Andrea Larissa Boesing

Landscape processes underpinning bird persistence and avian-mediated pest control in fragmented landscapes

São Paulo
2016

Andrea Larissa Boesing

Landscape processes underpinning bird
persistence and avian-mediated pest control in
fragmented landscapes

Persistência de aves e controle de pragas em
paisagens fragmentadas – uma perspectiva da
ecologia de paisagens

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências, na Área de Ecologia.

Orientador: Jean Paul Metzger
Co-orientadora: Elizabeth Nichols

São Paulo
2016

FichaCatalográfica

Boesing, Andrea Larissa

Persistência de aves e controle de pragas em paisagens fragmentadas – uma perspectiva da ecologia de paisagens

181 páginas

Tese (Doutorado) - Instituto de Biociências da Universidade de São Paulo. Departamento de Ecologia.

1.Estrutura da paisagem
2.Cobertura florestal
3.Mata Atlântica

Universidade de São Paulo. Instituto de Biociências. Departamento de Ecologia.

Comissão Julgadora:

_____   _____
Prof(a). Dr(a).   Prof(a). Dr(a).

_____   _____
Prof(a). Dr(a).   Prof(a). Dr(a).

_____
Prof. Dr. Jean Paul Metzger
Orientador(a)

Dedication

Epigraph

Hold fast to dreams
For if dreams die
Life is a broken-winged bird
That cannot fly.

Hold fast to dreams
For when dreams go
Life is a barren field
Frozen with snow.

Langston Hughes

Acknowledgments

Este trabalho é resultado de um esforço conjunto que envolveu muitas pessoas. Com toda certeza, agora que esta etapa esta próxima do fim, o sentimento é de gratidão para com cada pessoa que cruzou o meu caminho nesta empreitada. Sinto-me afortunada por todas as amizades e por todo o aprendizado durante esta caminhada e pelas experiências compartilhadas. Muito obrigada a todos que de uma maneira ou de outra, fizeram esta jornada tão especial, a qual foi uma etapa muito importante na minha vida. E sim, senta que lá vem história e cinco páginas de agradecimentos.

Agradeço primeiramente ao Jean por ter me acolhido no LEPaC há quatro anos atrás, por todo o apoio durante o desenvolvimento do projeto, pelas ideias compartilhadas, pelos puxões de orelha sempre em boa hora, e pela confiança em mim depositada. Aprendi muito neste período Jean, e lhe tenho como exemplo e fonte de inspiração para minha carreira. Sou muito grata pela oportunidade de ser parte do LEPaC.

Agradeço de coração à Liz, por todo auxilio e amizade durante o desenvolvimento deste trabalho, desde o inicio da fase de GIS e seleção das paisagens, de nossas primeiras aventuras à região da Cantareira, até os últimos instantes com correções, leitura, mais correções, puxões de orelha, motivação, mais puxões de orelha... Sou grata pelos tantos momentos compartilhados em campo ou fora dele. Obrigada pela motivação, por ter acentuado meu vício em café, pela troca de ideias, pelos 'insights de campo – 'IdC', e por tudo que me ensinou neste período.

Agradeço a todo o pessoal do LEPaC, pela parceria, convívio e experiência única de trabalhar com um grupo tão bacana. Este período não teria sido o mesmo sem o carisma e companheirismo de vocês. Sou grata por todo aprendizado e por tantos momentos que compartilhamos, em lab ou fora dele. Obrigada Isa, Ká, Chico, Feli, Juarez, Nati, Lê, Mel, Amanda, Paula, Camila, Caro, Vivi, por fazerem este período tão especial.

Um agradecimento especial também à "Veritchaa" (Vera Lucia), que faz nossa vida tão mais fácil no Departamento. Obrigada Vera pela força durante todo o processo, desde quando eu estava em campo, na gringolândia, ou em São Paulo, especialmente nas últimas semanas pelo apoio moral e psicológico.

I am thankful to Prof. Kathryn Sieving who hosted me during my Exchange at University of Florida, providing all logistical support. I really appreciate all Sieving's Lab members for the patience and discussions about my research.

I am thankful to Professor Scott Robinson, one of the most recognized tropical ornithologists in the world, for his kindly invitation to participate in his Lab meetings at University of Florida, and substantially contribute to bird's classification, and for sharing ideas on bird persistence in anthropogenic landscapes. I am thankful to Professor Bob Holt as well, who demonstrated so much interest for my work and also shared so many ideas and contribution to data discussion.

E agradeço àqueles que durante todo o período, não me deixaram surtar. Agradeço à minha família, em especial meu pai e meu irmão mais novo, sempre apoiadores das minhas decisões e sempre compreensíveis com meus campos e deadlines. Obrigada por apoiarem minha decisão de fazer o doutorado mesmo no momento mais difícil de nossas vidas. Meu agradecimento vai também em forma de pedido de desculpas, pela ausência neste período, pela ausência em muitos momentos que deveria estar presente, e pelos meses que fiquei sem dar as caras em casa.

Obrigada vai também à minha família buscapé (Tia Barbara, Tio Aroldo, Rodrigo(s) e Aline), por sempre me acolherem de braços abertos em cada fugida para casa, pelos assados de pinhão, cuca de banana, e o chimarrão sempre à espera. Agradeço especialmente a minha mãezinha "postiça" Tia Barbara, que tanto ajuda a preencher o vazio que minha mãe deixou e que olha meu little brô por mim enquanto estou nessa loucura.

Às moradoras do Refúgio, Meme e Pati, que me acolheram em São Paulo há 4 anos atrás e me aguentaram todo esse tempo mesmo ficando mais tempo em campo ou na USP do que em casa (talvez por isso me aguentam...). Obrigada também ao Jóqui,

pela companhia, apoio e histórias nas madrugadas em fase de escrita. Obrigada por tudo e devo desculpas a vocês também, pela ausência constante.

I am thankful to Harry Jones, who became my best friend and a whole inspiration during my stay in US. In spite being my coffee buddy, I'm so thankful for making my stay in your country so much easier, and for being such a loyal and present friend even 4,000 miles away. I have no words to describe how blessed I'm to have gotten met you.

Agradeço ao meu Brazilian crew na gringa: Sandev, Rafa e Takao, por tantos bons momentos compartilhados! Sandev, obrigada por todos os cafés, todos os almoços no chrisna, por todas as conversas malucas sem pé nem cabeça, por todas as cervejas boas, por toda ajuda em R quando eu penava, e por ser este doce de pessoa que não vê maldade no mundo. Takao, que foi imprescindível especialmente nos primeiros meses morando fora. Obrigada pela paciência, pela amizade verdadeira, e pelos doughnuts sempre em boa hora. Rafa querida, sempre tão calma e tranquila que transbordava positividade todos os dias e me deixava tranquila só com a presença dela.

Agradeço à Melina Melito, por ter se tornado uma irmã em São Paulo, na alegria e na tristeza, no vinho ou na cerveja, no temaki do postinho ou no hambúrguer do tio radialista, e em todas as fases de alegria e desespero de desenvolvimento da tese.

Agradeço ao Leleco (Leandro Pereira), que mesmo de longe está sempre por perto. O agradecimento não vai não só por esta fase, mas pelos mais de 6 anos de amizade, e por estar do meu lado em todos os momentos - sejam eles bons ou os piores que já passei.

Index

General Introduction

Globally, the current extent of conversion of native land cover to agricultural production is expanding faster than any time over the last 50 years (Grassini et al. 2013). Croplands and pastures have become the largest landscape components on the planet, occupying 40% of its land surface (Ramankutty and Foley 1999, Asner et al. 2004). Meanwhile, habitat loss is one of the main drivers of species extinction worldwide (Fahrig 1997, Dirzo and Raven 2003), reducing population sizes and increasing extinction probability due to demographic or environmental stochasticity (Burkey 1995). Although species extinction has always been part of Earth's history (Pimm et al. 1995), the current extinction crisis is occurring more rapidly than throughout geological time, prompting talk of a sixth mass extinction (Barnosky et al. 2011, Steffen et al. 2015).

The influence of habitat loss on biodiversity is tied to a series of non-linear relationships between the amount of native habitat remaining and landscape configuration that strongly affect isolation and connectivity processes determining both extinction and colonization rates (Andren 1994, Fahrig 2003, 2013). Different spatial configurations of a given habitat amount might affect species persistence due to functional connectivity (i.e. the degree to which landscapes actually facilitate or impede the movement of organisms; Fahrig 1998) – at least between certain thresholds of remaining habitat (Andren 1994, Villard and Metzger 2014). Extinction threshold theory predicts that there is a minimum suitable amount of habitat required by a given species or assemblage to persist in an environment (Andren 1994, Fahrig 1997). This theory predicts that as the proportion of habitat amount in a landscape decreases, species persistence is affected not only by habitat loss *per se*, but also by effects at the patch scale such as edge and area effects (Andren 1994, Villard and Metzger 2014).

Although habitat fragmentation theory is based on island biogeography and metapopulation theory (i.e. assuming matrix as inhospitable and homogeneous; (Haila 2002, Jules and Shahani 2003, Kupfer et al. 2006), the matrix surrounding habitat patches is often composed of a complex mosaic of land cover types (Ricketts 2001). Because of this heterogeneity, the matrix type where habitat

patches are embedded must play a key role affecting dispersal ability of species, influencing (re)colonization and extinction rates, and possibly changing extinction thresholds. Matrix composition can range from structurally simple matrices dominated by homogeneous arable lands to structurally complex ones, with high amounts of non-crop areas or components such as mixed plantations or agroforestry systems (Tscharntke et al. 2007), with different degrees of resistance to organisms' movement (Ricketts 2001). In addition to influencing species abundance and composition through movement and dispersal, the matrix surrounding habitat patches might also provide additional resources and affect the abiotic environment of patches (Driscoll et al. 2013, Prevedello et al. In press). While corridors and stepping stones have received much recent empirical attention (Levey et al. 2005, Haddad et al. 2014, Haddad 2015), the role of matrix composition in influencing biological processes such as dispersal and resources provisioning is still a challenging issue (Ricketts 2001, Prevedello and Vieira 2010, Driscoll et al. 2013).

Ultimately, landscape changes due anthropogenic disturbances are driving not only species loss *per se*, but also loss of functions performed by those species and their interactions (Mokross et al. 2014, Jordano 2016), and a whole evolutionary history is threatened as well (Hooper et al. 2005). As a consequence, losses in taxonomic diversity are accompanied by important changes in functional diversity (i.e. the diversity of functional traits across a community; Jarzyna and Jetz 2016), which may significantly impact ecosystem function (Bregman et al. 2014, Oliver et al. 2015), and by losses of phylogenetic diversity (i.e. the evolutionary history of a species assemblage; Webb 2000) that potentially curtail future resilience in both biodiversity and function (Frishkoff et al. 2014). A meta-analysis of biodiversity-ecosystem functions studies suggests that the impact of biodiversity losses on ecosystem functions is comparable (or even worse) in scale with that of other global changes such as climate change (Hooper et al. 2005). Moreover, declines in the number of individuals in local populations and changes in species composition in a community will strongly affect ecosystem functioning as well (Sekercioglu 2006).

Ultimately, biodiversity losses have been documented to undermine the provisioning of ecosystem services - defined as the benefits that humans derive

from nature (MEA 2005, TEEB 2010). Recent calls to create agricultural landscapes that simultaneously provide ecosystem services and support high biodiversity (Mooney et al. 2010, DeClerck et al. 2015) have highlighted the importance of understanding how landscape structure and composition influence the provisioning of ecosystem services (Turner et al. 2013, Wu 2013, Mitchell et al. 2015). Particularly, we need to estimate how much native habitat is required to maintain certain biodiversity standards and ecosystem functionality (Fahrig 2002, Ficetola and Denoel 2009), including providing some ecosystem services. As native land-cover provides critical habitat for many mobile organisms that offer ecosystem services in agricultural systems (Bianchi et al. 2006, Tscharntke et al. 2012, Karp et al. 2013), retaining native habitats nearby crop fields might result in considerable economic gain for landholders (Ostman et al. 2001, Karp et al. 2013) and might be a clear justification for habitat conservation in working agricultural landscapes.

Birds are an extremely useful taxon for investigating questions integrating effects of landscape structure and provisioning of ecosystem services. First, birds have an extremely diverse range of functional traits, allowing them to use a huge variety of resources (Sekercioglu et al. 2016), which makes them special from the perspective of ecosystem services provisioning (Whelan et al. 2008). Second, birds are especially mobile organisms, which allows them actively search and respond to pulses of resources in ways not generally possible for other vertebrates, allowing them to leave areas in which resources are no longer sufficient and relocate to more productive locations (Whelan et al. 2008). Finally, they have high mass-specific metabolic rates, which translates to a constant need for resources - especially during the breeding season, when nestlings require a protein-rich diet. In this context, insectivorous birds might play a significant role in controlling insect populations, making them special in terms of pest control services in agricultural landscapes (Van Bael et al. 2008). Moreover, insectivorous birds are ubiquitous, abundant, and essential components of most terrestrial ecosystems (Sekercioglu 2006), and by far the most diverse avian functional group with more than 7,400 species worldwide.

Herbivorous insects are responsible destroying one fifth of the world's total crop production, with an estimated economic impact of billion dollars annually

(Bonning and Chougule 2014). Pest proliferation leads, especially in monocultures, not only to problems related to crop losses (Matson et al. 1997, Laxminarayan and Simpson 2000), but also to serious concerns related to the long-term environmental sustainability of agricultural systems. Natural pest control can be considered as an alternative method to minimize these problems (Bianchi et al. 2006, Losey and Vaughan 2006, Oerke 2006). Taking advantage of natural enemies for pest suppression can enhance and stabilize yield resilience in crop production systems, avoiding complex collapses due to eroded natural regulation (Bommarco et al. 2011, Bommarco et al. 2013). For example, pest control services provided by biodiversity prevent approximately $13.6 billion in agricultural losses in the Unites States annually (Losey and Vaughan 2006). However, the effect of landscape components on the rate and magnitude of pest-control services has rarely been quantified (Tscharntke et al. 2007, Schellhorn et al. 2008), preventing a general understanding of how landscape structure regulates pest-control services.

The main objective of this thesis is to move beyond our current understanding about landscape processes underpinning bird persistence in fragmented landscapes and avian-mediated pest control. We start this work by systematically reviewing the literature for empirical evidence of landscape structure effects on avian-mediated pest control in agricultural systems worldwide. Then, using bird data collected in fragmented landscapes in the Brazilian Atlantic forest, we test for community-level extinction thresholds across a range of biodiversity facets (taxonomic, functional, and phylogenetic diversity) in order to evaluate how much habitat is need to maintain sustainable ecosystem functioning and ecosystem resilience, and how matrix composition might affect these thresholds. Finally, we investigate one of the main processes regulating avian-mediated pest control in tropical regions as determined in our literature review: cross-habitat spillover. The main justification and objectives of each chapter are detailed below.

The **chapter one** is based on a systematic literature review investigating current empirical evidence of the influence of landscape structure on avian-mediated pest control. Despite increasing evidence that landscape composition and configuration strongly influence patch-level diversity, abundance, and composition (Pardini et al. 2010, Banks-Leite et al. 2014), landscape structure has

seldom been explicitly linked with rate and magnitude of pest-control services (Tscharntke et al. 2012). We identify the main landscape features affecting avian-mediated pest control worldwide, in both tropical and temperate biomes and across a range of avian predator types varying in habitat association and diet specialization. We present a conceptual model of the landscape processes and biodiversity mechanisms underlining these relationships, and use this model to identify key research gaps and opportunities for future studies. This chapter is under review in the journal *Landscape Ecology*.

In order to evaluate how much habitat is need to maintain sustainable biodiversity patterns aiming to sustain ecosystem functioning and ecosystem resilience, **chapter two** investigates how matrix composition might modulate extinction thresholds of taxonomic, functional and phylogenetic diversity of Brazilian Atlantic forest avifauna. Biodiversity is one of multiple factors that govern ecosystem properties, and changes to both number and identity of species, and functional diversity imposed by human actions can yield ecosystem effects that vary from small to far-reaching and cascading (Naeem et al. 2012, Jordano 2016). Using approaches incorporating both functional attributes and life history patterns might increase our predictive power about the impacts of land use conversion and fragmentation. Even though it is suggested that extinction thresholds for avian taxonomic diversity occur at around 18-33% of habitat remaining (Betts et al. 2007, Banks-Leite et al. 2014, Richmond et al. 2015), the influence of matrix composition on these thresholds and the thresholds for other measures of biodiversity are unknown.

Cross-habitat spillover is often defined as the movement (e.g. encompassing dispersal and foraging) of organisms from one habitat type to another (Tscharntke et al. 2012). Among the knowledge gaps identified in chapter one, cross-habitat spillover of forest-dependent species into agricultural matrices is a process that deserves particular attention and is thus the subject of **chapter three**. Natural habitats adjacent to crop fields are often seen as source habitat for species providing beneficial regulating ecosystem services such as pest control and pollination in agricultural areas (Bianchi et al. 2006, Kremen et al. 2007). Understanding how habitat configuration and matrix permeability affect the movement of service-providing biodiversity is a key applied management concern

(Blitzer et al. 2012), especially in light of the current agricultural expansion. This chapter investigates these related ideas, testing how landscape structure and matrix composition affect avian cross-habitat spillover of forest-dependent species into the agricultural matrices using field data collected in fragmented landscapes in the Brazilian Atlantic forest, an imperiled ecosystem.

Finally, we conclude this dissertation with a general discussion of our results and their implications for landscape-level management. We discuss how to improve agricultural areas via the maintenance of biodiversity-friendly crop fields, the persistence of forest specialized species in these highly fragmented landscapes, and the enhancement of the provisioning of ecosystem services.

Literature cited

Andren H. (1994). Effects of habitat fragmentation in birds and mammals in landscapes with different proportions of suitable habitat - a review. *Oikos*, 71, 355-366.

Asner G.P., Elmore A.J., Olander L.P., Martin R.E. & Harris A.T. (2004). Grazing systems, ecosystem responses, and global change. *Annu Rev Env Resour*, 29, 261-299.

Banks-Leite C., Pardini R., Tambosi L.R., Pearse W.D., Bueno A.A., Bruscagin R.T., Condez T.H., Dixo M., Igari A.T., Martensen A.C. & Metzger J.P. (2014). Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science*, 345, 1041-1045.

Barnosky A.D., Matzke N., Tomiya S., Wogan G.O.U., Swartz B., Quental T.B., Marshall C., McGuire J.L., Lindsey E.L., Maguire K.C., Mersey B. & Ferrer E.A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51-57.

Betts M.G., Forbes G.J. & Diamond A.W. (2007). Thresholds in songbird occurrence in relation to landscape structure. *Conserv Biol*, 21, 1046-1058.

Bianchi F.J.J.A., Booij C.J.H. & Tscharntke T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *P Roy Soc B-Biol Sci*, 273, 1715-1727.

Blitzer E.J., Dormann C.F., Holzschuh A., Klein A.-M., Rand T.A. & Tscharntke T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agr Ecosyst Environ*, 146, 34-43.

Bommarco R., Kleijn D. & Potts S.G. (2013). Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol Evol*, 28, 230-238.

Bommarco R., Miranda F., Bylund H. & Bjorkman C. (2011). Insecticides Suppress Natural Enemies and Increase Pest Damage in Cabbage. *J Econ Entomol*, 104, 782-791.

Bonning B.C. & Chougule N.P. (2014). Delivery of intrahemocoelic peptides for insect pest management. *Trends Biotechnol*, 32, 91-98.

Bregman T.P., Sekercioglu C.H. & Tobias J.A. (2014). Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. *Biol Conserv*, 169, 372-383.

Burkey T.V. (1995). Extinction rates in archipelagoes - implications for populations in fragmented habitats. *Conserv Biol*, 9, 527-541.

DeClerck F., Estrada-Carmona N., Garbach K. & Martinez-Salinas A. (2015). Biodiversity and Ecosystem Services of Agricultural Landscapes: reversing agriculture's externalities. In: *Agroecology for Food Security and Nutrition Proceedings of the FAO International Symposium*. FAO Rome, Italy, pp. 140-157.

Dirzo R. & Raven P.H. (2003). Global state of biodiversity and loss. *Annu Rev Env Resour*, 28, 137-167.

Driscoll D.A., Banks S.C., Barton P.S., Lindenmayer D.B. & Smith A.L. (2013). Conceptual domain of the matrix in fragmented landscapes. *Trends Ecol Evol*, 28, 605-613.

Fahrig L. (1997). Relative effects of habitat loss and fragmentation on population extinction. *J Wildlife Manage*, 61, 603-610.

Fahrig L. (1998). When does fragmentation of breeding habitat affect population survival? *Ecol Model*, 105, 273-292.

Fahrig L. (2002). Effect of habitat fragmentation on the extinction threshold: A synthesis. *Ecol Appl*, 12, 346-353.

Fahrig L. (2003). Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol S*, 34, 487-515.

Fahrig L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *J Biogeogr*, 40, 1649-1663.

Ficetola G.F. & Denoel M. (2009). Ecological thresholds: an assessment of methods to identify abrupt changes in species-habitat relationships. *Ecography*, 32, 1075-1084.

Frishkoff L.O., Karp D.S., M'Gonigle L.K., Mendenhall C.D., Zook J., Kremen C., Hadly E.A. & Daily G.C. (2014). Loss of avian phylogenetic diversity in neotropical agricultural systems. *Science*, 345, 1343-1346.

Grassini P., Eskridge K.M. & Cassman K.G. (2013). Distinguishing between yield advances and yield plateaus in historical crop production trends. *Nat Commun*, 4.

Haddad N.M. (2015). Corridors for people, corridors for nature. *Science*, 350, 1166-1167.

Haddad N.M., Brudvig L.A., Damschen E.I., Evans D.M., Johnson B.L., Levey D.J., Orrock J.L., Resasco J., Sullivan L.L., Tewksbury J.J., Wagner S.A. & Weldon A.J. (2014). Potential Negative Ecological Effects of Corridors. *Conserv Biol*, 28, 1178-1187.

Haila Y. (2002). A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecol Appl*, 12, 321-334.

Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setala H., Symstad A.J., Vandermeer J. & Wardle D.A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol Monogr*, 75, 3-35.

Jarzyna M.A. & Jetz W. (2016). Detecting the multiple facets if biodiversity. *Trends Ecol Evol*, In press.

Jordano P. (2016). Chasing ecological interactions. *Plos Biol*, 14, 1-4.

Jules E.S. & Shahani P. (2003). A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. *J Veg Sci*, 14, 459-464.

Karp D.S., Mendenhall C.D., Sandi R.F., Chaumont N., Ehrlich P.R., Hadly E.A. & Daily G.C. (2013). Forest bolsters bird abundance, pest control and coffee yield. *Ecol Lett*, 16, 1339-1347.

Kremen C., Williams N.M., Aizen M.A., Gemmill-Herren B., LeBuhn G., Minckley R., Packer L., Potts S.G., Roulston T.a., Steffan-Dewenter I., Vazquez D.P., Winfree R., Adams L., Crone E.E., Greenleaf S.S., Keitt T.H., Klein A.-M., Regetz J. & Ricketts T.H. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol Lett*, 10, 299-314.

Kupfer J.A., Malanson G.P. & Franklin S.B. (2006). Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecol Biogeogr*, 15, 8-20.

Laxminarayan R. & Simpson R.D. (2000). *Biological limits on agricultural intensification: an example from resistance management*. Resources for the Nature, Washington, DC.

Levey D.J., Bolker B.M., Tewksbury J.J., Sargent S. & Haddad N.M. (2005). Effects of landscape corridors on seed dispersal by birds. *Science*, 309, 146-148.

Losey J.E. & Vaughan M. (2006). The economic value of ecological services provided by insects. *Bioscience*, 56, 311-323.

Matson P.A., Parton W.J., Power A.G. & Swift M.J. (1997). Agricultural intensification and ecosystem properties. *Science*, 277, 504-509.

MEA (2005). *Millennium Ecosystem Assessment Synthesis*, United Nations.

Mitchell M.G.E., Suarez-Castro A.F., Martinez-Harms M., Maron M., McAlpine C., Gaston K.J., Johansen K. & Rhodes J.R. (2015). Reframing landscape fragmentation's effects on ecosystem services. *Trends Ecol Evol*, 30, 190-198.

Mokross K., Ryder T.B., Cortes M.C., Wolfe J.D. & Stouffer P.C. (2014). Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. *P Roy Soc B-Biol Sci*, 281.

Mooney K.A., Gruner D.S., Barber N.A., Van Bael S.A., Philpott S.M. & Greenberg R. (2010). Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *P Natl Acad Sci USA*, 107, 7335-7340.

Naeem S., Duffy J.E. & Zavaleta E. (2012). The Functions of Biological Diversity in an Age of Extinction. *Science*, 336, 1401-1406.

Oerke E.C. (2006). Crop losses to pests. *J Agr Sci*, 144, 31-43.

Oliver T.H., Isaac N.J.B., August T.A., Woodcock B.A., Roy D.B. & Bullock J.M. (2015). Declining resilience of ecosystem functions under biodiversity loss. *Nat Commun*, 6.

Ostman O., Ekbom B. & Bengtsson J. (2001). Landscape heterogeneity and farming practice influence biological control. *Basic Appl Ecol*, 2, 365-371.

Pardini R., Bueno A.D., Gardner T.A., Prado P.I. & Metzger J.P. (2010). Beyond the Fragmentation Threshold Hypothesis: Regime Shifts in Biodiversity Across Fragmented Landscapes. *Plos One*, 5.

