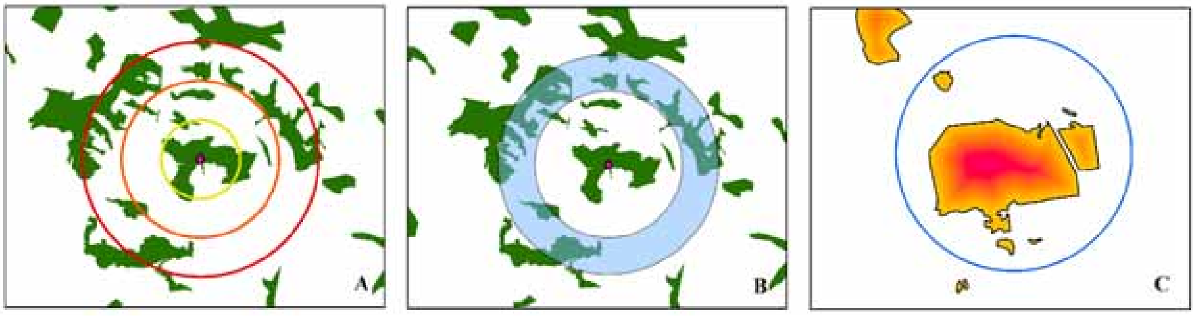


FIGURE S2: Map showing the buffers used to calculate the forest cover variables: A- Buffers of local forest cover around the centroid of the sample palms (pink dot) in three scales: 1500 m (red); 1000 m (orange); 500 m (yellow). B- Buffer zone of regional forest cover, where only the habitat within the area closer than 1500 m and farther that 1000 m is counted to the variable. C – First step in the calculation of the fragment shape variable: The fragment area is divided in a grid with cell of 5x5 meters and the Euclidean distance from each grid cell to the nearest edge is calculated, the color in the figure express the Euclidean distance from that cell to the nearest edge.

TABLE S3: List of the tested models.

Models
GLM/GAM0: VD ~ Mean (Null Model)
GLM/GAM1: VD ~ Edge Distance
GLM/GAM2: VD ~ Fruit Number
GLM/GAM3: VD ~ Fragment Area
GLM/GAM4: VD ~ Fragment Shape
GLM/GAM5: VD ~ Local Forest Cover*
GLM/GAM6: VD ~ Regional Forest Cover
GLM/GAM7: VD ~ Fruit Number + Edge Distance
GLM/GAM8: VD ~ Fragment Area + Edge Distance
GLM/GAM9: VD ~ Fragment Area + Fragment Shape
GLM/GAM10: VD ~ Local Forest Cover* + Edge Distance
GLM/GAM11: VD ~ Regional Forest Cover + Local Forest Cover (500 m)
† GLM/GAM12: VD ~ Squirrel predation
† GLM/GAM13: VD ~ Edge distance + Squirrel predation
† GLM/GAM14: VD ~ Fragment area + Squirrel predation
† GLM/GAM15: VD ~ Local forest cover* + Squirrel predation

* Variable used only in the best scale, † Model used only in the invertebrate tests

TABLE S4: List of landscapes with the respective number of fruits sampled and the predation rate of each predator group.

Landscape	Fruit number per landscape	Overall seed predation (%)	Invertebrate predation (%)	Squirrel predation (%)	Terrestrial rodent predation (%)
1	692	44.36	42.19	0	2.16
2	3823	73.92	43.57	0	30.34
3	945	67.3	31.85	0	35.44
4	12111	91.55	89.58	0	1.966
5	13444	85.46	78.95	0	6.5
6	7377	74.43	7.52	66.88	0.02
7	4493	56.99	28.62	22.79	5.58
8	5935	43.06	41.43	0	1.63
9	9549	54.72	50.06	0	4.66
10	11019	84.88	22.82	60.73	1.33
11	4561	78.42	8	69.19	1.22
12	25139	58.35	49.67	0	8.67
13	8781	74.58	65.66	8.87	0.04