Pimm S.L., Russell G.J., Gittleman J.L. & Brooks T.M. (1995). The future of biodiversity. *Science*, 269, 347-350.

Prevedello J.A., Gotelli N. & Metzger J.P. (In press). A stochastic model for landscape patterns of biodiversity. *Ecol Monogr*.

Prevedello J.A. & Vieira M.V. (2010). Does the type of matrix matter? A quantitative review of the evidence. *Biodivers Conserv*, 19, 1205-1223.

Ramankutty N. & Foley J.A. (1999). Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochem Cy*, 13, 997-1027.

Richmond S., Jenkins E., Couturier A. & Cadman M. (2015). Thresholds in forest bird richness in response to three types of forest cover in Ontario, Canada. *Landscape Ecol*, 30, 1273-1290.

Ricketts T.H. (2001). The matrix matters: Effective isolation in fragmented landscapes. *Am Nat*, 158, 87-99.

Schellhorn N.A., Macfadyen S., Bianchi F.J.J.A., Williams D.G. & Zalucki M.P. (2008). Managing ecosystem services in broadacre landscapes: what are the appropriate spatial scales? *Aust J Exp Agr*, 48, 1549-1559.

Sekercioglu C.H. (2006). Foreword on the ecological significance of bird populations In: *Handbook of birds of the world* (eds. Del Hoyo J, Elliott A & Christie DA). Lynx Edicions Barcelona, pp. 15-51.

Sekercioglu C.H., Wenny D.G. & Whelan C.J. (2016). *Why birds matter: avian ecological function and ecosystem services*. The University of Chicago Press, Chicago, London.

Steffen W., Richardson K., Rockstrom J., Cornell S.E., Fetzer I., Bennett E.M., Biggs R., Carpenter S.R., de Vries W., de Wit C.A., Folke C., Gerten D., Heinke J., Mace G.M., Persson L.M., Ramanathan V., Reyers B. & Sorlin S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, 347.

TEEB (2010). Mainstreaming the Economics of Nature: A Synthesis of the Approach, Conclusions and Recommendations of TEEB. In: *Conference of Parties to the CBD* (eds. P. S, H. W, C. S-S, C. N, J. B, Pt. B, H. G, P. K & B. S) Nagoya, Japan.

Tscharntke T., Bommarco R., Clough Y., Crist T.O., Kleijn D., Rand T.A., Tylianakis J.M., van Nouhuys S. & Vidal S. (2007). Conservation biological control and enemy diversity on a landscape scale. *Biol Control*, 43, 294-309.

Tscharntke T., Tylianakis J.M., Rand T.A., Didham R.K., Fahrig L., Batary P., Bengtsson J., Clough Y., Crist T.O., Dormann C.F., Ewers R.M., Frund J., Holt R.D., Holzschuh A., Klein A.M., Kleijn D., Kremen C., Landis D.A., Laurance W., Lindenmayer D., Scherber C., Sodhi N., Steffan-Dewenter I., Thies C., van der Putten W.H. & Westphal C. (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol Rev*, 87, 661-685.

Turner M.G., Donato D.C. & Romme W.H. (2013). Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. *Landscape Ecol*, 28, 1081-1097.

Van Bael S.A., Philpott S.M., Greenberg R., Bichier P., Barber N.A., Mooney K.A. & Gruner D.S. (2008). Birds as predators in tropical agroforestry systems. *Ecology*, 89, 928-934.

Villard M.-A. & Metzger J.P. (2014). Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. *J Appl Ecol*, 51, 309-318.

Webb C.O. (2000). Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *Am Nat*, 156, 145-155.

Whelan C.J., Wenny D.G. & Marquis R.J. (2008). Ecosystem services provided by birds. *Year in Ecology and Conservation Biology 2008*, 1134, 25-60.

Wu J. (2013). Landscape sustainability science: ecosystem services and human well-being in changing landscapes. . *Landscape Ecol*, 28, 999-1023.

Chapter 1

Effects of landscape structure on avian-mediated insect pest control services

Andrea L. Boesing, Elizabeth Nichols, Jean P. Metzger

Foto: Luiz Frare

(Submitted to Landscape Ecology)

Abstract

Insect crop pests cause massive annual economic loss through the destruction of crop yields. Despite increasing evidence that landscape composition and configuration strongly influence the community structure of potential pest-regulators, landscape structure has seldom been explicitly linked with rate and magnitude of pest-control services. We conducted a systematic literature review to (1) characterize our existing understanding of the empirical relationships between landscape structure and avian-mediated insect pest control services in agricultural systems, (2) identify gaps in our current understanding, and (3) develop a new conceptual model of landscape structural influences avian-mediated pest control. We found that on-farm pest suppression by birds was often higher in landscapes with higher native habitat cover, higher compositional heterogeneity, and in agricultural patches in closer proximity to native habitat. We identified more than 200 bird species that provide pest control services across both temperate and tropical regions. While most avian predators are insectivorous and habitat-generalist species, we found that a substantial fraction of pest control services in tropical regions was mediated by native habitat-dependent species, suggesting a link between conservation management and the maintenance of these pest control services. We identified a three-part research agenda for future investigations of the relationships between landscape structure and avian-mediated pest control services. This framework focuses on an improved understanding of the mechanisms related to: (1) predator-prey interactions and landscape modulation of trophic relationships, (2) bird dispersal ability and landscape connectivity, and (3) cross-habitat spillover of habitat-dependent avian predators. These findings can be applied to efforts to manage and design landscapes capable of supporting both biodiversity and ecosystem services.

Keywords: Avian predators. Birds. Conservation. Crop fields. Ecosystem services. Insect pests. Landscape ecology. Pest suppression. Sustainability. Tropical Forest.

Introduction

As humans continue to modify natural ecosystems around the world, land conversion and intensification for agricultural production continues to drive a significant reduction in biodiversity and associated ecosystem services (Foley et al. 2005, MEA 2005, Cardinale et al. 2012). Simultaneously, efforts to create sustainable agricultural landscapes that support ecosystem services and biodiversity have highlighted several key knowledge gaps, including how landscape structure influences service provision (Turner et al. 2013, Wu 2013, Mitchell et al. 2015).

Pest regulation ecosystem services are particularly critical in agricultural landscapes. Herbivorous insects destroy approximately one fifth of the world's total crop production annually, with an estimated annual economic impact of billions of dollars (Bonning and Chougule 2014). The use of natural enemies for pest suppression can enhance and stabilize yields in crop production systems, as well as increase overall crop resilience by aiding in the avoidance of crop failure when chemical-based regulation fails (Bommarco et al. 2011, Bommarco et al. 2013).

Pest control services depend fundamentally on the spatial and temporal distribution of natural enemies at the patch-level, within and around crop fields (Hooper et al. 2005, Gagic et al. 2015). As most natural enemies are mobile organisms that move within and across habitats to access different resources (Jirinec et al. 2011, Karp et al. 2013), their local diversity and abundance is also strongly influenced by landscape-level structure and processes. For example, the amount and configuration (i.e. spatial arrangement) of both native and anthropogenic habitats within a landscape strongly influence natural enemy community structure within patches (Bianchi et al. 2006, Tscharntke et al. 2012, Karp et al. 2013, Martin et al. 2013), and movement between patches (Tscharntke et al. 2005), with subsequent impacts on rates of crop pest suppression (Ostman et al. 2001, Karp et al. 2013). While we increasingly understand how local biodiversity patterns are influenced by components of landscape structure, including composition, configuration, heterogeneity, and connectivity (Estavillo et al. 2013, Fahrig 2013, Banks-Leite et al. 2014), similar links between landscape structure and biodiversity-mediated pest-control services are scarce (Schellhorn et

al. 2008, Tscharntke et al. 2008b). This precludes a more general understanding of how landscape structure may influence this key suite of ecosystem services.

Insectivorous birds provide significant pest control services (Karp et al. 2013, Maas et al. 2013, Maas et al. 2015), and may complement or replace chemical-based pest control strategies agricultural systems (Bianchi et al. 2006, Maas et al. 2015). However, the links between landscape structure and avian-mediated insect pest control services are poorly known. We review the existing empirical evidence that links landscape structure and avian-mediated pest control services in agricultural systems around the world. We target two questions: (1) What are the taxonomic identities and habitat associations of those bird species that provide pest control in agricultural landscapes, and (2) How does landscape structure modulate avian-mediated pest control? After summarizing what is currently known, we present a conceptual model of the processes and mechanisms that underpin these patterns. We conclude by using this model to identify key research gaps and opportunities within a future research framework to better understand landscape structure effects on avian-mediated pest suppression.

Literature review

Methods

We conducted a systematic literature review to investigate the role of landscape structure on avian-mediated pest control services in agricultural landscapes. We performed an ISI Web of Science search with keywords (pest* AND (control OR suppression OR regulation OR predation OR reduction OR insectivory OR consumption) AND land* AND (bird* OR avian OR farmland OR insectivorous OR predators OR "natural enemies" OR "biological control agent")), with a last view August 2016. A total of 876 papers were returned, of which 62 papers were directly related with pest control and birds in agricultural systems. We examined the references cited for these 62 papers, as well as all peer-reviewed articles that cited one or more of these articles, to arrive at a total of 151 relevant papers (see Table S1). We restricted our focus to agricultural systems, encompassing both perennial and annual plantations. Further, we limited our review to insect agricultural pests, excluding rodents and plant pests (weeds).

We classified these 151 papers into four classes, those that: (A) highlighted the importance of birds on pest control in agricultural fields without explicit measurements of pest control; (B) reported some measurement of avian-mediated pest control, but without explicitly reporting their links with landscape structure; (C) reported some measurement of pest control by birds and reported links with landscape structure; or (D) used non-empirical data (quantitative meta-analysis, modeling or simulations) to infer pest control by birds (see Table S1).

To understand the identity and habitat association of those bird species involved in pest control in crop fields, we retrieved all papers from categories B and C that reported the identity of avian predators (n = 25), commonly through foraging observation, isotopic analysis, camera traps, or DNA barcoding. We used an existing database of bird traits (del Hoyo et al. 2014) to classify these species according their diet and habitat association. For diet, we used five categories: restrictive insectivore (exclusive insect feeders); generalist insectivore (insect feeders that complement their diet with fruits or seeds); occasional insectivore (species that feed predominantly on non-insect resources but occasionally ingest insects); omnivore (that feeds on any available resource including insects, fruits, grains or garbage), or non-insectivore (restrictive granivores, carnivores or frugivores). For habitat association, we classified species as habitat-specialist (species requiring native habitat to persist and/or breed) or habitat-generalists (species able to use both native and anthropogenic habitats).

Results

The literature linking landscape structure to avian-mediated pest control services is recent, with 85% of papers (n =135) published within the last decade (Fig. 1). Nearly 60% of studies (n = 85) highlighted the importance of birds to pest suppression in agricultural fields without actual measurements of pest control (paper class A). Over 19% of studies (n = 29) presented empirical evidence of avian-mediated pest suppression without explicit links to landscape structure (class B), while 18% (n = 27) reported similar evidence with explicit links between pest control and landscape structure (class C). Finally, ten papers (3%) reported results from quantitative meta-analyses or reviews (class D).
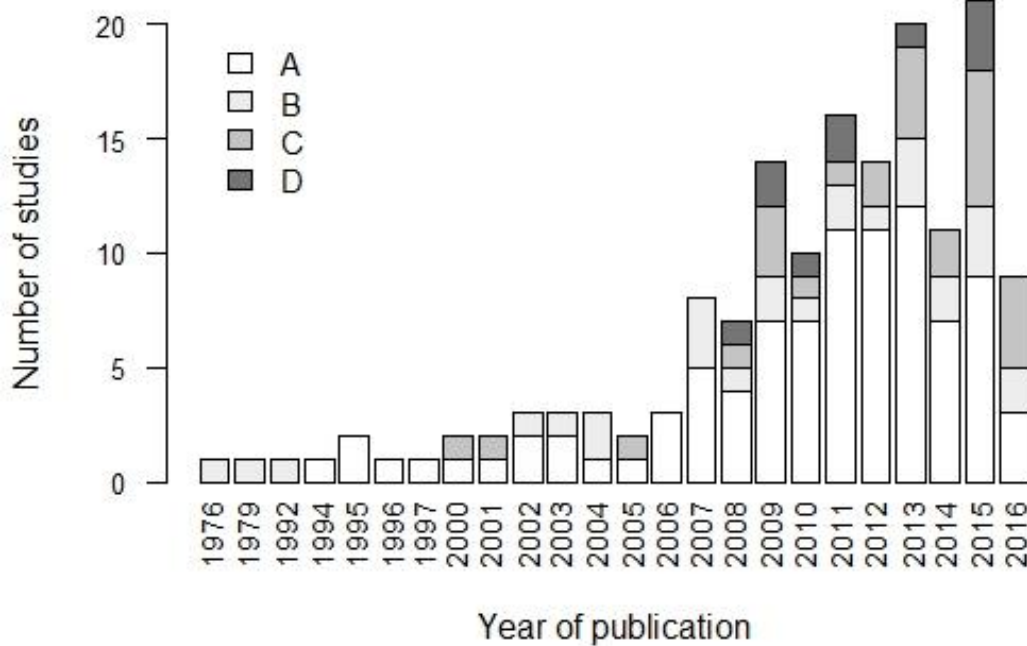
Figure 1. Papers published January 1976 - August 2016 that investigate avian-mediated pest control in agricultural fields. (A) highlighted the importance of birds on pest control in agricultural fields without explicit measurement of pest control (n = 85); (B) reported some measurement of avian-mediated pest control without explicitly reporting landscape metrics (n = 29); (C) reported some measurement of pest control by birds and reported landscape metrics associated to this service (n = 27); or (D) used quantitative meta-analysis, modeling or simulations using a priori empirical evidence to infer pest control by birds (n = 10).

Most empirical studies were based in tropical regions and focused on few crop types with correspondingly few pest species (Fig. 2). Tropical studies overwhelmingly focused on control of the coffee borer beetle (*Hypothenemus hampei*) in coffee plantations, while temperate zone studies predominantly focused on control of the codling moth pest (*Cydia pomonella*) in apple orchards. Pooling across both regions, 80% of all studies were conducted in ecosystems originally dominated by forest cover.

Taxonomic correlates and habitat associations
A total of 226 bird species were identified as providing pest control services (see Table S2). A total of 139 species from 46 families were reported from tropical

crops, with five families most frequently represented: Parulidae, Turdidae, Muscicapidae, Sturnidae, and Troglodytidae. Another 101 species from 36 families were reported in temperate crops, with the families Icteridae, Parulidae, Emberezidae, Turdidae, and Phasianidae most commonly reported. The majority of avian predators across both regions (69%) were habitat-generalists. Within tropical studies, 37% of avian predators reported were habitat-specialists, while 23% were reported as habitat-specialists in temperate region studies. While the diet of avian predators from both regions was unsurprisingly overwhelmingly insectivorous, we found regional differences in the diet of habitat-specialist species. Restrictive insectivores composed 64% of tropical habitat-specialists, but only 37% of temperate habitat-specialists. Even for habitat-generalist species, restrictive insectivory was a more common strategy in tropical than temperate regions (37% versus 20% respectively; Fig. 3).
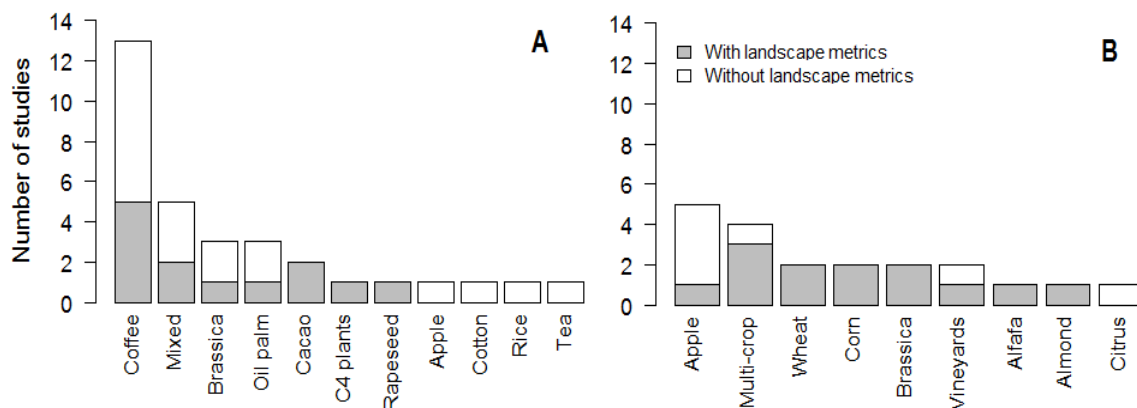
Figure 2. Experimental studies published January 1976 - August 2016 (n = 56) that investigated avian-mediated pest control in different crops. Grey bars show studies that considered the influence of landscape structure on the provision of pest control services, while white bars show studies that did not consider this influence. A: tropical regions, B: temperate regions.

Landscape structure

Across the 27 studies that considered landscape structure in their evaluation of avian-mediated pest control, the most frequently evaluated landscape features included isolation (i.e. linear distance from the closest native habitat remnant; n = 14), the areal extent of either native habitat (n = 10) or crop cover (n = 3),

landscape composition (i.e. land-use and land-cover proportion or heterogeneity; n = 4), edge density (n = 2), and native habitat patch size (n = 1).
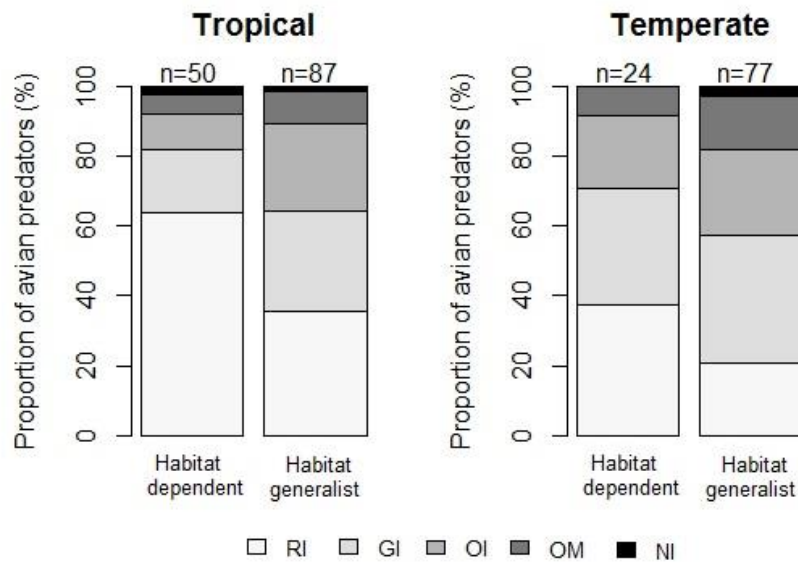
Figure 3. Diet of both native habitat-dependent and habitat-generalist avian predators in tropical and temperate biomes. RI: restrictive insectivores; GI: generalist insectivores; OI: occasional insectivores; OM: omnivores; NI: non-insectivores.

Isolation was reported as having a negative association with avian-mediated pest control in 71% of studies (n = 10; Table 1). The areal extent of native habitat was frequently reported as positively associated with both avian predator richness and abundance (50 %; n= 5), which was subsequently associated with reductions in pest infestation or herbivory in crop fields (Table 1). Two of three studies evaluating landscape heterogeneity reported that compositional heterogeneity (i.e. diversity of both land-use and land-cover types) was positively related with pest suppression. Similarly, two of three studies found that increasing crop extension and homogeneity led to decreased pest suppression. Finally, we found that while few studies evaluated the influence of patch size or edge density (n = 3), those that did reported positive relationship between pest control rates and both patch size and edge density (Table 1).

Table 1. Empirical studies investigating avian-mediated insect pest control that incorporate a landscape perspective in their evaluation. *Region.* Temperate (Temp); Tropical (Trop). Symbols of the effect of landscape structure in pest control service denote positive (✚), negative (▬) or neutral effects (⊘).

Region	Crop	Pest	Landscape metrics	Landscape effect	Landscape process/service description	Reference
Trop	Coffee *Coffea arabica*	Coffee-borer beetle *Hypothenemus hampei*	Proximity to habitat patches	✚⊘	Avian predator abundance or presence increases near edge but does not increase pest suppression. Distance range 0-120 m.	Kellerman et al. 2008
Trop	Coffee *C. arabica*	Coffee-borer beetle *H. hampei*	Proximity to habitat patches	✚	Avian predators increase near habitat patches reducing insect damage.	Johnson et al. 2009
Trop	Coffee *C. arabica*	Coffee-borer beetle *H. hampei*	Forest cover	✚	Increase in avian predators tied to forest cover leads to a decrease on infestation rates.	Karp et al. 2013
Trop	Coffee *C. arabica*	Invertebrates	Patch size	✚	Predation by birds increases with patch size.	Jordani et al. 2015
Trop	Coffee *C.arabica*	Fake caterpillars	Proximity to habitat patches	✚	Predation increase nearby habitat patches. Predation increased with increase in bird richness.	Milligan et al. 2015
Trop	Cacao *Theobroma cacao*	Invertebrates	Proximity to habitat patches	⊘	Pest suppression similar along distance gradient. Distance range 0-3500 m.	Maas et al. 2013
Trop	Cacao *T. cacao*	Invertebrates	Shade tree cover; Distance from habitat patches	⊘ ✚	Predation intensity increases with proximity with forest edges but similar along shade tree cover gradient. Distance range 0-2500 m.	Maas et al. 2015
Trop	Mixed	Invertebrates	Matrix heterogeneity; Crop diversity	✚ ✚	Higher number of avian predators foraging on insect pests in heterogeneous landscapes and more diversified crops.	Jones et al. 2005
Trop	Mixed	Invertebrates	Vegetation cover	⊘	Vegetation cover does not affect avian predation intensity.	Lemessa et al. 2015
Trop	Apple *Malus domestica*	Codling moth *Cydia pomonella*	Proximity to habitat patches	✚⊘	Higher species richness near native habitat patches, but distance does not affect damage.	Pesley et al. 2016
Trop	Brassica *Brassica oleracea*	Invertebrates	Forest cover	▬	Forest cover leads to increased tri trophic interactions (birds foraging on other natural enemies of pests).	Martin et al. 2013
Trop	C4 plants	Invertebrates	Proximity to habitat patches	⊘	Proportion of C4 source does not change along the distance gradient. Distance range 0-3500 m.	Ferger et al. 2013
Trop	Oil palm *Elaeis guineensis*	Bagworm (mimic)	Forest cover; Corridor width	⊘ ⊘	Intensity of predation does not change with forest cover or corridor width.	Gray and Lewis 2014
Trop	Rapeseeds *B. napus*	Cabbage flea beetles, aphids, lepdopteran skeletonizers and lepidopteran chewing larvae	Tree cover	⊘	Tree cover leads to higher avian predators but does not affect leaf damage by herbivores.	Lemessa et al. 2015
Temp	Wheat *Triticum aestivum*	Aphids *(Acyrthosiphon pisum)*	Crop cover; Matrix heterogeneity	▬ ✚	Higher crop cover decreases pest suppression, and pest suppression increases with heterogeneity.	Winqvist et al. 2011
Temp	Wheat *T. aestivum*	Aphids *(A. pisum)*	Crop cover	▬	Increased crop cover decreases the potential biological control.	Geiger et al. 2009
Temp	Wheat and Barley *Triticum aestivum Hordeum vulgare*	Aphids	Forest cover	✚	Forest cover is related with decreased infestation.	Tamburini et al. 2016
Temp	Brassica *Brassica oleracea*	Lepidopteran pests	Proximity to habitat patches	✚	Higher number of predation close to habitat patches; Birds remove pests but there is a weak correlation with bird richness.	Garfinkel and Johnson 2015

Temp	Brassica *B. oleracea*	Aphids	Forest cover	**+**	Forest cover leads to decreased infestation when evaluated for all natural enemies.	Martin et al. 2015
Temp	Corn *Zea mays*	Cutworms (*Agrottis* spp) Weevils (*Sphenophorus spp*)	Proximity to habitat patches	**+**	Higher pest suppression near habitat patches (mainly within 0-7 m). Distance range 0 -25 m.	Tremblay et al. 2001
Temp	Corn *Zea mays*	Invertebrates	Proximity to habitat patches	**+**	High number of foraging events near habitat patches (mainly within 0-20 m). Distance range 0-50 m.	Puckett et al. 2009
Temp	Mixed	Invertebrates	Crop cover; Matrix heterogeneity	**+** **–**	Higher crop cover increases frequency of pest insects brought to the nest. Matrix heterogeneity decrease insect pests brought to the nest.	Girard et al. 2012
Temp	Mixed	Herbivorous in general	Matrix heterogeneity; Edge density	**+** **–+**	More land uses decreases herbivory. Both edges and heterogeneity tend to increase both bird richness and abundance (and richness of natural enemies in general).	Martin et al 2016
Temp	Alfafa *Medicago sativa*	Wheevils	Proximity to habitat patches; Edge density	∅ **+**	Distance does not affect weevil infestation. Higher edge density leads to increased avian biodiversity and reduction of weevil abundance.	Kross et al. 2016
Temp	Almond *Prunus dulcis*	Navel Orangeworm (*Amyelois transitella*)	Forest cover; Proximity to habitat patches	**+** **–+**	Higher forest cover increase feeding. Both infestation rates and feeding lower near habitat patches. Distance ranges 0-100 m.	Eilers and Klein 2009
Temp	Apple *M. domestica*	Invertebrates	Tree cover	**+**	Higher tree cover increases bird foraging events.	Luck et al. 2012
Temp	Vineyards *Vitis spp.*	Lepidopteran pests	Proximity to habitat patches	∅	No effect of distance on intensity of pest removal.	Howard and Johnson 2014

Discussion

Although more studies are required to better understand how landscape context modulates pest suppression in different crops, some general statements can be made based on our literature review. First, although the majority of avian predators that provide pest-control services are habitat-generalists, a substantial proportion (~ 35%) of avian predators that provide services in tropical regions are habitat-specialists. Most existing studies on avian-mediated pest control are conducted in tropical zones, and consider relatively few crops (main focus in coffee plantations) and/or pest regulation systems, highlighting an urgently need to expansion of research efforts focusing in different crops and systems. Second, multiple aspects of landscape structure appear clearly linked to avian-mediated pest control rates. In general, we found avian-mediated pest suppression to be positively related to land-use heterogeneity, increased native habitat cover, and close proximity to native habitat patches. Identifying how different landscape

features might enhance avian-mediated pest control is an expanding research area with important implications for landscape planning and management to maintain both biodiversity and ecosystem services provision.

We found that while most avian predators are habitat-generalist species, a substantial proportion of avian predators that provide pest regulation services in the tropics are dependent on native tropical forest habitats. This suggests that conservation of remaining native tropical forests may broadly benefit pest-regulation services in agricultural landscapes (Tscharntke et al. 2012). It is important to point out that the identity and species traits of avian predators may matter as much or more to actual service provision than overall richness or abundance per se (Gagic et al. 2015). Even for well-studied systems such as coffee plantations and apple orchards, robust data about the identity of species that provide pest control or the per capita impact on insect pest density is remarkably scare (Letourneau et al. 2009).

Overall, we found that pest suppression by avian predators is often intensified nearby native habitat patches. Authors often attributed this pattern to habitat patches being a source of bird predators (e.g. Kellermann et al. 2008, Johnson et al. 2009, Pesley et al. 2016). Alternatively, predation intensity might be higher near native habitat patches because many forest dependent species avoid crossing long distances of non-habitat (Uezu et al. 2008). For example, Puckett and colleagues observed the majority of avian predators species (76%) foraging mainly within 20 m of the woody edge in temperate maize plantations (Puckett et al. 2009). Additionally, Maas and colleagues found higher number of predations marks by birds near forest edges in tropical cacao agroforestry, in an experimental study using plasticine caterpillars (Maas et al. 2015).

Another frequently reported pattern was higher rates avian-mediated pest control in more forested landscapes. This pattern is likely due to the positive impact on avian predator populations provided by larger extents of high quality habitat (Karp et al. 2013, Milligan et al. 2016). This should be particularly important in tropical regions, where approximately 35% of avian predators are forest-dependent species. In coffee plantations in Costa Rica, Karp and colleagues showed that more forested landscapes had an increased abundance of avian consumers of the coffee borer beetle, as well as lower borer beetle infestation rates

(Karp et al. 2013). However, we also found evidences that these relationships between native habitat cover and ecosystem services are complex and may be context-dependent (Martin et al. 2013, Martin et al. 2016). For example, Martin and colleagues used exclusion experiments to demonstrate that landscapes with higher natural and semi-natural habitat cover in South Korea may correlate with negative or neutral pest control effects, because avian predators additionally consume insect pest predators that otherwise would have contributed to pest suppression. They reported that in landscapes with more than 25% of semi-natural habitat, crop damage reduction by predator insects was significantly weaker in the presence of avian predators (Martin et al. 2013).

We found that increases in landscape heterogeneity were frequently positively correlated with avian-mediated pest suppression (e.g., Winqvist et al. 2011, Martin et al. 2016). A higher diversity of land-uses or land-covers can promote the persistence of avian predators through enhanced landscape complementation and supplementation processes (see below; Metzger and Brancalion 2016). When landscape heterogeneity was diminished because the areal extent of croplands increased, pest suppression commonly declined (Geiger et al. 2010, Winqvist et al. 2011). For example, in a study across five European regions, decreasing landscape heterogeneity through an increase arable land cover from 20 to 100% led to a substantial decline in both bird species richness and aphid predation rates (Winqvist et al. 2011). Jones and colleagues (2005) showed that highest abundance of insectivorous birds foraging insects in crop fields was associated with mixed crop plantings (i.e. more heterogeneous matrix land-use) and with the presence of native field borders.

We found relatively few studies that evaluated the impacts of patch size or edge effects on avian-mediated insect pest suppression. Nevertheless, the existing evidence (using dummy caterpillars in coffee plantations in Southern Brazil) suggests that average native habitat patch size positively influences predation intensity (Jordani et al. 2015). Similarly, pest suppression appears intensified in areas of higher edge density (Kross et al. 2016), mainly due to the increase of bird richness and abundance at forest-farm field edges (Kross et al. 2016, Martin et al. 2016).

A conceptual model of landscape-level avian-mediated pest control

We propose a new conceptual model to promote further studies on the role of landscape structure on the provisioning of avian-mediated insect pest control services (Fig. 4). This model considers that pest control services in agricultural landscapes fundamentally depend on how landscape structure (i.e. composition and configuration; Column 1 in Fig. 4) will affect landscape-level processes (i.e. those processes that relate two or more landscape units; Column 2, Fig. 4) that ultimately influence mechanisms related to avian-mediated pest control, including: 1) the persistence of avian predators in agricultural habitats; 2) the dispersal ability of avian predators into and through crop fields, and 3) trophic interactions between assemblages of natural enemies and pests (Column 3; Fig. 4). We summarize these main landscape processes and their impacts on pest control outcomes below (Column 4, Fig. 4).

Landscape complementation & supplementation effects

Landscape composition and complexity affect the distribution of both avian predators and insect pests, particularly for those species requiring resources dispersed across multiple and distinct habitat patches. This use of resources across multiple habitat patches to either *complement* or *supplement* resource access (Dunning et al. 1992), is closely related to avian predator persistence and service provision in agricultural landscapes. *Landscape complementation* is the capacity of a landscape to provide different resources, usually located in different landscape units or patches (Metzger and Brancalion 2016). For example, avian predators that forage in crop fields may also require hedgerows, habitat strips or forest to roost or breed. *Landscape supplementation* is a related concept that refers to the capacity of a landscape to provide the same kind of resource, distributed across distinct patches (Metzger and Brancalion 2016). This process is likely to mediate food resource provision for avian predators in agricultural landscapes, for example by when active foraging across multiple fields buffers an avian predator from the negative effects of low prey availability in any given field (Bianchi et al. 2006). These two processes contribute to the frequent observation that more heterogeneous landscapes are able to maintain avian predator abundance and diversity.

34

Habitat cover effects

The amount of native habitat available to a given species (Fahrig 2013) is a central driver of many of the ecological mechanisms proposed to influence avian-mediated pest control (Column 3, Fig. 4). This is because the occurrence and abundance of any given species (including avian predators) should increase with the amount of its preferred habitat (Villard and Metzger 2014). Additionally, higher amounts of native habitat increase landscape connectivity, which increases the accessibility of even small fragments that are situated in landscapes with high native habitat coverage (Fahrig 2013). Despite providing avian predators and increasing landscape connectivity, an increase in habitat amount (up to a certain level) also leads to an increase in landscape heterogeneity. These native habitat patches despite providing habitat-dependent predators, they are also important for those habitat-generalist predators, providing a huge variety of resources yearlong (i.e. landscape supplementation and complementation). Some studies, however, have demonstrated that this increase on landscape heterogeneity besides influence positively pest suppression, can also leads to neutral or negative effects (Letourneau et al. 2009, Martin et al. 2013) related to an increase on complexity of natural enemies assemblages and potential changes in trophic interactions.

Edge & cross-habitat spillover effects

Edge effects can be defined as the mutual influences of adjacent landscape units (Villard and Metzger 2014). Native habitat patches can act as sources of avian predators that influence adjacent landscape units (e.g. crop fields) as a result of cross-habitat spillover (Tscharntke et al. 2012). We could expect that an increase in edge density (i.e. increased contact between crop and native habitat units) increases the probability that native habitat-dependent avian predators spill over from native habitats into crop fields (Mitchell et al. 2015, Boesing et al. In prep). In addition, larger extents of native habitat that supports avian predators should allow greater predator movement into crop fields where the pest control is provided. Cross-habitat spillover seems to occur mainly in more forested landscapes (> 30% of forest cover; Estavillo et al. 2013), and may therefore be an especially important edge process in tropical regions, where around 35% of described avian predators are habitat-dependent species. Increasing distance from

native habitat edge is associated with both reduced spillover (Tscharntke et al. 2008a) and reduced predation intensity because these areas can provide more resources to avian predators (Johnson et al. 2009, Puckett et al. 2009) or because they can facilitate the dispersal of those species in the landscape (Metzger 2000). The matrix composition seems play an important role driving dispersal and spill over processes as the capacity of different edge types to facilitate movement will likely vary according the structure of adjacent land uses (i.e. matrix) and the biological features of the focal species. Further, the spillover of avian predators from natural habitats into neighboring crop fields may also affect trophic interactions and its directions through changes on assemblages of natural enemies (Martin et al. 2013).
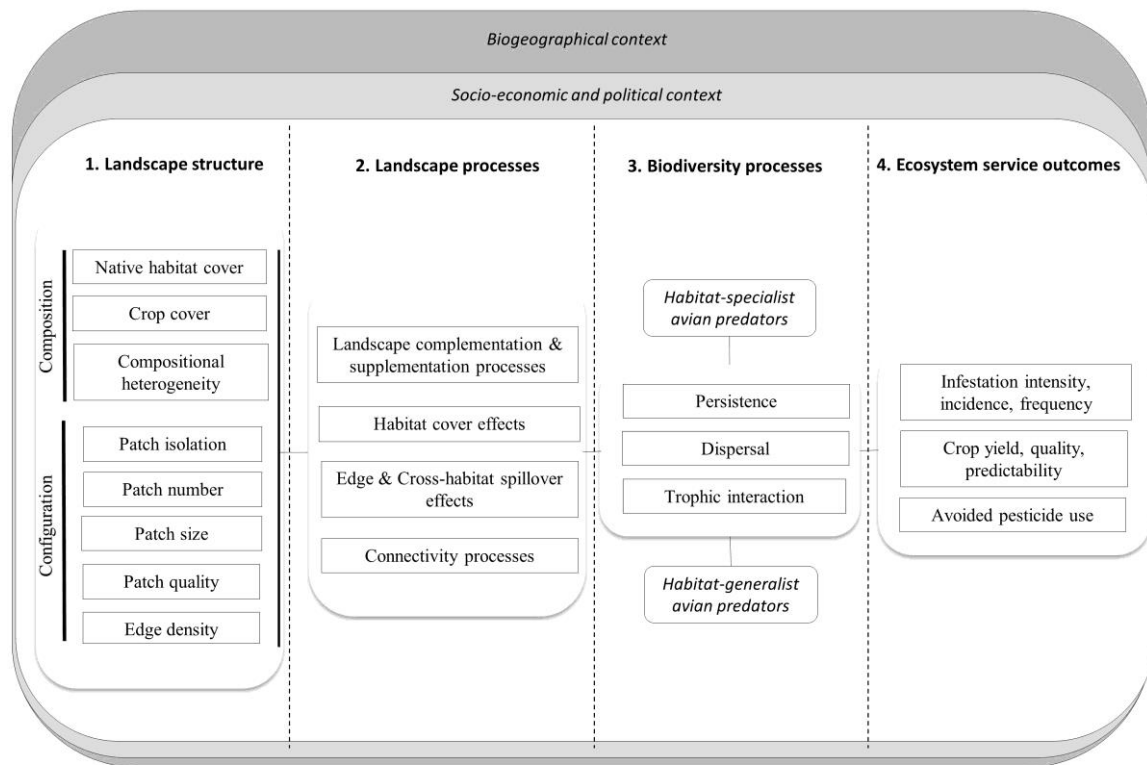
Figure 4. Conceptual model showing multiple mechanisms by which landscape structure can modulate avian-mediated insect pest control services. Provision of pest control services in agricultural landscapes (Column 4) depends on how landscape structure (i.e. composition and configuration; Column 1) will affect landscape processes (i.e. processes that link two or more landscape units; Column 2) and associated ecological mechanisms that regulate pest control, including: 1) the persistence of avian predators in agricultural environments; 2) the dispersal ability of avian predators into and through crop fields, and 3) trophic interactions between the entire assemblage of natural enemies and pests (Column 3).

Connectivity processes

Landscape connectivity is defined as the capacity of landscape to facilitate the movement of organisms (Taylor et al. 1993). Both landscape configuration and composition strongly influence connectivity (Belisle et al. 2001), and consequently, influences how avian predators disperse through agricultural landscapes (Villard and Metzger 2014). Individual landscape units such as trees, hedgerows or wind-breaks may act as stepping-stones (Boscolo et al. 2008, Uezu et al. 2008, Robertson and Radford 2009) that facilitate the movement of avian predators moving from native patches to agricultural areas. In addition, matrix types that are more permeable (i.e. structurally more similar to native habitat patches) often increase inter-patch colonization rates (Prevedello and Vieira 2010) by positively influencing avian movement across the matrix (Ricketts 2001, Driscoll et al. 2013). However, functional connectivity depends not only on the structural characteristics of the landscape, but also on the species-specific dispersal ability of the species under consideration (Gascon et al. 1999).

Opportunities for future research

Several processes operating at the landscape-level appear to mediate the interactions between landscape structure and avian-mediated pest control. We need to understand how both these processes operate individually and how they interact to contribute to pest control to improve landscape management for enhanced avian-mediated pest control, and predict synergisms and tradeoffs in ecosystem services provision. We identified three main gaps for future investigations of the relationships between landscape structure and avian-mediated pest control services.

1. How does landscape structure affect trophic interactions related to avian-mediated pest control?

Interactions among diverse enemy assemblages may lead to negative, neutral or positive consequences for ecosystem functioning (Finke and Denno 2004, Tylianakis and Romo 2010). We cannot predict these directions without knowing the identity of species interacting and their role within trophic chains. Most studies measure 'biodiversity' of natural enemies in the simple metrics of

species richness or abundance (Garfinkel and Johnson 2015, Martin et al. 2016), without reference to either the habitat associations of these species or their functional traits related to pest control provision. We need to improve our understanding of how landscape processes affect key trophic interactions and influence the representation of relevant functional traits, considering the effects of habitat amount, landscape heterogeneity, and cross-habitat spillover processes. Some experimental studies adding and removing predators (e.g. Martin et al. 2013) are a good way to start the achievement of this understanding. Investigations about the landscape effects modulating trophic chains in agricultural landscapes is a flourishing field of investigation which will allow us understand the directions of these interactions and contribute to design and manage multi-functional landscapes.

2. Can increasing landscape heterogeneity increase the attractiveness of crop fields to avian predators to promote pest control service delivery?

High landscape compositional heterogeneity can enhance landscape complementation processes, and can thus contribute to more diversified avian predator communities, with likely positive effects on pest control. At the same time, as landscapes with more heterogeneous configurations have higher edge density, the positive benefits of heterogeneity may be offset by the costs of lower rates of those processes contingent on large extents of native habitat, including cross-habitat spillover and functional connectivity. Different mechanisms can thus be involved in the relationship between landscape heterogeneity and pest control depending on if we consider the compositional or configurational component of heterogeneity (Fahrig et al. 2011). Furthermore, this heterogeneity can be enhanced by considering either natural landscape units (including those across a spectrum of disturbance or successional stage) or alternatively by considering more anthropogenic units (e.g. different matrix types, including crops, fallow fields, and urban or semi-urban areas).Which of those heterogeneity components (composition or configuration) and units (more native or more anthropogenic land uses) more effectively modulate pest control? An expanded effort to investigate these questions in different crop systems, considering heterogeneity in composition and configuration, within native or matrix landscape units, and using

different focal avian predators is needed. Experimental approaches capable of clarifying causal relationships between landscape heterogeneity and pest control processes are particularly welcome, for example using predator enrichment approaches such as hunting perches, intercropping additional resources (Jones and Sieving 2006), or installing nest boxes to attract birds to breeding and foraging in the matrix (Mols and Visser 2002). These efforts could be efficient ways to understand which component of the landscape heterogeneity is important to enhance the potential pest reduction services by avian predators.

3. How does landscape structure facilitate the cross-habitat spillover of habitat-dependent avian predators to crop fields?

In those contexts where a significant portion of the avian predator community that provides pest control services is composed by native habitat-specialists, cross-habitat spillover from native to agricultural habitats should be a key feature of any agricultural landscape management strategy. However, we know surprisingly little about what elements of landscape design will best promote spillover. Are relevant spillover processes mediated by the amount of edge, or type of edge contrast between native and agricultural patches? Or is spillover mediated instead by the relative degree of agricultural matrix permeability, by the size of habitat patches, or the areal extent of agricultural fields? Do specific species of functionally important avian predators avoid gap crossing, or have other behavioral barriers (Harris and Reed 2002) that require assessment? Careful future studies that consider both landscape structural characteristics and the species-specific behaviors, and pest control contributions of the avian predators in questions will be required to tease out the relative contributions of specific species identity from more general principals regarding the influence of landscape-level structure on avian-mediated insect pest regulation.

Concluding remarks

Our review identifies a series of key landscape factors that positively contribute to avian-mediated pest control: high landscape heterogeneity, higher habitat amount, and enhanced landscape connectivity. Moreover, we found that most avian species

providing pest control services in agricultural ecosystems are habitat generalists, but a considerable proportion of habitat dependent species might provide pest control services in tropical regions. Based on our findings, our conceptual model for linking landscape structure to avian pest control highlights the role of four key landscape processes: landscape supplementation and complementation, native habitat cover effects, edge and cross-habitat spillover effects and landscape connectivity. Given the limited number and biased distribution of studies across regions and crops, an expansion of research efforts identifying avian predators, understanding trophic interactions, and clarifying predator movement patterns across the crop/non-crop interface will be required to make stronger generalizations about the influence landscape structure on the efficacy of avian-mediated pest control, and contributions of landscape design to sustainable and multi-functional landscapes.

Acknowledgments

Literature cited

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

Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources **29**:261-299.

Banks-Leite, C., R. Pardini, L. R. Tambosi, W. D. Pearse, A. A. Bueno, R. T. Bruscagin, T. H. Condez, M. Dixo, A. T. Igari, A. C. Martensen, and J. P. Metzger. 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science **345**:1041-1045.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? Nature **471**:51-57.

Belisle, M., A. Desrochers, and M. J. Fortin. 2001. Influence of forest cover on the movements of forest birds: A homing experiment. Ecology **82**:1893-1904.

Betts, M. G., G. J. Forbes, and A. W. Diamond. 2007. Thresholds in songbird occurrence in relation to landscape structure. Conservation Biology **21**:1046-1058.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B-Biological Sciences **273**:1715-1727.

Blitzer, E. J., C. F. Dormann, A. Holzschuh, A.-M. Klein, T. A. Rand, and T. Tscharntke. 2012. Spillover of functionally important organisms between managed and natural habitats. Agriculture Ecosystems & Environment **146**:34-43.

Boesing, A. L., E. Nichols, and J. P. Metzger. In prep. How does landscape structure affects avian cross-habitat spillover?

Bommarco, R., D. Kleijn, and S. G. Potts. 2013. Ecological intensification: harnessing ecosystem services for food security. Trends in Ecology & Evolution **28**:230-238.

Bommarco, R., F. Miranda, H. Bylund, and C. Bjorkman. 2011. Insecticides Suppress Natural Enemies and Increase Pest Damage in Cabbage. Journal of Economic Entomology **104**:782-791.

Bonning, B. C. and N. P. Chougule. 2014. Delivery of intrahemocoelic peptides for insect pest management. Trends in Biotechnology **32**:91-98.

Boscolo, D., C. Candia-Gallardo, M. Awade, and J. P. Metzger. 2008. Importance of interhabitat gaps and stepping-stones for lesser woodcreepers (Xiphorhynchus fuscus) in the Atlantic forest, Brazil. Biotropica **40**:273-276.

Bregman, T. P., C. H. Sekercioglu, and J. A. Tobias. 2014. Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. Biological Conservation **169**:372-383.

Burkey, T. V. 1995. Extinction rates in archipelagoes - implications for populations in fragmented habitats. Conservation Biology **9**:527-541.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature **486**:59-67.

DeClerck, F., N. Estrada-Carmona, K. Garbach, and A. Martinez-Salinas. 2015. Biodiversity and Ecosystem Services of Agricultural Landscapes: reversing agriculture's externalities. Pages 140-157 Agroecology for Food Security and Nutrition Proceedings of the FAO International Symposium. FAO, Rome, Italy.

del Hoyo, J., A. Elliott, J. Sargatal, D. A. Christie, and E. Juana. 2014. Handbook of the Birds of the World Alive. Linx Edicions, Barcelons.

Dirzo, R. and P. H. Raven. 2003. Global state of biodiversity and loss. Annual Review of Environment and Resources **28**:137-167.

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 & Evolution **28**:605-613.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**:169-175.

Estavillo, C., R. Pardini, and P. L. Bernardo da Rocha. 2013. Forest Loss and the Biodiversity Threshold: An Evaluation Considering Species Habitat Requirements and the Use of Matrix Habitats. Plos One **8**.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management **61**:603-610.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modelling **105**:273-292.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecological Applications **12**:346-353.

Fahrig, L. 2003. Effects 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., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J.-L. Martin. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes Ecology Letters **14**:101-112.

Ficetola, G. F. and M. Denoel. 2009. Ecological thresholds: an assessment of methods to identify abrupt changes in species-habitat relationships. Ecography **32**:1075-1084.

Finke, D. L. and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature **429**:407-410.

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.

Frishkoff, L. O., D. S. Karp, L. K. M'Gonigle, C. D. Mendenhall, J. Zook, C. Kremen, E. A. Hadly, and G. C. Daily. 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. Science **345**:1343-1346.

Gagic, V., I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tscharntke, W. Weisser, and R. Bommarco. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proceedings of the Royal Society B-Biological Sciences **282**.

Garfinkel, M. and M. Johnson. 2015. Pest-removal services provided by birds on small organic farms in northern California. Agriculture Ecosystems & Environment **211**:24-31.

Gascon, C., T. E. Lovejoy, R. O. Bierregaard, J. R. Malcolm, P. C. Stouffer, H. L. Vasconcelos, W. F. Laurance, B. Zimmerman, M. Tocher, and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation **91**:223-229.

Geiger, F., J. Bengtsson, F. Berendse, W. W. Weisser, M. Emmerson, M. B. Morales, P. Ceryngier, J. Liira, T. Tscharntke, C. Winqvist, S. Eggers, R. Bommarco, T. Part, V. Bretagnolle, M. Plantegenest, L. W. Clement, C. Dennis, C. Palmer, J. J. Onate, I. Guerrero, V. Hawro, T. Aavik, C. Thies, A. Flohre, S. Hanke, C. Fischer, P. W. Goedhart, and P. Inchausti. 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology **11**:97-105.

Grassini, P., K. M. Eskridge, and K. G. Cassman. 2013. Distinguishing between yield advances and yield plateaus in historical crop production trends. Nature Communications **4**.

Haddad, N. M. 2015. Corridors for people, corridors for nature. Science **350**:1166-1167.

Haddad, N. M., L. A. Brudvig, E. I. Damschen, D. M. Evans, B. L. Johnson, D. J. Levey, J. L. Orrock, J. Resasco, L. L. Sullivan, J. J. Tewksbury, S. A. Wagner, and A. J. Weldon. 2014. Potential Negative Ecological Effects of Corridors. Conservation Biology **28**:1178-1187.

Haila, Y. 2002. A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. Ecological Applications **12**:321-334.

Harris, R. J. and J. M. Reed. 2002. Behavioral barriers to non-migratory movements of birds. Annales Zoologici Fennici **39**:275-290.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs **75**:3-35.

Jarzyna, M. A. and W. Jetz. 2016. Detecting the multiple facets if biodiversity. Trends in Ecology & Evolution:In press.

Jirinec, V., B. R. Campos, and M. D. Johnson. 2011. Roosting behaviour of a migratory songbird on Jamaican coffee farms: landscape composition may affect delivery of an ecosystem service. Bird Conservation International **21**:353-361.

Johnson, M. D., N. J. Levy, J. L. Kellermann, and D. E. Robinson. 2009. Effects of shade and bird exclusion on arthropods and leaf damage on coffee farms in Jamaica's Blue Mountains. Agroforestry Systems **76**:139-148.

Jones, G. A. and K. E. Sieving. 2006. Intercropping sunflower in organic vegetables to augment bird predators of arthropods. Agriculture Ecosystems & Environment **117**:171-177.

Jordani, M. X., E. Hasui, and V. Silva. 2015. Natural enemies depend on remnant habitat size in agricultural landscapes. Journal of Forestry Research **26**:469-477.

Jordano, P. 2016. Chasing ecological interactions. Plos Biology **14**:1-4.

Jules, E. S. and P. Shahani. 2003. A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. Journal of Vegetation Science **14**:459-464.

Karp, D. S., C. D. Mendenhall, R. F. Sandi, N. Chaumont, P. R. Ehrlich, E. A. Hadly, and G. C. Daily. 2013. Forest bolsters bird abundance, pest control and coffee yield. Ecology Letters **16**:1339-1347.

Kellermann, J. L., M. D. Johnson, A. M. Stercho, and S. C. Hackett. 2008. Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms. Conservation Biology **22**:1177-1185.

Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. a. Roulston, I. Steffan-Dewenter, D. P. Vazquez, R. Winfree, L. Adams, E. E. Crone, S. S. Greenleaf, T. H. Keitt, A.-M. Klein, J. Regetz, and T. H. Ricketts. 2007. Pollination and other ecosystem services produced by mobile

organisms: a conceptual framework for the effects of land-use change. Ecology Letters **10**:299-314.

Kross, S. M., T. R. Kelsey, C. J. McColl, and J. M. Townsend. 2016. Field-scale habitat complexity enhances avian conservation and avian-mediated pest-control services in an intensive agricultural crop. Agriculture Ecosystems & Environment **225**:140-149.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 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.

Laxminarayan, R. and R. D. Simpson. 2000. Biological limits on agricultural intensification: an example from resistance management. Resources for the Nature, Washington, DC.

Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. 2009. Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. Annual Review of Ecology Evolution and Systematics **40**:573-592.

Levey, D. J., B. M. Bolker, J. J. Tewksbury, S. Sargent, and N. M. Haddad. 2005. Effects of landscape corridors on seed dispersal by birds. Science **309**:146-148.

Losey, J. E. and M. Vaughan. 2006. The economic value of ecological services provided by insects. Bioscience **56**:311-323.

Maas, B., Y. Clough, and T. Tscharntke. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. Ecology Letters **16**:1480-1487.

Maas, B., T. Tscharntke, S. Saleh, D. D. Putra, and Y. Clough. 2015. Avian species identity drives predation success in tropical cacao agroforestry. Journal of Applied Ecology **52**:735-743.

Martin, E. A., B. Reineking, B. Seo, and I. Steffan-Dewenter. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. Proceedings of the National Academy of Sciences of the United States of America **110**:5534-5539.

Martin, E. A., B. Seo, C. R. Park, B. Reineking, and I. Steffan-Dewenter. 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. Ecological Applications **26**:448-462.

Matson, P. A., W. J. Parton, A. G. Power, and M. J. Swift. 1997. Agricultural intensification and ecosystem properties. Science **277**:504-509.

MEA. 2005. Millennium Ecosystem Assessment Synthesis, United Nations.

Metzger, J. P. 2000. Tree functional group richness and spatial structure in a tropical fragmented landscape (SE Brazil). Ecological Applications **10**:1147-1161.

Metzger, J. P. and P. H. S. Brancalion. 2016. Landscape ecology and restoration processes. Pages 90-120 *in* M. A. Palmer, J. B. Zeller, and D. A. Falk, editors. Foundation of restoration ecology. Island Press, Washington, DC.

Milligan, M. C., M. D. Johnson, M. Garfinkel, C. J. Smith, and P. Njoroge. 2016. Quantifying pest control services by birds and ants in Kenyan coffee farms. Biological Conservation **194**:58-65.

Mitchell, M. G. E., A. F. Suarez-Castro, M. Martinez-Harms, M. Maron, C. McAlpine, K. J. Gaston, K. Johansen, and J. R. Rhodes. 2015. Reframing landscape fragmentation's effects on ecosystem services. Trends in Ecology & Evolution **30**:190-198.

Mokross, K., T. B. Ryder, M. C. Cortes, J. D. Wolfe, and P. C. Stouffer. 2014. Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. Proceedings of the Royal Society B-Biological Sciences **281**.

Mols, C. M. M. and M. E. Visser. 2002. Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology **39**:888-899.

Mooney, K. A., D. S. Gruner, N. A. Barber, S. A. Van Bael, S. M. Philpott, and R. Greenberg. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proceedings of the National Academy of Sciences of the United States of America **107**:7335-7340.

Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The Functions of Biological Diversity in an Age of Extinction. Science **336**:1401-1406.

Oerke, E. C. 2006. Crop losses to pests. Journal of Agricultural Science **144**:31-43.

Oliver, T. H., N. J. B. Isaac, T. A. August, B. A. Woodcock, D. B. Roy, and J. M. Bullock. 2015. Declining resilience of ecosystem functions under biodiversity loss. Nature Communications **6**.

Ostman, O., B. Ekbom, and J. Bengtsson. 2001. Landscape heterogeneity and farming practice influence biological control. Basic and Applied Ecology **2**:365-371.

Pardini, R., A. D. Bueno, T. A. Gardner, P. I. Prado, and J. P. Metzger. 2010. Beyond the Fragmentation Threshold Hypothesis: Regime Shifts in Biodiversity Across Fragmented Landscapes. Plos One **5**.

Pesley, R. K., M. E. Saunders, and G. W. Luck. 2016. Cost-benefit trade-offs of bird activity in apple orchards. Peerj:1-20.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science **269**:347-350.

Prevedello, J. A., N. Gotelli, and J. P. Metzger. In press. A stochastic model for landscape patterns of biodiversity. Ecological Monographs.

Prevedello, J. A. and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation **19**:1205-1223.

Puckett, H. L., J. R. Brandle, R. J. Johnson, and E. E. Blankenship. 2009. Avian foraging patterns in crop field edges adjacent to woody habitat. Agriculture Ecosystems & Environment **131**:9-15.

Ramankutty, N. and J. A. Foley. 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. Global Biogeochemical Cycles **13**:997-1027.

Richmond, S., E. Jenkins, A. Couturier, and M. Cadman. 2015. Thresholds in forest bird richness in response to three types of forest cover in Ontario, Canada. Landscape Ecology **30**:1273-1290.

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist **158**:87-99.

Robertson, O. J. and J. Q. Radford. 2009. Gap-crossing decisions of forest birds in a fragmented landscape. Austral Ecology **34**:435-446.

Schellhorn, N. A., S. Macfadyen, F. J. J. A. Bianchi, D. G. Williams, and M. P. Zalucki. 2008. Managing ecosystem services in broadacre landscapes: what are the appropriate spatial scales? Australian Journal of Experimental Agriculture **48**:1549-1559.

Sekercioglu, C. H. 2006. Foreword on the ecological significance of bird populations Pages 15-51 *in* J. Del Hoyo, A. Elliott, and D. A. Christie, editors. Handbook of birds of the world. Lynx Edicions, Barcelona.

Sekercioglu, C. H., D. G. Wenny, and C. J. Whelan. 2016. Why birds matter: avian ecological function and ecosystem services. The University of Chicago Press, Chicago, London.

Steffen, W., K. Richardson, J. Rockstrom, S. E. Cornell, I. Fetzer, E. M. Bennett, R. Biggs, S. R. Carpenter, W. de Vries, C. A. de Wit, C. Folke, D. Gerten, J. Heinke, G. M. Mace, L. M. Persson, V. Ramanathan, B. Reyers, and S. Sorlin. 2015. Planetary boundaries: Guiding human development on a changing planet. Science **347**.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos **68**:571-573.

TEEB. 2010. Mainstreaming the Economics of Nature: A Synthesis of the Approach, Conclusions and Recommendations of TEEB.*in* S. P., W. H., S.-S. C., N. C., B. J., B. Pt., G. H., K. P., and S. B., editors. Conference of Parties to the CBD, Nagoya, Japan.

Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control **43**:294-309.

Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2008a. Conservation biological control and enemy

diversity on a landscape scale (Reprinted from Biol. Control, vol 43, pg 294-309, 2007). Biological Control **45**:238-253.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecology Letters **8**:857-874.

Tscharntke, T., C. H. Sekercioglu, T. V. Dietsch, N. S. Sodhi, P. Hoehn, and J. M. Tylianakis. 2008b. Landscape constraints on functional diversity of birds and insects in a tropical agroecosystem (vol 89, pg 944, 2008). Ecology **89**.

Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batary, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Frund, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews **87**:661-685.

Turner, M. G., D. C. Donato, and W. H. Romme. 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. Landscape Ecology **28**:1081-1097.

Tylianakis, J. M. and C. M. Romo. 2010. Natural enemy diversity and biological control: Making sense of the context-dependency. Basic and Applied Ecology **11**:657-668.

Uezu, A., D. D. Beyer, and J. P. Metzger. 2008. Can agroforest woodlots work as stepping stones for birds in the Atlantic Forest region? . Biodiversity and Conservation **17**:1907-1922.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology **89**:928-934.

Villard, M.-A. and J. P. Metzger. 2014. Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology **51**:309-318.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. American Naturalist **156**:145-155.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. Year in Ecology and Conservation Biology 2008 **1134**:25-60.

Winqvist, C., J. Bengtsson, T. Aavik, F. Berendse, L. W. Clement, S. Eggers, C. Fischer, A. Flohre, F. Geiger, J. Liira, T. Paert, C. Thies, T. Tscharntke, W. W. Weisser, and R. Bommarco. 2011. Mixed effects of organic farming and landscape complexity on

farmland biodiversity and biological control potential across Europe. Journal of Applied Ecology **48**:570-579.

Wu, J. 2013. Landscape sustainability science: ecosystem services and human well-being in changing landscapes. . Landscape Ecology **28**:999-1023.

Supplementary material

Table S1: List of 151 papers found in the literature review according the study category: (A) highlighted the importance of birds on pest control in agricultural fields without explicit measurements of pest control; (B) reported some measurements of avian-mediated pest control without explicitly reporting their links with the landscape structure; (C) reported some measurements of pest control by birds and reported the links with landscape metrics; or (D) used non-empirical data (quantitative meta-analysis, modeling or simulations) to infer pest control by birds.

Class	Author	Biome	Crop	Landscape metrics
D	Maas et al.2015	review	review	review
D	Mantyla et al. 2011	review	agricultural and natural areas	review
D	Mooney et al. 2010	review	agricultural and natural areas	review
D	Pesley et al. 2015	review	review	review
D	Philphot et al. 2009	tropical	coffee	review
D	Pumarinõ et al. 2015	review	review	review
D	Railsback & Johson 2011	review	review	review
D	Railsback & Johson 2014	review	review	review
D	Van Bael et al. 2008	tropical-temperate	agroforests	review
D	Vickery et al. 2009	review	review	review
C	Eilers & Klein 2009	temperate	almond orchard	habitat cover + edge distance
C	Ferger et al. 2013	tropical	C4 plants	distance
C	Garfinkel and Johnson 2014	temperate	brassica	distance
C	Geiger et al. 2010	temperate	mainly wheat	landscape composition (% land use)
C	Girard 2012	temperate	corn, weat (mixed)	landscape composition (% land use)
C	Gray and Lewis 2014	tropical	oil palm	habitat cover/corridor width
C	Howard & Johnson 2014	temperate	vineyards	distance
C	Johnson et al. 2009	tropical	coffee	landscape composition (% land use) + edge distance

C	Jones et al. 2005	tropical	mixed crops	landscape composition (% land use)
C	Jordani et al. 2015	tropical	coffee	patch size (6-105.9ha)
C	Karp et al. 2013	tropical	coffee	habitat cover
C	Kellerman et al. 2008	tropical	coffee	distance
C	Kross et al. 2016	temperate	alfalfa	no
C	Lemessa et al. 2015b	tropical	rapeseeds	tree cover
C	Lemessa et al.2015a	tropical	homegardens	habitat cover
C	Luck et al. 2012	temperate	apple orchards	tree cover
C	Maas et al.2013	tropical	cacao	distance
C	Maas et al. 2015	tropical	cacao	shade tree cover and distance from forest remnant
C	Martin et al. 2013	tropical	brassica	habitat cover
C	Martin et al. 2015	temperate	brassica	habitat cover
C	Martin et al. 2016	temperate	mixed crops	composition (land uses), habitat amount, Edge density
C	Milligan 2016	tropical	coffee	distance
C	Pesley et al. 2016	savanna, tropical	apple orchards	distance
C	Puckett et al. 2009	temperate	corn	distance
C	Tamburini 2016	temperate	wheat and barley	habitat cover (1.2 to 22%)
C	Tremblay et al. 2001	temperate	corn	distance
C	Winqvist et al. 2011	temperate	weat	landscape composition (% land use)
B	Borkhataria et al. 2006	tropical	coffee	-
B	Borkhataria et al. 2012c	tropical	rice	-
B	Chenon & Sunsanto 2009	tropical	oil palm	-
B	Classen 2014	tropical	coffee	-
B	Gamez-Virues 2007	tropical	shelterbelts adjacent mixed crops and pastures	-
B	Greenberg et al. 2000	tropical	coffee	-
B	Hooks et al. 2003	tropical	brassica	-

B	Howe et al. 2015	tropical	cotton	-
B	Jedlika et al. 2011	temperate	vineyards	-
B	Johnson et al. 2010	tropical	coffee	-
B	Jones and Sieving 2006	tropical	agroforests	-
B	Karp and Daily 2014	tropical	coffee	-
B	King et al. 2015	temperate	reedbeds	-
B	Koh et al. 2008	tropical	oil palm	-
B	Mols & Visser 2002	temperate	apple orchards	-
B	Mols & Visser 2007	temperate	apple orchards	-
B	Ndang'ang'a et al. 2013a	tropical	mixed crops	-
B	Ndang'ang'a et al. 2013b	tropical	brassica	-
B	Orlowski et al. 2015	temperate	multicrops	-
B	Perfecto et al. 2004	tropical	coffee	-
B	Peters & Greenberg 2013	tropical	coffee	-
B	Philphot et al. 2004	tropical	coffee	-
B	Pinol et al. 2010	temperate	citrus grove	-
B	Sanchez-Zapata et al. 2007	arid	multicrops	-
B	Saunders and Luck 2016	savanna, tropical	apple orchards	-
B	Sinu 2011	tropical	tea	-
B	Solomon & Glen 1976	temperate	apple orchards	-
B	Solomon & Glen 1979	temperate	apple orchards	-
B	Wearing & MacCarthy 1992	tropical	apple orchards	-
A	Anderson et al. 2007	-	-	-
A	Bailey et al. 2010	-	-	-
A	Barbaro & Battisti 2011	-	-	-
A	Barbaro et al. 2014	-	-	-
A	Barbaro et al. 2012	-	-	-
A	Batary et al. 2010	-	-	-

A	Beecher 2002	-	-	-
A	Beenhower et al. 2013	-	-	-
A	Bianchi et al. 2006	-	-	-
A	Bisseaua 2013	-	-	-
A	Blaauw & Isaacs 2015	-	-	-
A	Blommers et al. 1994	-	-	-
A	Borkataria et al. 2012a	-	-	-
A	Borkataria et al. 2012b	-	-	-
A	Bradbury et al. 2010	-	-	-
A	Buechley et al. 2015	-	-	-
A	Charles-Bouvier et al. 2011	-	-	-
A	Clough et al. 2011	-	-	-
A	Clough et al. 2009	-	-	-
A	Colding & Folke 2009	-	-	-
A	Dale & Polasky 2007	-	-	-
A	DeClerck et al. 2010	-	-	-
A	Deikumah et al. 2013	-	-	-
A	Develey & Pongiluppi 2010	-	-	-
A	Dix et al. 1995	-	-	-
A	Edwards et al. 2014	-	-	-
A	Evenden 1995	-	-	-
A	Evans-Ogden 2007	-	-	-
A	Fisher et al. 2010	-	-	-
A	Flynn et al. 2009	-	-	-
A	Gavier-Pizarro et al. 2012	-	-	-
A	Gojiman et al. 2015	-	-	-
A	Green & Elmberg 2014	-	-	-
A	Haslam et al. 2002	-	-	-

A	Hernandez et al. 2013	-	-	-
A	Jacobson et al. 2003	-	-	-
A	Jedlika et al. 2013	-	-	-
A	Jirinic et al. 2011	-	-	-
A	Jobin et al. 2001	-	-	-
A	Karp et al. 2011	-	-	-
A	Karp et al. 2012	-	-	-
A	Karpa et al. 2015	-	-	-
A	Kirk 1996	-	-	-
A	Komar et al. 2006	-	-	-
A	Landis et al.2000	-	-	-
A	Laterneou et al. 2009	-	-	-
A	Luck 2013	-	-	-
A	Luck et al. 2015	-	-	-
A	Luck et al. 2013	-	-	-
A	Luck et al. 2009	-	-	-
A	Lundberg & Moberg 2003	-	-	-
A	Martin et al. 2012	-	-	-
A	Mulwa et al. 2012	-	-	-
A	Munoz et al.2013	-	-	-
A	Myczko et al. 2013	-	-	-
A	Newbold et al.2014	-	-	-
A	Perfecto et al.2007	-	-	-
A	Philpott 2008	-	-	-
A	Philpott & Bichier 2012	-	-	-
A	Pimentel 1997	-	-	-
A	Poceda et al. 2008	-	-	-
A	Poch & Simoneti 2013	-	-	-

A	Power 2010	-	-	-
A	Prabowo et al. 2016	-	-	-
A	Rush et al. 2014	-	-	-
A	Rush et al. 2016	-	-	-
A	Sagoff et al. 2011	-	-	-
A	Sarwar et al. 2016	-	-	-
A	Sauders et al. 2015	-	-	-
A	Schackermann et al. 2015	-	-	-
A	Sekercioglu 2012	-	-	-
A	Sekercioglu 2006	-	-	-
A	Sekercioglu 2004	-	-	-
A	Thompson et al. 2014	-	-	-
A	Thuiller et al. 2014	-	-	-
A	Triplet et al. 2012	-	-	-
A	Tscharntke et al.2008	-	-	-
A	Tscharntke et al.2011	-	-	-
A	Tscharntke et al. 2005	-	-	-
A	Tschumi et al. 2015	-	-	-
A	Wenny et al. 2011	-	-	-
A	Werling et al. 2014	-	-	-
A	Whelan et al. 2008	-	-	-
A	Wilsey et al. 2011	-	-	-
A	Zhang et al. 2007	-	-	-

Literature review

Andersson, E., S. Barthel, and K. Ahrne. 2007. Measuring social-ecological dynamics behind the generation of ecosystem services. Ecological Applications **17**:1267-1278.

Bailey, D., M. H. Schmidt-Entling, P. Eberhart, J. D. Herrmann, G. Hofer, U. Kormann, and F. Herzog. 2010. Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. Journal of Applied Ecology **47**:1003-1013.

Barbaro, L. and A. Battisti. 2011. Birds as predators of the pine processionary moth (Lepidoptera: Notodontidae). Biological Control **56**:107-114.

Barbaro, L., E. G. Brockerhoff, B. Giffard, and I. van Halder. 2012. Edge and area effects on avian assemblages and insectivory in fragmented native forests. Landscape Ecology **27**:1451-1463.

Barbaro, L., B. Giffard, Y. Charbonnier, I. van Halder, and E. G. Brockerhoff. 2014. Bird functional diversity enhances insectivory at forest edges: a transcontinental experiment. Diversity and Distributions **20**:149-159.

Batary, P., T. Matthiesen, and T. Tscharntke. 2010. Landscape-moderated importance of hedges in conserving farmland bird diversity of organic vs. conventional croplands and grasslands. Biological Conservation **143**:2020-2027.

Beecher, N. A., R. J. Johnson, J. R. Brandle, R. M. Case, and L. J. Young. 2002. Agroecology of birds in organic and nonorganic farmland. Conservation Biology **16**:1620-1631.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B-Biological Sciences **273**:1715-1727.

Bisseleua, H. B. D., D. Fotio, Yede, A. D. Missoup, and S. Vidal. 2013. Shade Tree Diversity, Cocoa Pest Damage, Yield Compensating Inputs and Farmers' Net Returns in West Africa. Plos One **8**.

Blaauw, B. R. and R. Isaacs. 2015. Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. Biological Control **91**:94-103.

Blommers, L. H. M. 1994. Integrated Pest-Management in European Apple Orchards. Annual Review of Entomology **39**:213-241.

Borkhataria, R., J. A. Collazo, M. J. Groom, and A. Jordan-Garcia. 2012a. Shade-grown coffee in Puerto Rico: Opportunities to preserve biodiversity while reinvigorating a struggling agricultural commodity. Agriculture Ecosystems & Environment **149**:164-170.

Borkhataria, R. R., J. A. Collazo, and M. J. Groom. 2006. Additive effects of vertebrate predators on insects in a Puerto Rican coffee plantation. Ecological Applications **16**:696-703.

Borkhataria, R. R., J. A. Collazo, and M. J. Groom. 2012b. Species abundance and potential biological control services in shade vs. sun coffee in Puerto Rico. Agriculture Ecosystems & Environment **151**:1-5.

Borkhataria, R. R., G. S. Nuessly, E. Pearlstine, and R. H. Cherry. 2012c. Effects of Blackbirds (Agelaius Phoenicius) on Stink Bug (Hemiptera: Pentatomidae) Populations, Damage, and Yield in Florida Rice. Florida Entomologist **95**:143-149.

Bouvier, J. C., B. Ricci, J. Agerberg, and C. Lavigne. 2011. Apple Orchard Pest Control Strategies Affect Bird Communities in Southeastern France. Environmental Toxicology and Chemistry **30**:212-219.

Bradbury, R. B., C. Stoate, and J. R. B. Tallowin. 2010. Lowland farmland bird conservation in the context of wider ecosystem service delivery. Journal of Applied Ecology **47**:986-993.

Buechley, E. R., C. H. Sekercioglu, A. Atickem, G. Gebremichael, J. K. Ndungu, B. A. Mahamued, T. Beyene, T. Mekonnen, and L. Lens. 2015. Importance of Ethiopian shade coffee farms for forest bird conservation. Biological Conservation **188**:50-60.

Chenon, R. D. and A. Susanto. 2006. Ecological observations on diurnal birds in Indonesian oil palm plantations. Journal of Oil Palm Research:122-143.

Classen, A., M. K. Peters, S. W. Ferger, M. Helbig-Bonitz, J. M. Schmack, G. Maassen, M. Schleuning, E. K. V. Kalko, K. Bohning-Gaese, and I. Steffan-Dewenter. 2014. Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. Proceedings of the Royal Society B-Biological Sciences **281**.

Clough, Y., J. Barkmann, J. Juhrbandt, M. Kessler, T. C. Wanger, A. Anshary, D. Buchori, D. Cicuzza, K. Darras, D. D. Putra, S. Erasmi, R. Pitopang, C. Schmidt, C. H. Schulze, D. Seidel, I. Steffan-Dewenter, K. Stenchly, S. Vidal, M. Weist, A. C. Wielgoss, and T. Tscharntke. 2011. Combining high biodiversity with high yields in tropical agroforests. Proceedings of the National Academy of Sciences of the United States of America **108**:8311-8316.

Clough, Y., D. D. Putra, R. Pitopang, and T. Tscharntke. 2009. Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. Biological Conservation **142**:1032-1041.

Colding, J. and C. Folke. 2009. The Role of Golf Courses in Biodiversity Conservation and Ecosystem Management. Ecosystems **12**:191-206.

Dale, V. H. and S. Polasky. 2007. Measures of the effects of agricultural practices on ecosystem services. Ecological Economics **64**:286-296.

De Beenhouwer, M., R. Aerts, and O. Honnay. 2013. A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. Agriculture Ecosystems & Environment **175**:1-7.

DeClerck, F. A. J., R. Chazdon, K. D. Holl, J. C. Milder, B. Finegan, A. Martinez-Salinas, P. Imbach, L. Canet, and Z. Ramos. 2010. Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future. Biological Conservation **143**:2301-2313.

Deikumah, J. P., C. A. McAlpine, and M. Maron. 2013. Matrix Intensification Alters Avian Functional Group Composition in Adjacent Rainforest Fragments. Plos One **8**.

Develey, P. F. and T. Pongiluppi. 2010. Potential impacts of the changes proposed in the Brazilian Forest Code on birds. Biota Neotropica **10**:43-45.

Dix, M. E., R. J. Johnson, M. O. Harrell, R. M. Case, R. J. Wright, L. Hodges, J. R. Brandle, M. M. Schoeneberger, N. J. Sunderman, R. L. Fitzmaurice, and L. J. Young. 1995. Influences of Trees on Abundance of Natural Enemies of Insect Pests - a Review. Agroforestry Systems **29**:303-311.

Edwards, F. A., D. P. Edwards, S. Sloan, and K. C. Hamer. 2014. Sustainable Management in Crop Monocultures: The Impact of Retaining Forest on Oil Palm Yield. Plos One **9**.

Eilers, E. J. and A. M. Klein. 2009. Landscape context and management effects on an important insect pest and its natural enemies in almond. Biological Control **51**:388-394.

Evans-Ogden, L. J., D. B. Lank, and S. Bittman. 2007. Use of agricultural land by shorebirds in the Fraser River Delta. Canadian Journal of Plant Science **87**:528-529.

Evenden, M. D. 1995. The labors of Nature: Economic ornithology and the role of birds as agents of biological pest control in North American agriculture, ca 1880-1930. Forest & Conservation History **39**:172-183.

Ferger, S. W., K. Bohning-Gaese, W. Wilcke, Y. Oelmann, and M. Schleuning. 2013. Distinct carbon sources indicate strong differentiation between tropical forest and farmland bird communities. Oecologia **171**:473-486.

Fischer, J., A. Zerger, P. Gibbons, J. Stott, and B. S. Law. 2010. Tree decline and the future of Australian farmland biodiversity. Proceedings of the National Academy of Sciences of the United States of America **107**:19597-19602.

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters **12**:22-33.

Gamez-Virues, S., R. S. Bonifacio, G. M. Gurr, C. Kinross, A. Raman, and H. I. Nicol. 2007. Arthropod prey of shelterbelt-associated birds: linking faecal samples with biological control of agricultural pests. Australian Journal of Entomology **46**:325-331.

Garfinkel, M. and M. Johnson. 2015. Pest-removal services provided by birds on small organic farms in northern California. Agriculture Ecosystems & Environment **211**:24-31.

Gavier-Pizarro, G. I., N. C. Calamari, J. J. Thompson, S. B. Canavelli, L. M. Solari, J. Decarre, A. P. Goijman, R. P. Suarez, J. N. Bernardos, and M. E. Zaccagnini. 2012. Expansion and intensification of row crop agriculture in the Pampas and Espinal of Argentina can reduce ecosystem service provision by changing avian density. Agriculture Ecosystems & Environment **154**:44-55.

Geiger, F., J. Bengtsson, F. Berendse, W. W. Weisser, M. Emmerson, M. B. Morales, P. Ceryngier, J. Liira, T. Tscharntke, C. Winqvist, S. Eggers, R. Bommarco, T. Part, V. Bretagnolle, M. Plantegenest, L. W. Clement, C. Dennis, C. Palmer, J. J. Onate, I. Guerrero, V. Hawro, T. Aavik, C. Thies, A. Flohre, S. Hanke, C. Fischer, P. W. Goedhart, and P. Inchausti. 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology **11**:97-105.

Girard, J., A. Baril, P. Mineau, and L. Fahrig. 2012. Foraging habitat and diet of Song Sparrows (Melospiza melodia) nesting in farmland: a stable isotope approach. Canadian Journal of Zoology-Revue Canadienne De Zoologie **90**:1339-1350.

Goijman, A. P., M. J. Conroy, J. N. Bernardos, and M. E. Zaccagnini. 2015. Multi-Season Regional Analysis of Multi-Species Occupancy: Implications for Bird Conservation in Agricultural Lands in East-Central Argentina. Plos One **10**.

Graya, C. L. and O. T. Lewis. 2014. Do riparian forest fragments provide ecosystem services or disservices in surrounding oil palm plantations? Basic and Applied Ecology **15**:693-700.

Green, A. J. and J. Elmberg. 2014. Ecosystem services provided by waterbirds. Biological Reviews **89**:105-122.

Greenberg, R., P. Bichier, A. C. Angon, C. MacVean, R. Perez, and E. Cano. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. Ecology **81**:1750-1755.

Haslam, S. M. and A. Vella. 2002. Birds associated with agricultural crops in Malta. Avian Landscape Ecology: Pure and Applied Issues in the Large-Scale Ecology of Birds:238-241.

Hernandez, S. M., B. J. Mattsson, V. E. Peters, R. J. Cooper, and C. R. Carroll. 2013. Coffee Agroforests Remain Beneficial for Neotropical Bird Community Conservation across Seasons. Plos One **8**.

Hooks, C. R. R., R. R. Pandey, and M. W. Johnson. 2003. Impact of avian and arthropod predation on lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem. Ecological Entomology **28**:522-532.

Howard, K. A. and M. D. Johnson. 2014. Effects of natural habitat on pest control in california vineyards. Western Birds **45**:276-283.

Howe, A. G., G. Nachman, and G. L. Lovei. 2015. Predation pressure in Ugandan cotton fields measured by a sentinel prey method. Entomologia Experimentalis Et Applicata **154**:161-170.

Jacobson, S. K., K. E. Sieving, G. A. Jones, and A. Van Doorn. 2003. Assessment of farmer attitudes and behavioral intentions toward bird conservation on organic and conventional Florida farms. Conservation Biology **17**:595-606.

Jedlicka, J. A., R. Greenberg, and D. K. Letourneau. 2011. Avian Conservation Practices Strengthen Ecosystem Services in California Vineyards. Plos One **6**.

Jedlika, J. A., A. M. Sharma, and R. P. P. Almeida. 2013. Molecular tools reveal diets of insectivorous birds from predator fecal matter. Conservation Genetics Resources **5**:879-885.

Jirinec, V., B. R. Campos, and M. D. Johnson. 2011. Roosting behaviour of a migratory songbird on Jamaican coffee farms: landscape composition may affect delivery of an ecosystem service. Bird Conservation International **21**:353-361.

Jobin, B., L. Choiniere, and L. Belanger. 2001. Bird use of three types of field margins in relation to intensive agriculture in Quebec, Canada. Agriculture Ecosystems & Environment **84**:131-143.

Johnson, M. D., J. L. Kellermann, and A. M. Stercho. 2010. Pest reduction services by birds in shade and sun coffee in Jamaica. Animal Conservation **13**:140-147.

Johnson, M. D., N. J. Levy, J. L. Kellermann, and D. E. Robinson. 2009. Effects of shade and bird exclusion on arthropods and leaf damage on coffee farms in Jamaica's Blue Mountains. Agroforestry Systems **76**:139-148.

Jones, G. A. and K. E. Sieving. 2006. Intercropping sunflower in organic vegetables to augment bird predators of arthropods. Agriculture Ecosystems & Environment **117**:171-177.

Jones, G. A., K. E. Sieving, and S. K. Jacobson. 2005. Avian diversity and functional insectivory on north-central Florida farmlands. Conservation Biology **19**:1234-1245.

Jordani, M. X., E. Hasui, and V. Silva. 2015. Natural enemies depend on remnant habitat size in agricultural landscapes. Journal of Forestry Research **26**:469-477.

Karp, D. S. and G. C. Daily. 2014. Cascading effects of insectivorous birds and bats in tropical coffee plantations. Ecology **95**:1065-1074.

Karp, D. S., C. D. Mendenhall, R. F. Sandi, N. Chaumont, P. R. Ehrlich, E. A. Hadly, and G. C. Daily. 2013. Forest bolsters bird abundance, pest control and coffee yield. Ecology Letters **16**:1339-1347.

Karp, D. S., A. J. Rominger, J. Zook, J. Ranganathan, P. R. Ehrlich, and G. C. Daily. 2012. Intensive agriculture erodes beta-diversity at large scales. Ecology Letters **15**:963-970.

Karp, D. S., G. Ziv, J. Zook, P. R. Ehrlich, and G. C. Daily. 2011. Resilience and stability in bird guilds across tropical countryside. Proceedings of the National Academy of Sciences of the United States of America **108**:21134-21139.

Karpa, D. S., C. D. Mendenhall, E. Callaway, L. O. Frishkoff, P. M. Kareiva, P. R. Ehrlich, and G. C. Daily. 2015. Confronting and resolving competing values behind conservation objectives. Proceedings of the National Academy of Sciences of the United States of America **112**:11132-11137.

Kellermann, J. L., M. D. Johnson, A. M. Stercho, and S. C. Hackett. 2008. Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms. Conservation Biology **22**:1177-1185.

King, R. A., W. O. C. Symondson, and R. J. Thomas. 2015. Molecular analysis of faecal samples from birds to identify potential crop pests and useful biocontrol agents in natural areas. Bulletin of Entomological Research **105**:261-272.

King, W. B. 1980. Ecological basis of extinction in birds. Acta Congressus Internationalis Ornithologici **2**:905-911.

Kirk, A. 1996. Past and current attempts to evaluate the role of birds as predators of insect pests in temperate agriculture. Current Ornithology **13**:175-269.

Koh, L. P. 2008. Birds defend oil palms from herbivorous insects. Ecological Applications **18**:821-825.

Komar, O. 2006. Ecology and conservation of birds in coffee plantations: a critical review. Bird Conservation International **16**:1-23.

Kross, S. M., T. R. Kelsey, C. J. McColl, and J. M. Townsend. 2016. Field-scale habitat complexity enhances avian conservation and avian-mediated pest-control services in an intensive agricultural crop. Agriculture Ecosystems & Environment **225**:140-149.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology **45**:175-201

Lemessa, D., P. A. Hamback, and K. Hylander. 2015a. Arthropod but Not Bird Predation in Ethiopian Homegardens Is Higher in Tree-Poor than in Tree-Rich Landscapes. Plos One **10**.

Lemessa, D., U. Samnegard, P. A. Hamback, and K. Hylander. 2015b. Tree cover mediates the effect on rapeseed leaf damage of excluding predatory arthropods, but in an unexpected way. Agriculture Ecosystems & Environment **211**:57-64.

Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. 2009. Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. Annual Review of Ecology Evolution and Systematics **40**:573-592.

Luck, G. W. 2013. The net return from animal activity in agroecosystems: trding off benefits from ecosystem services against costs from crop damage. F1000 Research **2**:1-20.

Luck, G. W., A. Carter, and L. Smallbone. 2013. Changes in Bird Functional Diversity across Multiple Land Uses: Interpretations of Functional Redundancy Depend on Functional Group Identity. Plos One **8**.

Luck, G. W., R. Harrington, P. A. Harrison, C. Kremen, P. M. Berry, R. Bugter, T. P. Dawson, F. de Bello, S. Diaz, C. K. Feld, J. R. Haslett, D. Hering, A. Kontogianni, S. Lavorel, M. Rounsevell, M. J. Samways, L. Sandin, J. Settele, M. T. Sykes, S. van den Hove, M. Vandewalle, and M. Zobel. 2009. Quantifying the Contribution of Organisms to the Provision of Ecosystem Services. Bioscience **59**:223-235.

Luck, G. W., K. Hunt, and A. Carter. 2015. The species and functional diversity of birds in almond orchards, apple orchards, vineyards and eucalypt woodlots. Emu **115**:99-109.

Luck, G. W., S. Lavorel, S. McIntyre, and K. Lumb. 2012. Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. Journal of Animal Ecology **81**:1065-1076.

Lundberg, J. and F. Moberg. 2003. Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. Ecosystems **6**:87-98.

Maas, B., Y. Clough, and T. Tscharntke. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. Ecology Letters **16**:1480-1487.

Maas, B., D. S. Karp, S. Bumrungsri, K. Darras, D. Gonthier, J. C. C.-. HUang, C. A. Lindell, J. J. Maine, L. Mestre, N. L. Michel, E. B. Morrinson, I. Prerfecto, S. Philpott, C. H. Sekercioglu, R. M. Silva, P. J. Taylor, T. Tscharntke, S. A. Van Bael, C. J. Whelan, and K. Willians-Guillén. 2015a. Bird and bat predation services in tropical forests and agroforestry landscapes. Biological Reviews:1-21.

Maas, B., T. Tscharntke, S. Saleh, D. D. Putra, and Y. Clough. 2015b. Avian species identity drives predation success in tropical cacao agroforestry. Journal of Applied Ecology **52**:735-743.

Mantyla, E., T. Klemola, and T. Laaksonen. 2011. Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. Oecologia **165**:143-151.

Martin, E. A., B. Reineking, B. Seo, and I. Steffan-Dewenter. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. Proceedings of the National Academy of Sciences of the United States of America **110**:5534-5539.

Martin, E. A., B. Reineking, B. Seo, and I. Steffan-Dewenter. 2015. Pest control of aphids depends on landscape complexity and natural enemy interactions. Peerj **3**.

Martin, E. A., B. Seo, C. R. Park, B. Reineking, and I. Steffan-Dewenter. 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. Ecological Applications **26**:448-462.

Martin, E. A., M. Viano, L. Ratsimisetra, F. Laloe, and S. M. Carriere. 2012. Maintenance of bird functional diversity in a traditional agroecosystem of Madagascar. Agriculture Ecosystems & Environment **149**:1-9.

Milligan, M. C., M. D. Johnson, M. Garfinkel, C. J. Smith, and P. Njoroge. 2016. Quantifying pest control services by birds and ants in Kenyan coffee farms. Biological Conservation **194**:58-65.

Mols, C. M. M. and M. E. Visser. 2002. Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology **39**:888-899.

Mols, C. M. M. and M. E. Visser. 2007. Great Tits (Parus major) Reduce Caterpillar Damage in Commercial Apple Orchards. Plos One **2**.

Mooney, K. A., D. S. Gruner, N. A. Barber, S. A. Van Bael, S. M. Philpott, and R. Greenberg. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proceedings of the National Academy of Sciences of the United States of America **107**:7335-7340.

Mulwa, R. K., K. Bohning-Gaese, and M. Schleuning. 2012. High Bird Species Diversity in Structurally Heterogeneous Farmland in Western Kenya. Biotropica **44**:801-809.

Munoz, J. C., R. Aerts, K. W. Thijs, P. R. Stevenson, B. Muys, and C. H. Sekercioglu. 2013. Contribution of woody habitat islands to the conservation of birds and their potential ecosystem services in an extensive Colombian rangeland. Agriculture Ecosystems & Environment **173**:13-19.

Myczko, L., Z. M. Rosin, P. Skorka, P. Wylegala, M. Tobolka, M. Fliszkiewicz, T. Mizera, and P. Tryjanowski. 2013. Effects of management intensity and orchard features on bird communities in winter. Ecological Research **28**:503-512.

Ndang'ang'a, P. K., J. B. M. Njoroge, K. Ngamau, W. Kariuki, P. W. Atkinson, and J. Vickery. 2013a. Avian foraging behaviour in relation to provision of ecosystem services in a highland East African agroecosystem. Bird Study **60**:156-168.

Ndang'ang'a, P. K., J. B. M. Njoroge, and J. Vickery. 2013b. Quantifying the contribution of birds to the control of arthropod pests on kale, Brassica oleracea acephala, a key crop in East African highland farmland. International Journal of Pest Management **59**:211-216.

Newbold, T., J. P. W. Scharlemann, S. H. M. Butchart, C. H. Sekercioglu, L. Joppa, R. Alkemade, and D. W. Purves. 2014. Functional traits, land-use change and the structure of present and future bird communities in tropical forests. Global Ecology and Biogeography **23**:1073-1084.

Orlowski, G., J. Karg, and G. Karg. 2014. Functional Invertebrate Prey Groups Reflect Dietary Responses to Phenology and Farming Activity and Pest Control Services in Three Sympatric Species of Aerially Foraging Insectivorous Birds. Plos One **9**.

Peisley, R. K., M. E. Saunders, and G. W. Luck. 2015. A sistematic review of the benefits and costs of bird and insect activity in agroecosystems. Springer science reviews **3**:113-125.

Perfecto, I., I. Armbrecht, S. M. Philpott, L. Soto-Pinto, and T. V. Dietsch. 2007. Shaded coffee and the stability of rainforest margins in northern Latin America. Stability of Tropical Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation:227-263.

Perfecto, I., J. H. Vandermeer, G. L. Bautista, G. I. Nunez, R. Greenberg, P. Bichier, and S. Langridge. 2004. Greater predation in shaded coffee farms: The role of resident neotropical birds. Ecology **85**:2677-2681.

Pesley, R. K., M. E. Saunders, and G. W. Luck. 2016. Cost-benefit trade-offs of bird activity in apple orchards. Peerj:1-20.

Peters, V. E. and R. Greenberg. 2013. Fruit Supplementation Affects Birds but not Arthropod Predation by Birds in Costa Rican Agroforestry Systems. Biotropica **45**:102-110.

Philpott, S. M., W. J. Arendt, I. Armbrecht, P. Bichier, T. V. Diestch, C. Gordon, R. Greenberg, I. Perfecto, R. Reynoso-Santos, L. Soto-Pinto, C. Tejeda-Cruz, G. Williams-Linera, J. Valenzuela, and J. M. Zolotoff. 2008. Biodiversity Loss in Latin American Coffee Landscapes: Review of the Evidence on Ants, Birds, and Trees. Conservation Biology **22**:1093-1105.

Philpott, S. M. and P. Bichier. 2012. Effects of shade tree removal on birds in coffee agroecosystems in Chiapas, Mexico. Agriculture Ecosystems & Environment **149**:171-180.

Philpott, S. M., R. Greenberg, P. Bichier, and I. Perfecto. 2004. Impacts of major predators on tropical agroforest arthropods: comparisons within and across taxa. Oecologia **140**:140-149.

Philpott, S. M., O. Soong, J. H. Lowenstein, A. L. Pulido, D. T. Lopez, D. F. B. Flynn, and F. DeClerck. 2009. Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. Ecological Applications **19**:1858-1867.

Pimentel, D., C. Wilson, C. McCullum, R. Huang, P. Dwen, J. Flack, Q. Tran, T. Saltman, and B. Cliff. 1997. Economic and environmental benefits of biodiversity. Bioscience **47**:747-757.

Pinol, J., X. Espadaler, N. Canellas, J. Martinez-Vilalta, J. A. Barrientos, and D. Sol. 2010. Ant versus bird exclusion effects on the arthropod assemblage of an organic citrus grove. Ecological Entomology **35**:367-376.

Poch, T. J. and J. A. Simonetti. 2013. Ecosystem services in human-dominated landscapes: insectivory in agroforestry systems. Agroforestry Systems **87**:871-879.

Power, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2959-2971.

Prabowo, W. E., K. Darras, Y. Clough, M. Toledo-Hernandez, R. Arlettaz, Y. A. Mulyani, and T. Tscharntke. 2016. Bird Responses to Lowland Rainforest Conversion in Sumatran Smallholder Landscapes, Indonesia. Plos One **11**.

Puckett, H. L., J. R. Brandle, R. J. Johnson, and E. E. Blankenship. 2009. Avian foraging patterns in crop field edges adjacent to woody habitat. Agriculture Ecosystems & Environment **131**:9-15.

Pumarino, L., G. W. Sileshi, S. Gripenberg, R. Kaartinen, E. Barrios, M. N. Muchane, C. Midega, and M. Jonsson. 2015. Effects of agroforestry on pest, disease and weed control: A meta-analysis. Basic and Applied Ecology **16**:573-582.

Railsback, S. F. and M. D. Johnson. 2011. Pattern-oriented modeling of bird foraging and pest control in coffee farms. Ecological Modelling **222**:3305-3319.

Railsback, S. F. and M. D. Johnson. 2014. Effects of land use on bird populations and pest control services on coffee farms. Proceedings of the National Academy of Sciences of the United States of America **111**:6109-6114.

Rusch, A., K. Birkhofer, R. Bommarco, H. G. Smith, and B. Ekbom. 2014. Management intensity at field and landscape levels affects the structure of generalist predator communities. Oecologia **175**:971-983.

Rusch, A., R. Chaplin-Kramer, M. M. Gardiner, V. Hawro, J. Holland, D. Landis, C. Thies, T. Tscharntke, W. W. Weisser, C. Winqvist, M. Woltz, and R. Bommarco. 2016. Agricultural landscape simplification reduces natural pest control: a quantitative analysis. Agriculture, Ecosystems, and Environment **221**:198-204.

Sagoff, M. 2011. The quantification and valuation of ecosystem services. Ecological Economics **70**:497-502.

Sanchez-Zapata, J. A., J. A. Donazar, A. Delgado, M. G. Forero, O. Ceballos, and F. Hiraldo. 2007. Desert locust outbreaks in the Sahel: resource competition, predation and ecological effects of pest control. Journal of Applied Ecology **44**:323-329.

Sarwar, M., I. Hussain, M. Anwar, and S. N. Mirza. 2016. BASELINE DATA ON ANTHROPOGENIC PRACTICES IN THE AGRO-ECOSYSTEM OF POTHWAR PLATEAU, PAKISTAN. Journal of Animal and Plant Sciences **26**:850-857.

Saunders, M. E. and G. W. Luck. 2016. Combining Costs and Benefits of Animal Activities to Assess Net Yield Outcomes in Apple Orchards. Plos One **11**.

Schackermann, J., G. Pufal, Y. Mandelik, and A. M. Klein. 2015. Agro-ecosystem services and dis-services in almond orchards are differentially influenced by the surrounding landscape. Ecological Entomology **40**:12-21.

Sekercioglu, C. H. 2006. Increasing awareness of avian ecological function. Trends in Ecology & Evolution **21**:464-471.

Sekercioglu, C. H. 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. Journal of Ornithology **153**:S153-S161.

Sekercioglu, C. H., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences of the United States of America **101**:18042-18047.

Sinu, P. A. 2011. Avian pest control in tea plantations of sub-Himalayan plains of Northeast India: Mixed-species foraging flock matters. Biological Control **58**:362-366.

Solomon, M. E. and D. M. Glen. 1979. Prey Density and Rates of Predation by Tits (Parus Spp) on Larvae of Codling Moth (Cydia-Pomonella) under Bark. Journal of Applied Ecology **16**:49-59.

Solomon, M. E., D. M. Glen, D. A. Kendall, and N. F. Milsom. 1976. Predation of Overwintering Larvae of Codling Moth (Cydia-Pomonella -L) by Birds. Journal of Applied Ecology **13**:341-&.

Tamburini, G., S. De Simone, M. Sigura, F. Boscutti, and L. Marini. 2016. Conservation tillage mitigates the negative effect of landscape simplification on biological control. Journal of Applied Ecology **53**:233-241.

Thompson, I. D., K. Okabe, J. A. Parrotta, E. Brockerhoff, H. Jactel, D. I. Forrester, and H. Taki. 2014. Biodiversity and ecosystem services: lessons from nature to improve management of planted forests for REDD-plus. Biodiversity and Conservation **23**:2613-2635.

Thuiller, W., S. Pironon, A. Psomas, M. Barbet-Massin, F. Jiguet, S. Lavergne, P. B. Pearman, J. Renaud, L. Zupan, and N. E. Zimmermann. 2014. The European functional tree of bird life in the face of global change. Nature Communications **5**.

Tremblay, A., P. Mineau, and R. K. Stewart. 2001. Effects of bird predation on some pest insect populations in corn. Agriculture Ecosystems & Environment **83**:143-152.

Triplett, S., G. W. Luck, and P. G. Spooner. 2012. The importance of managing the costs and benefits of bird activity for agricultural sustainability. International Journal of Agricultural Sustainability **10**:268-288.

Tscharntke, T., Y. Clough, S. A. Bhagwat, D. Buchori, H. Faust, D. Hertel, D. Holscher, J. Juhrbandt, M. Kessler, I. Perfecto, C. Scherber, G. Schroth, E. Veldkamp, and T. C. Wanger. 2011. Multifunctional shade-tree management in tropical agroforestry landscapes - a review. Journal of Applied Ecology **48**:619-629.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecology Letters **8**:857-874.

Tscharntke, T., C. H. Sekercioglu, T. V. Dietsch, N. S. Sodhi, P. Hoehn, and J. M. Tylianakis. 2008. Landscape constraints on functional diversity of birds and insects in a tropical agroecosystem (vol 89, pg 944, 2008). Ecology **89**.

Tschumi, M., M. Albrecht, M. H. Entling, and K. Jacot. 2015. High effectiveness of tailored flower strips in reducing pests and crop plant damage. Proceedings of the Royal Society B-Biological Sciences **282**:189-196.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology **89**:928-934.

Vickery, J. A., R. E. Feber, and R. J. Fuller. 2009. Arable field margins managed for biodiversity conservation: A review of food resource provision for farmland birds. Agriculture Ecosystems & Environment **133**:1-13.

Wearing, C. H. and K. Mccarthy. 1992. Predation of Codling Moth Cydia-Pomonella L by the Silvereye Zosterops-Lateralis (Latham). Biocontrol Science and Technology **2**:285-295.

Wenny, D. G., T. L. DeVault, M. D. Johnson, D. Kelly, C. H. Sekercioglu, D. F. Tomback, and C. J. Whelan. 2011. The Need to Quantify Ecosystem Services Provided by Birds. Auk **128**:1-14.

Werling, B. P., T. L. Dickson, R. Isaacs, H. Gaines, C. Gratton, K. L. Gross, H. Liere, C. M. Malmstrom, T. D. Meehan, L. L. Ruan, B. A. Robertson, G. P. Robertson, T. M. Schmidt, A. C. Schrotenboer, T. K. Teal, J. K. Wilson, and D. A. Landis. 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. Proceedings of the National Academy of Sciences of the United States of America **111**:1652-1657.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. Year in Ecology and Conservation Biology 2008 **1134**:25-60.

Wilsey, C. B. and S. A. Temple. 2011. The Effects of Cropping Systems on Avian Communities in Cacao and Banana Agro-Forestry Systems of Talamanca, Costa Rica. Biotropica **43**:68-76.

Winqvist, C., J. Bengtsson, T. Aavik, F. Berendse, L. W. Clement, S. Eggers, C. Fischer, A. Flohre, F. Geiger, J. Liira, T. Paert, C. Thies, T. Tscharntke, W. W. Weisser, and R. Bommarco. 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. Journal of Applied Ecology **48**:570-579.

Zhang, W., T. H. Ricketts, C. Kremen, K. Carney, and S. M. Swinton. 2007. Ecosystem services and dis-services to agriculture. Ecological Economics **64**:253-260.

Table S2: Bird species providing pest control services in agricultural crops identified in literature review. The bird names follow the 2015 IOC Bird world list (Gill and Donsker 2015, available at: http://www.worldbirdnames.org/ioc-lists/). Numbers 1-14: enumerated literature from empirical studies in tropical biomes; 15-25: enumerated literature from empirical studies in temperate biome. Literature correspondent to each study is described below. *Diet.* RI: restrictive insectivores (exclusive insect feeders); GI: generalist insectivores (insect feeders that complement their diet with fruits or seeds); OI: occasional insectivores (species that feed predominantly on non-insect resources but occasionally ingest insects); NI: non-insectivores; OM: omnivores. *Habitat.* HD: native habitat-dependent; HG: habitat-generalist species.

Scientific name	Family	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Diet	Habitat
Corvus brachyrhynchos	Corvidae																				X					X	OM	HG
Carduelis tristis	Fringillidae																						X				OI	HG
Setophaga ruticilla	Parulidae												X								X						RI	HD
Turdus migratorius	Turdidae														X								X			X	GI	HG
Dendroica castanea	Parulidae																				X						GI	HD
Mniotilta varia	Parulidae					X							X								X						RI	HD
Dendroica striata	Parulidae																				X						OM	HD
Passerina caerulea	Cardinalidae																				X						GI	HG
Cyanocitta cristata	Corvidae																				X		X				OM	HG
Polioptila caerulea	Polioptilidae																				X						RI	HG
Quiscalus major	Icteridae																				X						OM	HG
Dolichonyx oryzivorus	Icteridae																				X						OI	HG
Taxostoma rufum	Mimidae																				X		X				OM	HG
Poecile carolinensis	Paridae																				X						GI	HD
Thryothorus ludovicianus	Troglodytidae																				X						GI	HG
Bulbucus ibis	Ardeidae																				X						GI	HG
Quiscalus quiscula	Icteridae																						X				OM	HG
Columbina passerina	Columbidae																				X						NI	HG
Geothlypis trichas	Parulidae												X								X						RI	HD

Species	Family																			Diet	Status
Dryobates pubescens	Picidae														X					RI	HG
Sialia sialis	Turdidae														X		X			GI	HD
Tyrannus tyrannus	Tyrannidae														X		X			GI	HG
Sturnella magna	Icteridae														X					GI	HD
Dumetella carolinensis	Mimidae														X		X			OM	HG
Myiarchus crinitus	Tyrannidae														X					RI	HG
Carpodacus mexicanus	Fringilidae														X			X		OI	HG
Passerina cyanea	Cardinalidae														X					OI	HG
Lanius ludovicianus	Laniidae														X					GI	HG
Zenaida macroura	Columbidae														X		X	X		OI	HG
Colinus virginianus	Odontophoridae														X					OI	HG
Cardinalis cardinalis	Cardinalidae				X										X		X			OI	HG
Mimus polyglotus	Mimidae														X					OM	HG
Parula americana	Parulidae						X								X					RI	HD
Icterus spurius	Icteridae														X		X			RI	HG
Melanerpes carolinus	Picidae														X					OM	HD
Melanerpes erythrocephalus	Picidae														X		X			OM	HG
Buteo lineatus	Accipitridae														X					OI	HG
Agelaius phoeniceus	Icteridae				X										X		X			GI	HG
Columba livia	Columbidae														X					OI	HG
Archilochus colubris	Trochilidae	X													X					OI	HD
Grus canadensis	Gruidae														X					OM	HG
Melospiza melodia	Emberezidae															X	X			OI	HG
Piranga rubra	Thraupidae	X													X					RI	HG
Dendroica palmarum	Parulidae						X								X					RI	HD
Meleagris gallopavo	Phasianidae														X					GI	HG
Elminia longicauda	Monarchidae					X														RI	HG
Muscicapa adusta	Muscicapidae					X														RI	HG
Terpsiphone viridis	Monarchidae					X														RI	HG
Ispidina picta	Alcedinidae					X														RI	HG
Dendroica pharetra	Parulidae						X													RI	HD
Ploceus baglafecht	Ploceidae		X			X														RI	HG
Icterus galbula	Icteridae	X															X			RI	HG

Species	Family								
Coereba flaveola	Thraupidae		X					OI	HG
Limosa limosa	Scolopacidae						X	RI	HG
Dendroica caerulescens	Parulidae		X					RI	HD
Vireo vireo (Vireo altiloquus)	Vireonidae		X					RI	HD
Vireo osburni	Vireonidae		X					RI	HD
Turdoides plebejus	Timaliidae	X						RI	HG
Tchagra australis	Malaconotidae	X						RI	HG
Molothrus ater	Icteridae				X	X		GI	HG
Automolus ochrolaemus	Furnariidae			X				RI	HD
Dendropicos fuscescens	Picidae	X						RI	HG
Platysteira cyanea	Platysteiridae	X						RI	HD
Cinnyrius cupreus	Nectariniidae	X						OI	HG
Emberiza calandra	Emberezidae						X	OM	HG
Crex crex	Rallidae						X	GI	HG
Galerida cristata	Alaudidae						X	GI	HG
Numenius arquata	Scolopacidae						X	GI	HG
Cisticola juncidis	Cisticolidae						X	RI	HG
Otis tarda	Otididae						X	GI	HG
Perdix perdix	Phasianidae						X	OI	HD
Todus todus	Todidae		X					RI	HD
Vanellus vanellus	Charadriidae						X	RI	HG
Chondestes grammacus	Emberezidae					X		OI	HG
Tetrax tetrax	Otididae						X	GI	HG
Circus aeruginosus	Accipitridae						X	NI	HG
Acrocephalus palustris	Sylviidae						X	RI	HG
Anthus pratensis	Motacillidae						X	RI	HD
Circus pygargus	Accipitridae						X	OI	HG
Melaenornis edolioides	Muscicapidae	X						RI	HG
Emberiza hortulana	Emberezidae						X	RI	HG
Seiurus aurocapillus	Parulidae		X					RI	HD
Haematopus ostralegus	Haematopodidae						X	OI	HG
Bradornis pallidus	Muscicapidae	X						RI	HG
Phasianus colchicus	Phasianidae						X	OI	HG

Species	Family																												
Dendroica discolor	Parulidae									X																	RI	HG
Coturnix coturnix	Phasianidae																				X			OI	HD
Alectoris rufa	Phasianidae																				X			OI	HG
Thryothorus rutilus	Troglodytidae								X															RI	HD
Basileuterus rufifrons	Parulidae			X		X				X														RI	HG
Calandrella brachydactyla	Alaudidae																				X			RI	HG
Cisticola cantans	Cisticolidae							X																RI	HD
Gallinago gallinago	Scolopacidae																				X			RI	HG
Ploceus ocularis	Ploceidae							X																RI	HD
Saxicola torquatus	Turdidae				X																X			RI	HG
Limnothlyps swaisonii	Parulidae								X															RI	HG
Anthus campestris	Motacillidae																				X			GI	HG
Prinia subflava	Cisticolidae	X						X																RI	HD
Vermivora peregrina	Parulidae			X				X																GI	HD
Laniarius aethiopicus	Malaconotidae							X																RI	HG
Oenanthe oenanthe	Turdidae																				X			RI	HD
Saxicola rubetra	Turdidae																				X			GI	HD
Cossypha heuglini	Turdidae							X																RI	HD
Erythropyigia leucophrys	Turdidae							X																RI	HG
Psalidoprocne albiceps	Hirundinidae							X																RI	HD
Elvira chionura	Trochilidae								X															OI	HG
Lullula arborea	Alaudidae																				X			GI	HG
Motacilla flava	Motacillidae																				X			GI	HG
Zosterops senegalensis	Zosteropidae							X																RI	HG
Emberiza citrinella	Emberezidae																				X			OI	HG
Dendroica coronata	Parulidae									X							X						X	GI	HD
Parus major	Paridae													X										GI	HG
Paroaria coronata	Emberezidae						X							X										GI	HG
Zosterops lateralis	Zosteropidae															X							X	GI	HG
Parus caerulescens	Paridae													X										GI	HG
Dicrurus leucophaeus	Dicruridae						X																	RI	HD
Artamus fuscus	Artamidae						X																	RI	HG

Species	Family								X																								
Sturnus contra	Sturnidae								X																						OM	HG	
Muscicapa dauurica	Muscicapidae								X																						GI	HD	
Chrysomma sinense	Timaliidae								X																						GI	HG	
Dicrurus macrocercus	Dicruridae								X																						RI	HG	
Oriolus xanthornus	Oriolidae								X																						OI	HG	
Dinopium benghalense	Picidae								X																						GI	HG	
Psilopogon asiaticus	Capitonidae								X																						OI	HG	
Merops leschenauti	Meropidae								X																						RI	HG	
Sturnia malabaricus	Sturnidae								X																						GI	HG	
Acridotheres tristis	Sturnidae								X																						OM	HG	
Megalaima haemacephala	Megalaimidae								X																						OI	HG	
Picoides canicapillus	Picidae								X																						RI	HD	
Oriolus oriolus	Oriolidae								X																						GI	HD	
Chrysocolaptes lucidus	Picidae								X																						RI	HD	
Merops orientalis	Meropidae								X																						RI	HG	
Culicicapa ceylonensis	Muscicapidae								X																						RI	HD	
Gracula religiosa	Sturnidae								X																						OM	HD	
Coracias benghalensis	Coraciidae								X																						GI	HG	
Acridotheres fuscus	Sturnidae								X																						GI	HG	
Coracina macei	Campephagidae								X																						GI	HG	
Dicrurus remifer	Dicruridae								X																						RI	HD	
Lanius schach	Laniidae								X																						GI	HG	
Pericrocotus ethologus	Campephagidae								X																						GI	HD	
Copsychus saularis	Turdidae								X																						GI	HG	
Cuculus saturatus	Cuculidae								X																						GI	HG	
Cyornis poliogenys	Muscicapidae								X																						RI	HD	
Cacomantis merulinus	Cuculidae								X																						GI	HG	
Pycnonotus cafer	Pycnonotidae								X																						OM	HG	
Pycnonotus jocosus	Pycnonotidae								X																						OM	HG	
Oriolus tenuirostris	Oriolidae								X																						OI	HG	
Dicrurus hottentottus	Dicruridae								X																						RI	HD	
Streptopelia chinensis	Columbidae								X																						NI	HG	
Dendrocitta vagabunda	Corvidae								X																						OM	HG	

Species	Family						GI/etc	HG/etc
Acridotheres cinereus	Sturnidae					X	GI	HG
Thryothorus pleuthorus	Troglodytidae					X	RI	HD
Amazilia cyanura	Trochilidae				X		OI	HG
Myiarchus tuberculifer	Tyrannidae			X	X		GI	HD
Thryothorus modestus	Troglodytidae			X	X		RI	HG
Thryothorus maculipectus	Troglodytidae				X		RI	HG
Piranga leucoptera	Thraupidae				X		OI	HG
Vireo flavoviridis	Vireonidae			X	X		GI	HG
Serinus striolatus	Fringillidae		X				OI	HG
Passer motitensis	Passeridae		X				NI	HD
Lanius collaris	Laniidae		X				GI	HG
Cisticola hunteri	Cisticolidae		X				RI	HD
Ploceus spekei	Ploceidae		X				OM	HG
Cossypha caffra	Turdidae		X				OM	HG
Serinus flavivertex	Fringillidae		X				OI	HG
Anthus cinnamomeus	Motacillidae		X				GI	HG
Streptopelia capicola	Columbidae		X				OI	HG
Corvus capensis	Corvidae		X				OM	HG
Colius striatus	Collidae		X				OI	HG
Serinus sulphuratus	Fringilidae		X				OI	HG
Nectarinia kilimensis	Nectariniidae		X				OI	HG
Wilsonia pusilla	Parulidae	X					RI	HD
Catharus aurantiirostris	Turdidae	X					GI	HG
Tiaris olivaceus	Emberezidae	X					OI	HG
Melozone leucotis	Emberezidae	X					GI	HG
Amazilia tzacatl	Trochilidae	X					OI	HG
Troglodites musculus	Troglodytidae	X					RI	HG
Thryophilus rufalbus	Troglodytidae	X					RI	HG
Momotus coeruliceps	Momotidae	X					OI	HD
Chlorostilbon canivetii	Trochilidae	X					OI	HG
Geothlypis poliocephala	Parulidae	X					RI	HG
Todirostrum cinereum	Tyrannidae	X					GI	HG

Species	Family																														
Euphonia hirundinacea	Thraupidae					X																									OI	HD
Dendroica petechia	Parulidae					X																									GI	HG
Amazilia sauceroteii	Trochilidae					X																									OI	HD
Dendroica pensylvanica	Parulidae					X																									GI	HD
Thraupis episcopus	Thraupidae					X																									OI	HG
Zimmerius vilissimus	Tyrannidae					X																									OI	HD
Spizella pallida	Emberezidae					X																									GI	HG
Cyclarhis gujanensis	Vireonidae					X																									OM	HD
Atlapetes albinucha	Emberezidae					X																									GI	HD
Chiroxiphia linearis	Pipridae					X																									OI	HD
Hylophilus decurtatus	Vireonidae					X																									RI	HD
Leptotila verreauxi	Columbidae					X																									OI	HG
Turdus viscivorus	Turdidae																	X													GI	HG
Sylvia melanocephala	Sylviidae																	X													GI	HG
Lanius senator	Laniidae																	X													GI	HG
Periparus ater	Paridae																	X													GI	HD
Surnus unicolor	Sturnidae																	X													OM	HG
Passer domesticus	Passeridae																	X													OM	HG
Passer montanus	Passeridae																	X													OI	HG
Acrocephalus scirpacues	Sylviidae				X																										RI	HG
Acrocephalus schoenobaenus	Sylviidae				X																										GI	HG
Cettia cetti	Sylviidae				X																										RI	HD
Apus apus	Apodidae			X																											RI	HG
Hirundo rustica	Hirundinidae			X																											GI	HG
Delichon urbica	Hirundinidae			X																											RI	HG
Zosterops chloris	Zosteropidae		X																												OI	HG
Camaroptera brachyura	Cisticolidae	X																													RI	HG
Cossypha semirufa	Turdidae	X																													RI	HD
Malurus cyaneus	Maluridae																											X			RI	HD
Ptilonorhynchus violaceus	Ptilonorhynchidae																											X			OI	HD
Cracticus tibicen	Cracticidae																											X			GI	HG

Species	Family					Diet	Habitat
European blackbird	Turdidae			X		GI	HG
Zonotrichia leucophris	Emberezidae				X	OI	HG
Callipepla californica	Odontophoridae				X	OI	HD
Euphagus cyanocephalus	Icteridae				X	OI	HG
Passerculus sandwichensis	Emberezidae				X	GI	HG
Anthus rubescens	Motacillidae				X	GI	HD
Petrochelidon pyrrhonota	Hirundinidae				X	RI	HG
Tachycineta bicolor	Hirundinidae				X	RI	HG
Sturnella neglecta	Icteridae				X	GI	HG
Aphelocoma californica	Corvidae	X	X			OM	HD
Sturnus vulgaris	Sturnidae	X				GI	HG
Sialia mexicana	Turdidae		X			GI	HD
Junco hyemalis	Emberezidae		X			OI	HD

Literature cited

(1) Lemessa D. Hamback PA, Hylander K (2015) Arthropod but Not Bird Predation in Ethiopian Homegardens Is Higher in Tree-Poor than in Tree-Rich Landscapes. Plos One 10(5)

(2) Maas B, Tscharntke T, Saleh S, Putra DD, Clough Y (2015) Avian species identity drives predation success in tropical cacao agroforestry. J Appl Ecol 52(3):735-743

(3) Orlowski G, Karg J, Karg G (2014) Functional Invertebrate Prey Groups Reflect Dietary Responses to Phenology and Farming Activity and Pest Control Services in Three Sympatric Species of Aerially Foraging Insectivorous Birds. Plos One 9(12)

(4) King RA, Symondson WOC, Thomas RJ (2015) Molecular analysis of faecal samples from birds to identify potential crop pests and useful biocontrol agents in natural areas. Bulletin of Entomological Research 105(3):261-272

(5) Peters VE, Greenberg R (2013) Fruit Supplementation Affects Birds but not Arthropod Predation by Birds in Costa Rican Agroforestry Systems. Biotropica 45(1):102-110

(6) Ndang'ang'a PK, Njoroge JBM, Ngamau K, Kariuki W, Atkinson PW, Vickery J (2013) Avian foraging behaviour in relation to provision of ecosystem services in a highland East African agroecosystem. Bird Study 60(2):156-168

(7) Perfecto I, Vandermeer JH, Bautista GL et al (2004) Greater predation in shaded coffee farms: The role of resident neotropical birds. Ecology 85(10):2677-2681

(8) Sinu PA (2011) Avian pest control in tea plantations of sub-Himalayan plains of Northeast India: Mixed-species foraging flock matters. Biol Control 58(3):362-366

(9) Borkhataria RR, Nuessly GS, Pearlstine E, Cherry RH (2012) Effects of Blackbirds (Agelaius Phoenicius) on Stink Bug (Hemiptera: Pentatomidae) Populations, Damage, and Yield in Florida Rice. Fla Entomol 95(1):143-149

(10) Hooks CRR, Pandey RR, Johnson MW (2003) Impact of avian and arthropod predation on lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem. Ecol Entomol 28(5):522-532

(11) Ferger SW, Boehning-Gaese K, Wilcke W, Oelmann Y, Schleuning M (2013) Distinct carbon sources indicate strong differentiation between tropical forest and farmland bird communities. Oecologia 171(2):473-486

(12) Kellermann JL, Johnson MD, Stercho AM, Hackett SC (2008) Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms. Conserv Biol 22(5):1177-1185

(13) Karp DS, Mendenhall CD, Sandi RF et al (2013) Forest bolsters bird abundance, pest control and coffee yield. Ecol Lett 16(11):1339-1347

(14) Garfinkel M. & Johnson M. (2015). Pest-removal services provided by birds on small organic farms in northern California. Agr Ecosyst Environ, 211, 24-31

(15) Howard, K. A. & Johnson, M. D. (2014). Effects of natural habitat on pest control in california vineyards. Western Birds 45: 276-283

(16) Pinol J, Espadaler X, Canellas N, Martinez-Vilalta J, Barrientos JA, Sol D (2010) Ant versus bird exclusion effects on the arthropod assemblage of an organic citrus grove. Ecol Entomol 35(3):367-376

(17) Solomon ME, Glen DM, Kendall DA, Milsom NF (1976) Predation of Overwintering Larvae of Codling Moth (Cydia-Pomonella -L) by Birds. J Appl Ecol 13(2):341-&

(18) Wearing CH, Mccarthy K (1992) Predation of Codling Moth Cydia-Pomonella L by the Silvereye Zosterops-Lateralis (Latham). Biocontrol Sci Techn 2(4):285-295

(19) Mols CMM, Visser ME (2002) Great tits can reduce caterpillar damage in apple orchards. J Appl Ecol 39(6):888-899

(19) Mols CMM, Visser ME (2007) Great Tits (Parus major) Reduce Caterpillar Damage in Commercial Apple Orchards. Plos One 2(2)

(20) Jones GA, Sieving KE, Jacobson SK (2005) Avian diversity and functional insectivory on north-central Florida farmlands. Conserv Biol 19(4):1234-1245

(21) Girard J, Baril A, Mineau P, Fahrig L (2012) Foraging habitat and diet of Song Sparrows (Melospiza melodia) nesting in farmland: a stable isotope approach. Can J Zool 90(11):1339-1350

(22) Puckett HL, Brandle JR, Johnson RJ, Blankenship EE (2009) Avian foraging patterns in crop field edges adjacent to woody habitat. Agr Ecosyst Environ 131(1-2):9-15

(23) Geiger F, Bengtsson J, Berendse F et al (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl Ecol 11(2):97-105

(24) Pesley R.K., Saunders M.E. & Luck G.W. (2016). Cost-benefit trade-offs of bird activity in apple orchards. PeerJ, 1-20.

(25) Kross S.M., Kelsey T.R., McColl C.J. & Townsend J.M. (2016). Field-scale habitat complexity enhances avian conservation and avian-mediated pest-control services in an intensive agricultural crop. Agr Ecosyst Environ, 225, 140-149.

Chapter 2

Taxonomic, functional, and phylogenetic thresholds are modulated by matrix composition

Andrea Larissa Boesing, Elizabeth Nichols, Jean Paul Metzger

Luis Ribenboim

Abstract

The biodiversity extinction threshold is an abrupt decline in species richness with habitat loss. It arises as declining landscape connectivity reduces dispersal and increases local species extinction across remaining native habitat patches. Matrix composition should influence threshold dynamics through its effects on landscape connectivity. Using 23 1,254 ha independent landscapes in the Brazilian Atlantic Rainforest, we evaluated how tropical avian biodiversity respond to native forest loss in agricultural matrices with different permeability contexts: lower-permeability (cattle pastures, n= 13) and higher-permeability (coffee plantations, n= 10). We defined biodiversity in three ways, as taxonomic (TD), functional (FD), and phylogenetic diversity (PD). We tested two hypotheses: i) that lower-permeability matrix is associated with more abrupt species loss than higher-permeability matrix, and ii) that thresholds using TD, FD, and PD occur in distinct amounts of remaining native habitat. We found that both matrix composition and choice of diversity metric strongly influenced the location of this threshold along the forest cover gradient. First, coffee matrices are able to maintain higher TD in lower amounts of remaining forest cover compared to pasture matrices. The extinction threshold for TD occurred at 35% remaining habitat in pasture matrices, and 19% remaining habitat in coffee matrices. Second, PD was lost almost at same time as TD (at 28% and 22% in pasture and coffee matrices respectively) and a strong phylogenetic clustering was found in coffee matrices, indicating environmental filter driving phylogenetic structure of assemblages. Finally, we found no clear predictor for FD – although there is a substantial reduction in FD below 20% remaining habitat in both matrices. These results highlight the importance of investigating different biodiversity indices when evaluating impacts of land use change on ecosystems, as well as the importance of matrix permeability in facilitating species movement among patches, maintaining higher biodiversity levels, and providing avian-mediated ecosystem services.

Key-words: Atlantic rainforest, Coffee plantations, Functional diversity, Habitat loss, Landscape structure, Pasture lands, Phylogenetic diversity.

Introduction

Anthropogenic habitat loss, particularly in tropical forests, is considered the principal driver of the ongoing biodiversity crisis (MEA 2005). Through a suite of deleterious effects on individual fitness (Foley et al. 2005), habitat loss causes well-described changes in species richness and community structure (Pardini et al. 2010). These losses in taxonomic diversity are accompanied by important changes in functional diversity that may significantly impact ecosystem function (Bregman et al. 2014, Oliver et al. 2015), and by losses of phylogenetic diversity that may curtail future resilience in both biodiversity and function (Frishkoff et al. 2014). From a practical standpoint, there is a strong interest in understanding how much native habitat is needed to maintain certain biodiversity standards and ecosystem functionality (Fahrig 2002, Ficetola and Denoel 2009).

While the relationship between taxonomic diversity and remaining native habitat cover varies across taxa and regions, it is typically non-linear and characterized by sharp thresholds of loss between 20-40% remaining habitat, with some variability depending on the region and taxonomic group: e.g. 30% for small tropical mammals (Estavillo et al. 2013), 30-40% for large tropical mammals (Ochoa-Quintero et al. 2015), 18-33% for forest birds (Betts et al. 2007, Banks-Leite et al. 2014, Richmond et al. 2015), and 30-40% for vascular plants (Goncalves Rigueira et al. 2013, Lima and Mariano-Neto 2014). Extinction threshold theory holds that biodiversity thresholds are largely governed by the degree of dispersal among native habitat fragments, and therefore influenced by landscape structural components such as the number and size of remaining patches and their isolation (Andren 1994).

These biodiversity thresholds are theoretically influenced by the composition of the non-native habitat matrix surrounding native habitat patches, which influences community composition and ecological processes, both by modulating organismal movement and dispersal and by influencing abiotic environment of native patches (Driscoll et al. 2013, Prevedello et al. In press). Matrix types range from structurally simple land-uses dominated by agriculture monocultures to complex and heterogeneous land-uses composed of different crop or vegetation types, which are more similar to native habitat patches (Tscharntke

et al. 2007). The type of matrix strongly influences organism movement and dispersal between native habitat patches (Driscoll et al. 2013). Theoretically, a more permeable matrix should facilitate native species movement through the landscape and thus should maintain species in habitat patches at lower levels of landscape-scale native habitat cover than would otherwise be possible, retarding species extinctions and postponing extinction thresholds along the process of landscape degradation (Fig. 1A). Explicit consideration of the matrix has remained surprisingly absent from the extinction threshold literature, and the majority of studies do not include matrix composition (Estavillo et al. 2013, Banks-Leite et al. 2014, Ochoa-Quintero et al. 2015) in spite of the fact that it strongly influences processes related to species persistence in fragmented landscapes (e.g.Bender and Fahrig 2005, Ewers and Didham 2006, Kupfer et al. 2006).

In addition, existing biodiversity threshold studies have overwhelming explored the effects of declining habitat on one measure of biological diversity - taxonomic diversity, defined either as species richness (Estavillo et al. 2013) or as community integrity (Banks-Leite et al. 2014). However, taxonomic diversity may not be the most effective measurement of diversity, particularly in terms of efforts to understanding the relationships between diversity and potential ecosystem functioning (Diaz and Cabido 2001, Fahrig 2013). Measures of functional and phylogenetic diversity also contain valuable information regarding ecosystem functioning (Petchey and Gaston 2006) and community evolutionary history (Ricotta 2005), and may thus be important complements to taxonomic diversity in efforts to identify the consequences of environmental change (Jarzyna and Jetz 2016). Functional diversity reflects the variety of functional traits within a community (Jarzyna and Jetz 2016) composing a major component of ecosystem functioning (Hooper et al. 2005), and it can be measured using different approaches (e.g. Tilman 2001, Petchey and Gaston 2002, Mason et al. 2003, Cornwell et al. 2006). Phylogenetic diversity is based on cladistics relationships (Faith 1992) and reflects the evolutionary history of a species assemblage (Webb 2000, Villeger et al. 2008) and many metrics can be used to capture it as well (Tucker et al. 2016). A common measure is the sum of the branches lengths in a dendogram (Faith 1992) representing differences among species in terms of forms or functions (Mouchet et al. 2008).

Extinction thresholds for taxonomic, functional, and phylogenetic diversity are likely to occur in different amounts of remaining native habitat (Fig. 1B). Taxonomic diversity should be the most sensitive index to habitat loss, as it is influenced by the loss of each individual species (Owens and Bennett 2000, Brooks et al. 2002). Functional diversity is likely to be slightly less sensitive than taxonomic diversity due to species replacement, as species may be lost without losing community-level representation of species' traits (Owens and Bennett 2000). Finally, phylogenetic diversity should be the least sensitive of the three metrics, as the loss of (even many) closely related species has relatively little impact on overall phylogenetic diversity (Frishkoff et al. 2014).

Here we provide an empirical assessment of the influence of matrix composition on taxonomic, functional, and phylogenetic extinction thresholds. We do this through a well-replicated and spatially-extensive sample of avian diversity in 23 independent landscapes, with habitat patches embedded in either lower-permeability matrix (cattle pasture), or higher-permeability matrix (sun coffee plantations) in southeastern Brazil. We test two central hypotheses: (1) that lower-permeability matrix is associated with more abrupt species loss than higher-permeability matrix (Fig. 1A), and (2) that thresholds of taxonomic, functional, and phylogenetic diversity occur in distinct amounts of remaining native habitat (Fig. 1B).
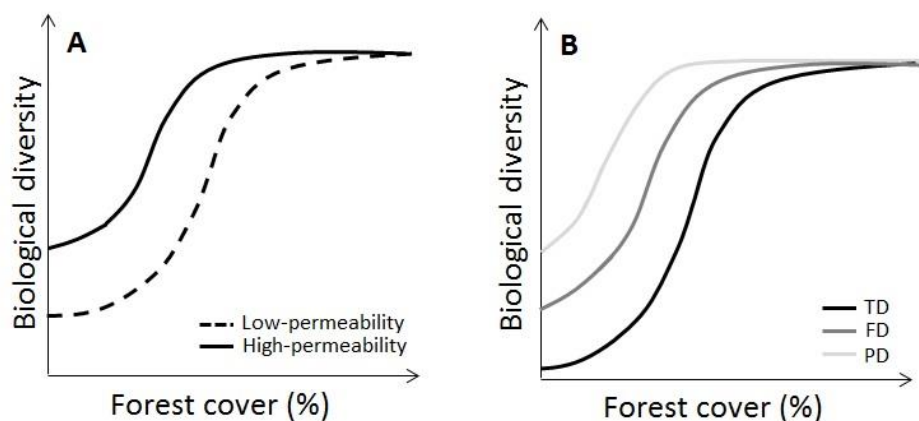
Figure 1. Expected relationships between forest cover and phylogenetic (PD), functional (FD), and taxonomic diversity (TD) of avian communities according to matrix type (**A**) and diversity metric (**B**). In **A** we hypothesize that biodiversity thresholds will occur first for all of the diversity metrics (TD, FD, PD) in low-permeability matrix (dashed lines) when compared with high-permeability

matrix (straight lines). In **B**, we hypothesize that TD is lost earlier along the forest cover gradient, followed by FD and lastly by PD.

Methods

Study region: The study was conducted in two regions of 2,000-3,000 km² each (Fig. 2) within the Brazilian Atlantic Rainforest, one of the world's most biodiverse and endangered ecosystems (Myers et al. 2000, Brooks et al. 2002, Ribeiro et al. 2011). In one region, the matrix is primarily composed of unmanaged cattle pastures owned by small landholders (lower-permeability matrix), while the other region has a matrix dominated by sun-coffee plantations (higher-permeability matrix), and lies in one of the most productive coffee regions in the world (CONAB 2013). The study region has a subtropical climate (UNICAMP 2016), with annual mean temperature varying from 11.3°C (minimum, in the colder season April-September) to 27.7°C (maximum, in the warmer season October-March), annual rainfall varying between 1,350 and 2,000 mm (Pompeu et al. 2009), and an elevation between 700-1700 m (Oliveira and Fontes 2000). Currently, the majority of the region's remaining tropical forest has been reduced to small fragments (< 50 ha) in different stages of regeneration (Ribeiro et al. 2009).

Landscape selection: We used the landscape selection approach of Pasher et al. (2013) to select independent landscapes that span a large range of landscape-level forest cover, while controlling for potentially confounding factors. We identified a total of 23 circular landscapes (2 km radius, or 1,256 ha), where each landscape was constrained between 800 and 1,300 m.a.s.l, with ferric red latosol or argisol soil, and where either extensive cattle production or sun coffee plantation was the predominant matrix land-use type (lower-permeability pasture matrix; N = 13; higher-permeability coffee matrix; N= 10; Fig. S1). We excluded major interstate highways and water reservoirs from focal landscapes and maintained a minimum distance of 6 km between the centroid of landscapes. Land-use in each 2 km focal landscape was mapped using high-resolution images (ArcGis 10.3 basemap imagery, DigitalGlobe satellites 2010-2011) with a reference scale of 1:5,000. Our final focal landscapes ranged from 6 to 54% of forest cover within the 2-km radius. Landscape-level forest cover did not vary more than 5% within 1, 2, or 3-km radii,

based on each landscape's centroid, showing that our landscape selection and forest-cover landscape ranking were little affected by landscape extent.
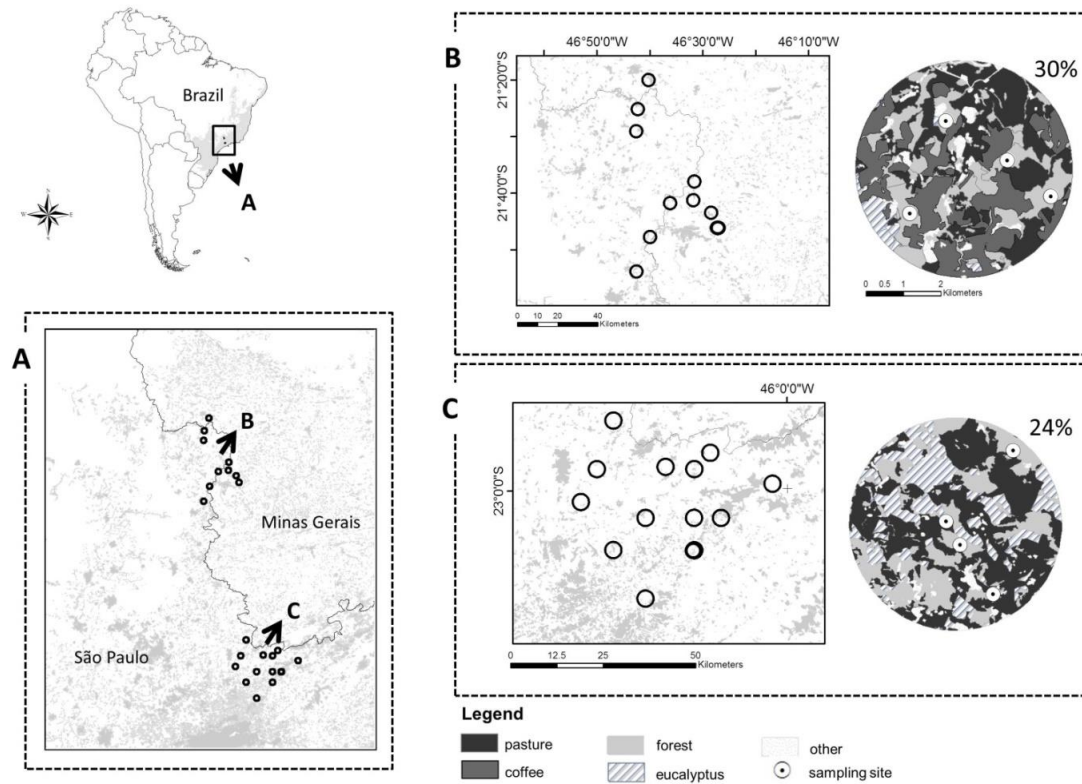
Figure 2. Study areas in the Brazilian Atlantic Rainforest domain (shaded area) between states of São Paulo and Minas Gerais (**A**). Landscapes with higher-permeability matrix (sun coffee plantation) are in the North (**B**) and low-permeability matrix (cattle pasture) are in the South (**C**). In both panels, we highlight the land use and distribution of sampling sites.

Study sites: To realistically reflect the distribution of forest across fragment sizes, we used a stratified random proportional design based on the largest fragment size to select the placement of four sampling sites in forest patches within each of the 23 focal landscapes (N= 92). We calculated the percentage of total forest cover represented by the largest forest fragment in each landscape and allocated that proportion of sampling sites to that fragment. For instance, if the largest fragment contained 50% of the landscape forest cover, 50% of sampling sites (N = 2) were located at this fragment, and 50% randomly distributed across the remaining forest fragments larger than 2.5 ha. For each selected forest patch, we randomly selected a point along the forest-matrix interface and placed a sampling site 100 m

(100.92 ± 12.97) from the edge within forest patch. All sampling sites were spaced a minimum of 800 m apart (1,591 ± 621; Fig. 2).

Bird sampling: In each sampling site, we performed 50 m fixed-radius point count (Blondel et al. 1970, Bibby et al. 2002) and recorded all bird species detected visually or orally during a 15 min sampling period. Studies in tropical regions indicate that 10 min point counts are enough to record 90% of tropical bird species (Esquivel and Peris 2008, Cavarzere et al. 2012). Bird species needed to be perched or singing inside the radius of detection to be recorded, and species flying above the canopy or flying through the sample area were not recorded (Bibby et al. 2002). All point counts were performed in the four hours after sunrise and in the last hour before sunset (Lynch 1995). Each point count was sampled in different times during the morning and evening periods in order to give the same chance of detection for all species. To increase detectability of more cryptic and rare species, each point count was replicated four times, between January-April and August-November of 2014 (23 landscapes, 92 sampling sites, N = 368 point counts). All point counts were performed by the same observer (A.L.B).

We restricted our analysis to forest-dependent species (Sick 1997, del Hoyo et al. 2014), as these are the species of conservation concern that predominantly respond to native habitat loss. Forest-dependent species were considered those species dependent of forest environments to breeding and survive (Sick 1997, del Hoyo et al. 2014). We quantified bird abundance with the Punctual Abundance Index (PAI), the most common index to quantify bird abundance in Neotropical regions (Blake 2007). The PAI was calculated as the number of detections of a given species in a given sampling site, divided by the total number of point counts (Blondel et al. 1970).

Functional trait selection: We collected information on four avian functional traits (Sick 1997, del Hoyo et al. 2014), three related to extinction-proneness associated with habitat loss (7 levels in 3 traits; McKinney 1997), and one related to resource use (6 levels). Extinction proneness traits included body mass, clutch size, and nest type. For resource use, we measured diet (insectivorous, frugivorous, granivorous, nectivorous, carnivorous, or herbivorous), performing a ranking of intensity of

resource use for each species *as per* De Coster et al. (2015) according to information available from the literature (Sick 1997, del Hoyo et al. 2014). For species with missing information, we took data for the most closely-related congener. More detail on traits selection and ranking of resources use is available in SOM1, and all traits values are available in Table S1.

Taxonomic richness: We defined taxonomic diversity (TD) as the total number of bird species (i.e. species richness) recorded in each sampling site.

Functional diversity: Because different functional traits may have values spanning several orders of magnitude, we first scaled trait values to avoid a single trait dominating trait diversity values (Villeger et al. 2008, Swenson 2014). We then performed a PCoA ordination to eliminate trait redundancy and included in our calculations those principal components explaining the majority (more than 95%) of variation. Finally, we estimated functional diversity using Rao's quadratic entropy, which is the sum, across species pairs, of the product of the distance between the two species in trait space and their two relative abundances (FD; Botta-Dukat 2005). Functional diversity was calculated using "FD" package (Laliberté et al. 2015). Rao's quadratic entropy is influenced by both species-abundance based diversity and differences among species, and it does not correlate with species richness (Botta-Dukat 2005).

Phylogenetic diversity: We calculated phylogenetic diversity (PD) using Faith's Index which provides a simple measure of the phylogenetic relatedness of a community based on the sum of all branch lengths in a phylogeny (Faith 1992, Thompson et al. 2015) using "Picante" package (Kembel et al. 2010) and the mean of 300 random phylogenetic trees. We obtained phylogenetic trees using backbone trees (BirdTree.org; Jetz et al. 2012, Jetz et al. 2014) derived from established deep avian relationships (Hackett et al. 2008; for further details, see Jetz et al. 2014). We used the total number of species in the whole sampling pool for each region as species pool. As PD frequently correlates with species richness, we also measured the *standardized effect size* (PD_{ses}) of phylogenetic community (Webb 2000, Pavoine and Bonsall 2011), which describes the difference between phylogenetic

distances in observed communities and null communities where taxa labels were shuffled across the tips of the phylogenetic tree 999 times (Swenson 2014). PD_{ses} can be interpreted in terms of which processes are important in community assembly. Positive PD_{ses} indicates phylogenetic evenness (i.e. a greater phylogenetic distance among co-occurring species) and indicates that competition is the main process driving the phylogenetic structure of communities (Swenson 2014). Negative PD_{ses} indicates phylogenetic clustering (i.e. a smaller phylogenetic distances among co-occurring species than expected by chance), and indicates an environmental filter structuring phylogeny (Swenson 2014).

Data analysis: All analyses were conducted in the R environment, version 3.3.1 (R Development Core Team 2016). To first assess the differences among ranges and central tendencies of TD, FD, PD, and PD_{ses}, metrics were pooled across all landscapes within both matrix types (pasture and coffee plantations) and we performed an independent paired t-test following data normality and homogeneity assumptions using "stats" package (R Development Core Team 2016). We assessed phylogenetic signal for all functional traits using Pagel's λ (Pagel 1999) and the "phytools" package (Revell et al. 2008) in order to determine how trait variation is correlated with phylogenetic relatedness of species. Phylogenetic signal can be defined as the statistical non-independence among trait values due their phylogenetic relatedness (Revell et al. 2008)

To test our first hypothesis that lower-permeability matrices (i.e. pasture matrices) are associated with abrupt species loss at higher levels of native habitat compared to higher-permeability matrices, we built three predictive models in response to forest cover for each biodiversity index (TD, FD, PD, PD_{ses}): a generalized linear mixed model (LR), a piecewise mixed model (PR), and a null mixed model (Null). Metrics were modeled using appropriate error distributions (Poisson for TD and Gaussian for FD, PD, and PD_{ses}), and focal landscape identity was used as random factor in all models. To identify the best predictive model, we performed a model selection procedure based on Akaike Information Criterion (AICc) corrected for small samples (Burnham & Anderson 2002), in which we compared AICc model weights across models. We considered those models with a ΔAICc below two as having the strongest empirical support (Burnham and

Anderson 2002). We used packages "bbmle" (Bolker 2016), "lme4" (Bates et al. 2016), and "segmented.lme" (Muggeo et al. 2014).

We used the forest cover amount in an 800 m radius around each sampling site as our predictor variable because this is the scale that reflects bird species response to both patch and landscape scale (Boscolo and Metzger 2009, Banks-Leite et al. 2011). Data on the movement of Brazilian Atlantic Forest birds revealed that most movements (85%) occur within 400 m from the focal site within the same forest fragment, and 15% occur within up to 1000 m (Marini 2010), supporting the use of 800 m radius scale. Previous results suggest that 800 m scale strongly reflects species response to landscape configuration, as we are focusing in a subset of forest-dependent species, mostly Passeriformes, with reduced dispersal distances, and small territories (Lira et al. 2012).

To test our second hypothesis that thresholds for taxonomic, functional, and phylogenetic diversity occur in distinct amounts of remaining native habitat, we used the estimated breakpoints given by the piecewise regression models. Piecewise regression models permit the estimatation of biodiversity thresholds by splitting explanatory variables (i.e. forest cover) in two or more linear regressions and locating where the linear trends change (Muggeo et al. 2014). Thresholds and respective confident intervals were obtained giving several starting points to the piecewise model in order to obtain those estimated values with lowest log-likelihood (Muggeo et al. 2014).

Results

Despite recording more forest-dependent species overall (a higher gamma diversity) in patches embedded in pasture matrix (85 species compared to 71 species in coffee matrix; Table S1), we found that matrix composition affects each of the diversity metrics differently. TD was higher in patches embedded in coffee matrices (t = 4.19, df = 88.97, p < 0.001; Fig. 3), while neither PD nor FD varied significantly between matrices (PD: t=-1.356; df =86.85; p = 0.178; FD: t = 0.258; df = 89.78; p = 0.796). In general, there was a strong phylogenetic signal among species' trait values (λ > 0.67; p < 0.01; Table S2), resulting in moderate correlation between FD and PD in both coffee and pasture matrices (r = 0.68 and r = 0.69 respectively; Fig. S2A), and similar patterns of ranges and central tendencies of FD

and PD (Fig. 3). Moreover, matrix composition also affected PD_{ses}: there was a stronger phylogenetic clustering of assemblages (i.e. a smaller phylogenetic distance among co-occurring species than expected by chance) in patches embedded in coffee matrices (t = 4.61, df = 73.8, p <0.001; Fig. 3), while values did not differ from what would be expected by chance in pasture matrices (PD_{ses} = 0). All calculated indexes are in Table S3.
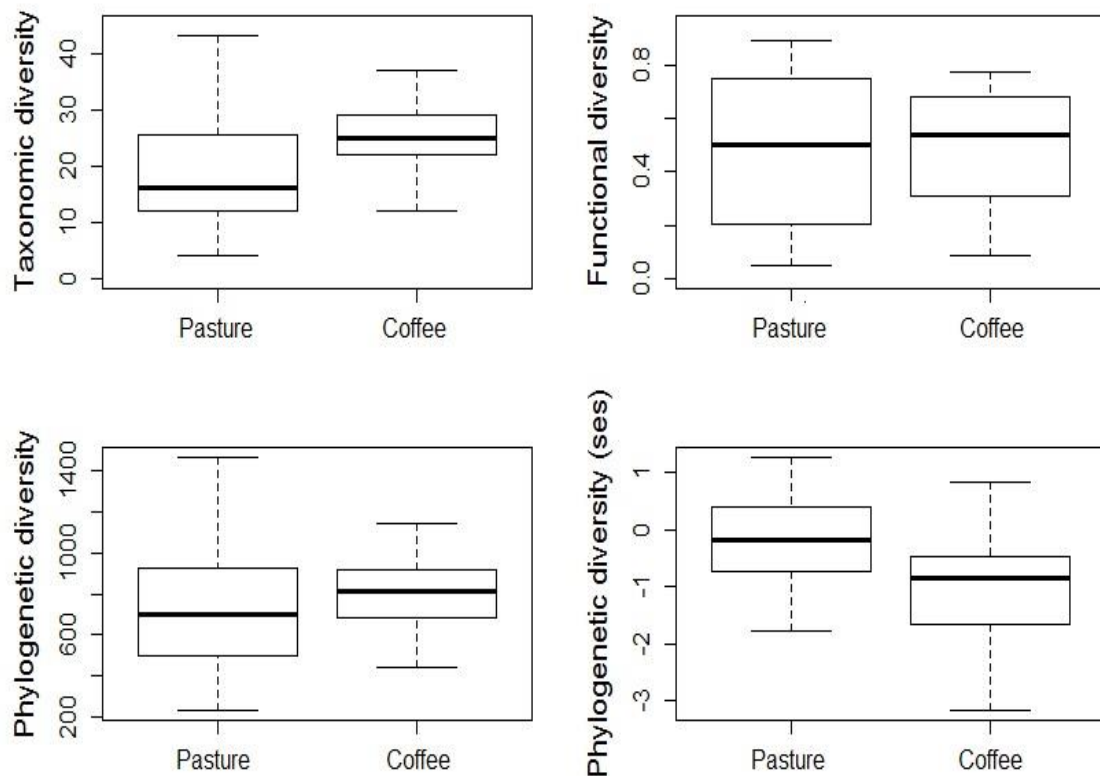
Figure 3. Central tendencies and ranges of taxonomic (TD), functional (FD), and phylogenetic (PD and PD_{ses}) avian diversity according matrix type (pasture and coffee plantations).

We found that different diversity metrics responded differently to habitat loss. A non-linear relationship with forest cover was found for TD and PD, while no clear relationship was observed for FD and PD_{ses} (Table 1). The best fitted model for TD in both matrices was the piecewise regression (Table 1). In patches embedded in coffee matrices, we found a taxonomic threshold at 19% remaining habitat (confident interval; CI: 11.7-23.4), with species loss occurring in a rate of 0.08 species per percent unit of forest cover before the threshold and increasing to 0.92 after the threshold (Table 1; Fig. 4A). For patches embedded in pasture matrices, the TD threshold occurred at 34% remaining habitat (CI: 25.1-43.4), with

species loss occurring in a rate of 0.14 species per unit of forest cover before the threshold and a more gradual reduction compared to coffee matrices (b = 0.51) below the threshold. We noticed that 60% of all bird species in the measured species pool were lost below the threshold in pasture matrices, and 30% were lost below the threshold in coffee matrices (Fig. 4B).
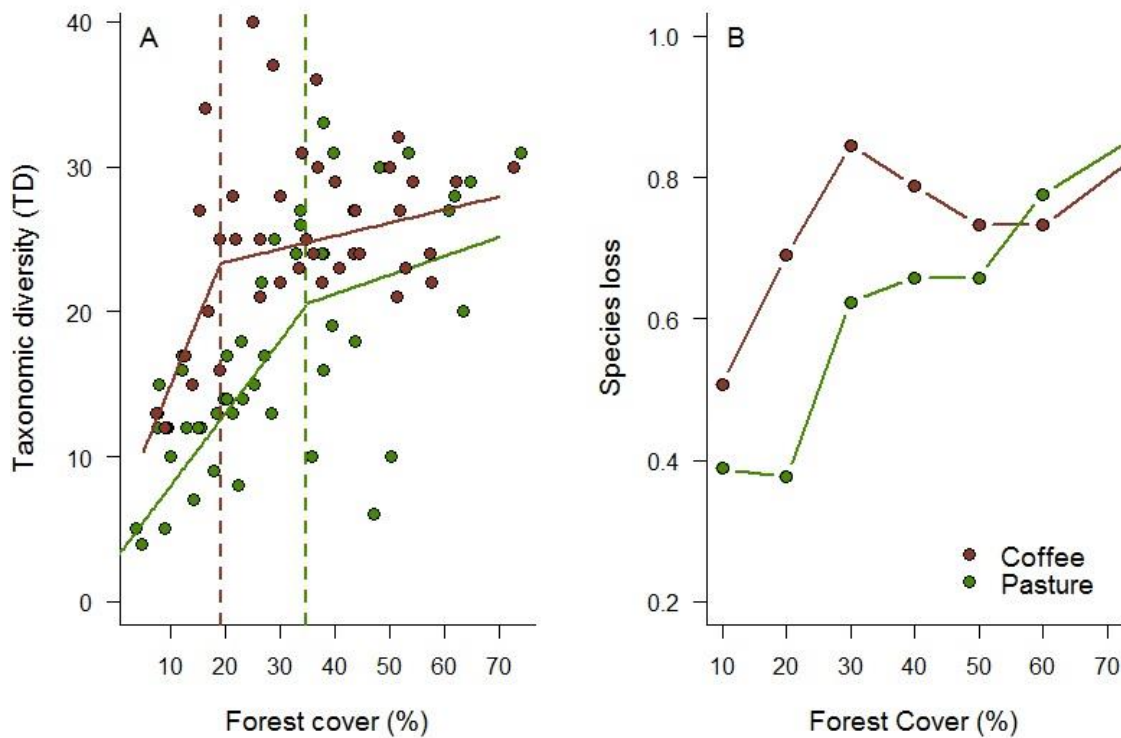
Figure 4. Fitted piecewise regressions for taxonomic diversity according matrix type (pasture and coffee plantations) (**A**), and species loss (normalized) in relation to regional species pool (**B**).

The best fitting model for PD in both matrices was also the piecewise model (Table 1). However, we found no statistical difference between thresholds for PD in the two matrices (Table 1; Fig. 5A), and a strong correlation between PD and TD in both coffee (r = 0.87) and pasture matrices (r = 0.97; Fig. S2B). In both matrix contexts, the estimated thresholds for PD were close the estimated values for TD (22% for coffee matrices and 29% for pasture matrices). Phylogenetic diversity in patches embedded in coffee matrices is lost at a rate of 264,000 evolutionary years per unit of forest cover (percent) before the phylogenetic threshold (22%; CI: 7.04-41.1), but the rate increases to 277,890 after the threshold. For patches embedded in pasture matrices, PD decreases at a similar rate of 275,540 evolutionary years per forest cover unit before the phylogenetic threshold (29%; CI: 11.7-46) which

increases to 286,700 below the threshold (29%). Unlike PD, our other measure of phylogenetic diversity that corrected for correlation with species richness (PD_{ses}) exhibited no relationship with forest cover (Table 1), but has shown a substantial difference in PD_{ses} according to matrix composition (Fig. 3; Fig. 5B).
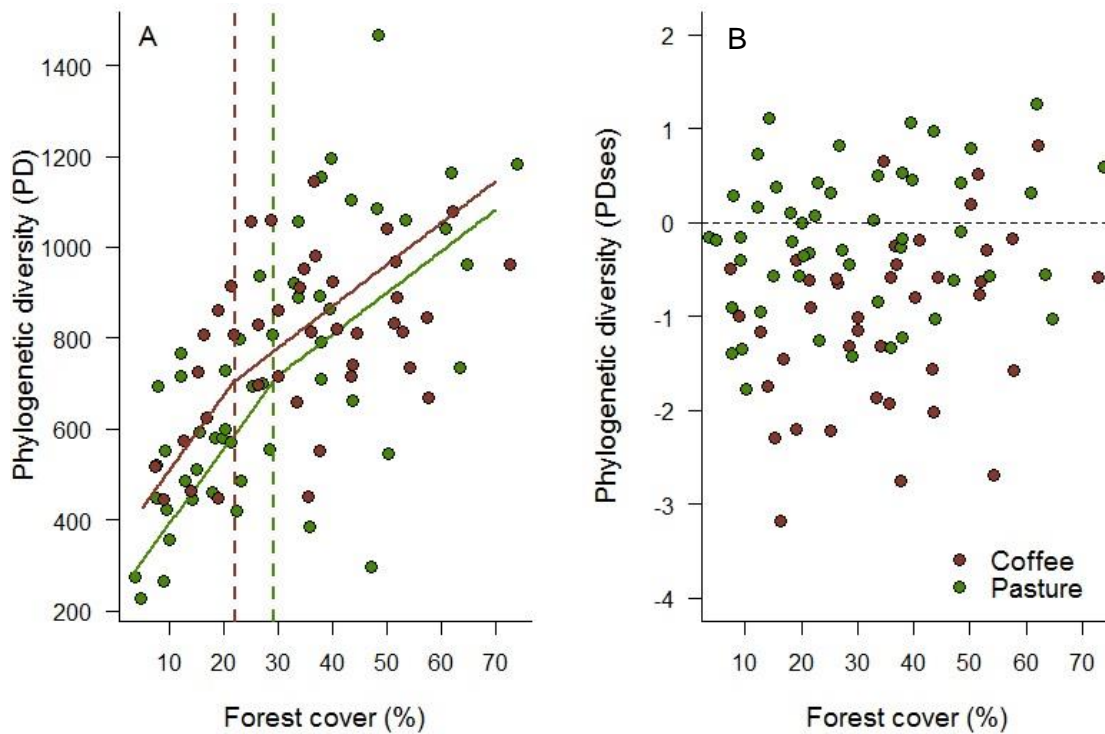
Figure 5. Fitted piecewise regressions for phylogenetic diversity (PD) according matrix type (pasture and coffee plantations) (**A**). PD_{ses} values according matrix type (**B**). Values above 0 indicate that competition is the main driver of phylogenetic structure of bird assemblages; values below 0 indicate an environmental filter.

Finally, even though traits all showed a moderate phylogenetic signal, and therefore FD could have been expected to behave like PD, no relationship between FD and forest cover was detected (Table 1). However, there is an evident reduction in FD below 20% remaining native habitat in both matrices (Fig. 6). Seed dispersers, insectivorous, and ecosystem engineers (i.e. species that contribute modifying the environment that most times brings benefits for other species) are reduced by 90, 50, and 65% respectively in pasture matrices, and by in 50, 40, and 40% in coffee matrices (Fig. S3). Birds of prey are completely lost in both matrices below this threshold.
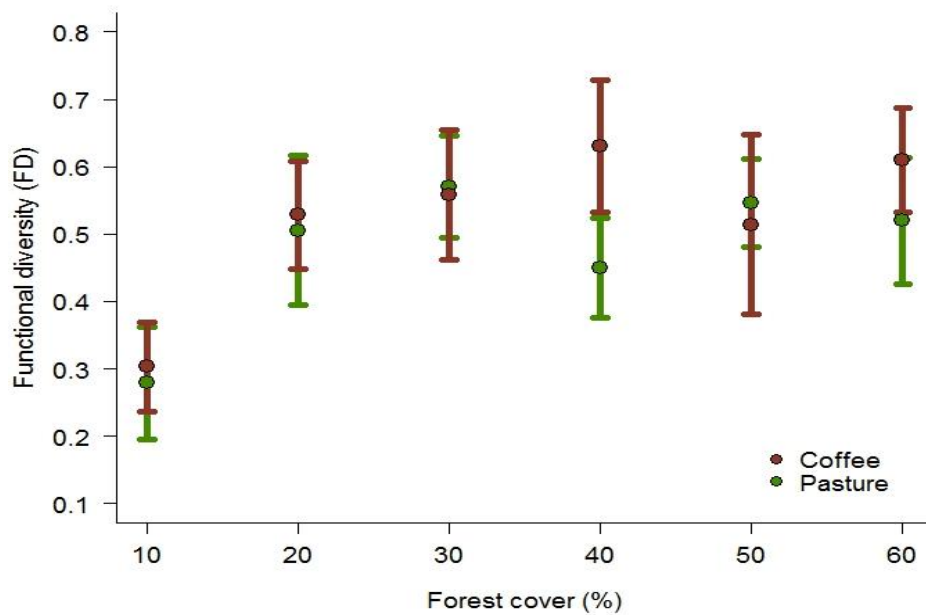
Figure 6. Mean and standard error of functional diversity (FD) in response to habitat loss according matrix type (pasture and coffee plantations).

Discussion

Through a large, comparative landscape field study, we found evidence for a strong influence of matrix composition on different diversity indexes, supporting at least partially our first hypothesis. Coffee matrices are able to maintain higher avian taxonomic diversity in forest patches in landscapes with smaller amounts of remaining forest cover than pasture matrices. As a result, the threshold for taxonomic diversity occurs at a lower amount of habitat cover in coffee matrices (ca. 20%) compared to pasture matrices (ca. 35%). Secondly, we also found partial support for our hypothesis that TD, PD, and FD are differentially influenced by forest cover loss. However, the order in which each type of diversity is lost is not what we predicted, and is dependent on matrix type. In habitat patches embedded in pasture matrices, TD and PD are lost practically at same time (probably due its correlation), and FD is lost later in the habitat loss process, while all diversity indexes seem be lost at same time (ca. 20%) in patches embedded in coffee matrices. In addition, a strong phylogenetic clustering (negative values of PD_{ses}) in coffee matrices suggests an environmental filter structuring the phylogenetic structure of bird assemblages that might be a result of the deforestation and

fragmentation history of the region. Finally, even though null model was the best predictor of FD in both matrices, there is a substantial reduction on FD below 20% of habitat remaining, which has implications in terms of ecosystem functioning. Our study is novel, contributing to the understanding of matrix composition as an important driver not only of patterns in biodiversity, but also of threshold dynamics in fragmented landscapes.

We found that matrix composition strongly affects biodiversity patterns within habitat patches, corroborating at least partially, our first hypothesis that more contrasting matrices are associated with abrupt species loss at higher levels of native habitat– at least for TD. Matrix might affect in-patch diversity in three ways at least. First, as inter-patch movement of organisms can be affected by different land-use types (Ricketts 2001, Ruffell et al. 2016, Prevedello et al. In press), matrix quality may be even more important than size and spatial arrangement of remnant patches in maintaining landscape connectivity (Tubelis et al. 2007, Driscoll et al. 2013). A higher-contrasting matrix, such as a cattle pasture, can strongly prevent avian dispersal among patches and consequently increase extinction rates in-patches, while reducing (re) colonization rates (Horner-Devine and Bohannan 2006, Webb et al. 2006). Second, even though the strongest effect of matrix composition on biodiversity is the way it regulates dispersal and movement and therefore drives colonization and extinction processes (Antongiovanni and Metzger 2005, Castellon and Sieving 2006, Neuschulz et al. 2013), matrix composition also plays important role modulating microclimate conditions at habitat edges (Saunders et al. 1991) and consequently might changes native species survival and reproductive success (Ewers and Didham 2006). Finally, the matrix surrounding habitat patches might function as source of additional nesting and foraging resources (Dunning et al. 1992, Ewers and Didham 2006, Caryl et al. 2012) and regulates the cross-habitat spillover between native and matrix habitats (Estavillo et al. 2013, Boesing et al. In prep). However, once habitat loss reaches the critical 20% threshold, even matrix composition cannot postpone species loss, and community stability is compromised.

Table 1. Model selection evaluating the response of taxonomic (TD), functional (FD), and phylogenetic diversity (PD, PD_{ses}) to forest cover (fc) according to matrix composition (pasture or coffee plantations). Model type indicates the model (PR: piecewise mixed model; LR: generalized linear mixed model; Null: null mixed model); AICc corresponds to Akaike information criteria corrected to small samples; ΔAICc is the difference between AICc from the best ranked model (ΔAICc); AICc ωi is the evidence weight; df is the degrees of freedom. Var1 (b) corresponds to the slope of regression (and in case of PR, the slope before threshold); Var2(c) is always the slope after the thresholds in a PR. Threshold (U) corresponds to estimated threshold given by the PR.

Models	Model type	AICc	ΔAIC	df	AICc ωi	Intercept (se)	Var1 (b)	Var2 (c)	Threshold U
Taxonomic diversity									
Pasture matrix									
TD ~ fc *(fc < U) + fc* (fc > U)	PR	329.8	0	6	0.963	19.74 (na)	0.51 (na)	-0.370 (na)	34.7 (25.0-43.4)
TD ~ fc	LR	336.3	6.5	3	0.037	2.812 (0.074)	0.223 (0.041)	-	-
TD ~ Null	Null	362.2	32.4	2	<0.001	2.824 (0.107)	-	-	-
Coffee matrix									
TD ~ fc *(fc < U) + fc* (fc > U)	PR	201.7	0	6	0.937	24.24 (na)	0.920 (na)	-0.832 (na)	19.1 (11.7-23.4)
TD ~ fc	LR	207.1	5.4	3	0.062	3.174 (0.034)	0.123 (0.034)	-	-
TD ~ Null	Null	216.3	14.6	2	<0.001	3.180 (0.043)	-	-	-
Phylogenetic diversity									
Pasture matrix									
PD ~ fc *(fc < U) + fc* (fc > U)	PR	425.8	0	6	1	718.92 (na)	286.7(na)	-12.163(na)	28.9 (11.7-46.0)
PD ~ fc	LR	676.6	250.9	4	<0.001	716.31 (41.28)	163.15 (30.43)	-	-
PD ~ Null	Null	704.5	278.8	3	<0.001	719.79 (63.92)	-	-	-
Coffee matrix									
PD ~ fc *(fc < U) + fc* (fc > U)	PR	425.8	0	6	0.908	731.35 (na)	277.89 (na)	-13.031 (na)	22.4 (7.04-41.1)

PD ~ fc	LR	430.4	4.6	4	0.092	784.20 (31.11)	101.27 (25.24)	-	-
PD ~ Null	Null	450.1	24.3	3	<0.001	782.3 (38.2)	-	-	-

Phylogenetic diversity (ses)

Pasture matrix

PD_{ses} ~ Null	Null	122.7	0	3	0.77	-0.173 (0.122)	-	-	-
PD_{ses} ~ fc	LR	125.2	2.5	4	0.23	-0.175 (0.108)	0.158 (0.105)		
PD_{ses} ~ fc *(fc < U) + fc* (fc > U)	PR	-	-	-		-	-	-	-

Coffee matrix

PD_{ses} ~ Null	Null	123.2	0	3	0.72	-0.179 (0.105)	-	-	-
PD_{ses} ~ fc	LR	125.1	1.9	4	0.28	-0.179 (0.103)	0.176 (0.104)	-	-
PD_{ses} ~ fc *(fc < U) + fc* (fc > U)	PR	-	-	-	-	-	-	-	-

Functional diversity

Pasture matrix

FD ~ Null	Null	21.3	0	3	0.61	0.491 (0.051)	-	-	-
FD ~ fc *(fc < U) + fc* (fc > U)	PR	23.5	2.2	6	0.2	1.199 (na)	0.813 (na)	-0.046 (na)	15.84 (9.3-22.6)
FD ~ fc	LR	23.6	2.3	4	0.19	0.491 (0.039)	0.095 (0.037)	-	-

Coffee matrix

FD ~ Null	Null	1.6	0	3	0.875	0.478 (0.046)	-	-	-
FD ~ fc	LR	5.5	3.9	4	0.122	0.478 (0.047)	0.064 (0.003)	-	-
FD ~ fc *(fc < U) + fc* (fc > U)	PR	14.1	12.6	6	0.001	0.758 (na)	0.318 (na)	-0.019 (na)	22.76 (8.2-37.2)

Differences in community structure in both matrix types might explain why the indices are all lost at same time in coffee matrices, while TD and PD are lost before FD in pasture matrices. Distinct deforestation and fragmentation histories and the absence of a source of colonizers might be lead to higher similarity among communities in patches embedded in coffee matrices than pasture matrices (Fig. S4). Landscapes with pasture matrices are located in a region surrounded by large forest remnant along the Cantareira and Mantiqueira mountains region, and might be more easily colonized or recolonized by species from adjacent regions. This could potentially lead to what we observed: more diverse clades and a higher phylogenetic distance among species in pasture matrices than in coffee matrices. This higher heterogeneity in bird composition in pasture matrices could explain why TD and PD are lost before FD, as species can be lost without losing functions, while in more homogeneous assemblages (coffee matrices) all indexes are lost around 20% of habitat remaining.

In spite of the fact that the ranges and central tendencies of total evolutionary history (PD) are similar between regions – especially due its correlation with TD, the strong phylogenetic clustering (PD_{ses}) in coffee matrices indicates a regional filter controlling the phylogenetic structure of bird communities. One reason for this clustered pattern in coffee plantations could be the historical context of fragmentation that carried a regional extinction of more distinctive species, leading to a higher phylogenetic similarity due the presence of closely related species with similar traits, and that are similarly adapted to this new condition (Cavender-Bares et al. 2009). While species distributions are determined largely by biogeographical processes, environmental filters are fundamental in determining species persistence at smaller spatial scales (Cavender-Bares et al. 2009). In addition, habitat loss and fragmentation might favor persistence of subsets of related clades that can thrive in highly disturbed and deforested landscapes (Frishkoff et al. 2014), and therefore particular branches of the phylogeny are at greater risk than others (Purvis et al. 2000). This pattern highlights the importance of maintaining more permeable matrices in order to increase species dispersal and movement, and also how important is to maintain large blocks of habitat that can act as a source of colonizers to increase community heterogeneity in fragmented landscapes.

Even though FD does not follow the same pattern as TD and PD, with clear thresholds along the habitat loss gradient in both matrices, there is a substantial reduction in FD below 20% remaining habitat in both matrices. The absence of an FD threshold might be a function of at least two factors. First, species turnover might be occurring, allowing different species performing similar functions to persist in altered forest patches (Banks-Leite et al. 2012, Dornelas et al. 2014), obscuring thresholds. Previous studies highlight that species may be lost without losing functions (Luck et al. 2013, De Coster et al. 2015), particularly when communities have significant amounts of functional trait redundancy (Fonseca and Ganade 2001). Second, the absence of threshold for FD might be due to the functional diversity metric used. Different functional indexes have different drawbacks and strengths (Cianciaruso et al. 2009). As Rao's entropy do not correlate with species richness and instead takes into account bird abundance (Botta-Dukat 2005), we expected it to be the most appropriate for this purpose; however, the choice of another metric might have revealed another pattern.

Implications for conservation

Our study demonstrates that matrix composition strongly affects in-patch assemblages of birds in the Brazilian Atlantic forest. This is the first empirical study demonstrating that less contrasting matrices might postpone abrupt loss of species from a threshold of 35% of forest cover to 20%. This strong influence of the matrix on in-patch diversity has important implications for conserving biodiversity in fragmented landscapes (Ruffell et al. 2016, Prevedello et al. In press, Prevedello and Vieira. 2010). Increasing matrix permeability through land uses that provide substantial resources, facilitates dispersal, and create lower-edge contrast (Kupfer et al. 2006) might reduce the impacts of habitat loss. However, since matrix management is constrained by both economic and social factors (Phalan et al. 2011), effective implementation of matrix management will require an interdisciplinary approach to harmonize biological needs with economic and social demands. Moreover, in terms of landscape management, it is important to understand how much matrix must be converted to high-quality uses in order to achieve conservation goals (Ruffell et al. 2016). Although the conversion of large

areas of high-contrasting matrices to lower-contrasting matrices is most of the time unfeasible, even minor changes to a small proportion of matrix, such as the inclusion of stepping stones (Boscolo et al. 2008, Uezu et al. 2008, Saura et al. 2014) may be a an effective conservation strategy (Renjifo 2001, Ruffell et al. 2016). In a recent demonstration of this pattern, Ruffell and colleagues (2016) showed that in the absence of arboreal elements in the matrix, 60% of in-patch bird species were lost by habitat loss, while when the matrix had plantations (even exotic tree plantations), the loss was reduced to 15%. Increasing landscape heterogeneity is a key management strategy, since complex-structured mosaics in spite to increase matrix suitability, it increases areas of contact between different habitats (Perovic et al. 2010) enhancing landscape connectivity and promoting long-term persistence in fragmented landscapes.

Increasing matrix permeability might not only guarantee species movement among patches, ensuring long-term persistence in fragmented landscapes, but also provide critical resources for some forest-dependent species that provide regulating ecosystem services (Sekercioglu et al. 2016), such as pest control and pollination in agricultural matrices (Bianchi et al. 2006, Blitzer et al. 2012, Naeem et al. 2012). The decrease in in-patch insectivorous might potentially affect pest control performed by avian predators—especially in coffee matrices where a substantial number of forest-dependent species often spill over into these plantations (Boesing et al. In prep). Many studies in both natural and managed areas demonstrate that birds not only have the potential to reduce herbivorous insect populations, but also that crops may respond with higher growth rates in the presence of avian predators (Whelan et al. 2008), increasing yield productivity (Johnson et al. 2009, Maas et al. 2013). In addition, frugivorous species are also strongly affected by habitat loss, and the absence or lower density of seed-dispersing frugivores might cause a smaller fraction of the fruit crop to be dispersed, resulting in changes on plant composition (Jordano et al. 2011). Moreover, more than 90% of tropical woody plant species depend on frugivorous to support their life cycles, and the disappearance of frugivorous species could unleash a cascade of effects and substantial changes in structure and function of an ecosystem (Jordano 2016).

For practical purposes, taxonomic diversity seems to be the best predictor index of loss in fragmented landscapes, since this is the first index to be affected - especially in high-contrasting matrices - and therefore detecting a minimal habitat threshold cover for taxonomic diversity can prevent subsequent functional and phylogenetic loss. Our results highlight the need to maintain sustainable amounts of habitat cover above thresholds (35% in the worse scenario) in order to maintain ecosystem functionality. Even though this threshold might not save most threatened species from extinction (Banks-Leite et al. 2014), it might prevent subsequent loss of functional and phylogenetic diversity. Importantly, once habitat loss reaches the critical 20% threshold, even a more permeable matrix cannot postpone species loss, and community stability is compromised.

Our results support the existence of a regime-shift occurring in avian community composition in heavily-deforested landscapes that is strongly modulated by matrix composition, and first detected by taxonomic diversity. We thus highlight the importance of considering matrix permeability and investigating different facets of biodiversity when evaluating the impacts of land use change on ecosystems composition and functions.

Acknowledgements

Literature cited

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

Antongiovanni, M. and J. P. Metzger. 2005. Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest framents. Biological Conservation **122**:441-451.

Banks-Leite, C., R. M. Ewers, V. Kapos, A. C. Martensen, and J. P. Metzger. 2011. Comparing species and measures of landscape structure as indicators of conservation importance. Journal of Applied Ecology **48**:706-714.

Banks-Leite, C., R. M. Ewers, and J. P. Metzger. 2012. Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. Ecology **93**:2560-2569.

Banks-Leite, C., R. Pardini, L. R. Tambosi, W. D. Pearse, A. A. Bueno, R. T. Bruscagin, T. H. Condez, M. Dixo, A. T. Igari, A. C. Martensen, and J. P. Metzger. 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science **345**:1041-1045.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, G. Grothendieck, and P. Green. 2016. lme4: Linear Mixed-Effects Models using 'Eigen' and S4. R package version 1.1-12.

Bender, D. J. and L. Fahrig. 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. Ecology **86**:1023-1033.

Betts, M. G., G. J. Forbes, and A. W. Diamond. 2007. Thresholds in songbird occurrence in relation to landscape structure. Conservation Biology **21**:1046-1058.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society B-Biological Sciences **273**:1715-1727.

Bibby, C. J., N. D. Burgess, D. A. Hill, and S. H. Mustoe. 2002. Bird Census Techniques. Second Edition edition. Academic Press, London, UK.

Blake, J. G. 2007. Neotropical forest bird communities: A comparison of species richness and composition at local and regional scales. Condor **109**:237-255.

Blitzer, E. J., C. F. Dormann, A. Holzschuh, A.-M. Klein, T. A. Rand, and T. Tscharntke. 2012. Spillover of functionally important organisms between managed and natural habitats. Agriculture Ecosystems & Environment **146**:34-43.

Blondel, J., C. Ferry, and B. Frochot. 1970. [The point count method to recording bird from hearing spots]. Alauda **38**:55-71.

Boesing, A. L., E. Nichols, and J. P. Metzger. In prep. How does landscape structure affects avian cross-habitat spillover?

Bolker, B. 2016. bbmle: tools for general maximum likelihood estimation. R package version 1.0.18. R package version 1.0.18.

Boscolo, D., C. Candia-Gallardo, M. Awade, and J. P. Metzger. 2008. Importance of interhabitat gaps and stepping-stones for lesser woodcreepers (Xiphorhynchus fuscus) in the Atlantic forest, Brazil. Biotropica **40**:273-276.

Boscolo, D. and J. P. Metzger. 2009. Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? Landscape Ecology **24**:907-918.

Botta-Dukat, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science **16**:533-540.

Bregman, T. P., C. H. Sekercioglu, and J. A. Tobias. 2014. Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. Biological Conservation **169**:372-383.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology **16**:909-923.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference. A practical information-theoritical approach. Springer, New York.

Caryl, F. M., C. P. Quine, and K. J. Park. 2012. Martens in the matrix: the importance of nonforested habitats for forest carnivores in fragmented landscapes. Journal of Mammalogy **93**:464-474.

Castellon, T. D. and K. E. Sieving. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. Conservation Biology **20**:135-145.

Cavarzere, V., T. V. Vieira da Costa, and L. F. Silveira. 2012. On the use of 10-minute point counts and 10-species lists for surveying birds in lowland Atlantic forests in Southeastern Brazil. Papeis Avulsos de Zoologia (Sao Paulo) **52**:333-340.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters **12**:693-715.

Cianciaruso, M. V., I. A. Silva, and M. A. Batalha. 2009. Diversidade filogenética e funcional: novas abordagens para a ecologia de comunidades. Biota Neotropica **9**:93-103.

CONAB. 2013. Acompanhamento da Safra Brasileira - Café Safra 2013. Companhia National de Abastecimento de Brasília.

Cornwell, W. K., D. W. Schwilk, and D. D. Ackerly. 2006. A trait-based test for habitat filtering: Convex hull volume. Ecology **87**:1465-1471.

De Coster, G., C. Banks-Leite, and J. P. Metzger. 2015. Atlantic forest bird communities provide different but not fewer functions after habitat loss. Proceedings of the Royal Society B-Biological Sciences **282**.

del Hoyo, J., A. Elliott, J. Sargatal, D. A. Christie, and E. Juana. 2014. Handbook of the Birds of the World Alive. Linx Edicions, Barcelons.

Diaz, S. and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution **16**:646-655.

Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. Science **344**:296-299.

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 & Evolution **28**:605-613.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**:169-175.

Esquivel, M. A. and S. Peris. 2008. Influence of time of day, duration and number of counts in point count sampling of birds in an Atlantic forest of Paraguay. Ornitologia Neotropical **19**:229-242.

Estavillo, C., R. Pardini, and P. L. Bernardo da Rocha. 2013. Forest Loss and the Biodiversity Threshold: An Evaluation Considering Species Habitat Requirements and the Use of Matrix Habitats. Plos One **8**.

Ewers, R. M. and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews **81**:117-142.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecological Applications **12**:346-353.

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

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation **61**:1-10.

Ficetola, G. F. and M. Denoel. 2009. Ecological thresholds: an assessment of methods to identify abrupt changes in species-habitat relationships. Ecography **32**:1075-1084.

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.

Fonseca, C. R. and G. Ganade. 2001. Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology **89**:118-125.

Frishkoff, L. O., D. S. Karp, L. K. M'Gonigle, C. D. Mendenhall, J. Zook, C. Kremen, E. A. Hadly, and G. C. Daily. 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. Science **345**:1343-1346.

Goncalves Rigueira, D. M., P. L. Bernardo da Rocha, and E. Mariano-Neto. 2013. Forest cover, extinction thresholds and time lags in woody plants (Myrtaceae) in the Brazilian Atlantic Forest: resources for conservation. Biodiversity and Conservation **22**:3141-3163.

Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K.-L. Han, J. Harshman, C. J. Huddleston, B. D. Marks, K. J. Miglia, W. S. Moore, F. H. Sheldon, D. W. Steadman, C. C. Witt, and T. Yuri. 2008. A phylogenomic study of birds reveals their evolutionary history. Science **320**:1763-1768.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs **75**:3-35.

Horner-Devine, M. C. and B. J. M. Bohannan. 2006. Phylogenetic clustering and overdispersion in bacterial communities. Ecology **87**:100-108.

Jarzyna, M. A. and W. Jetz. 2016. Detecting the multiple facets if biodiversity. Trends in Ecology & Evolution:In press.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature **491**:444-448.

Jetz, W., G. H. Thomas, J. B. Joy, D. W. Redding, K. Hartmann, and A. O. Mooers. 2014. Global Distribution and Conservation of Evolutionary Distinctness in Birds. Current Biology **24**:919-930.

Johnson, M. D., N. J. Levy, J. L. Kellermann, and D. E. Robinson. 2009. Effects of shade and bird exclusion on arthropods and leaf damage on coffee farms in Jamaica's Blue Mountains. Agroforestry Systems **76**:139-148.

Jordano, P. 2016. Chasing ecological interactions. Plos Biology **14**:1-4.

Jordano, P., P. M. Forget, J. E. Lambert, K. Bohning-Gaese, A. Traveset, and S. J. Wright. 2011. Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. Biology Letters **7**:321-323.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics **26**:1463-1464.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 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.

Laliberté, E., P. Legendre, and B. Shipley. 2015. Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. Package 'FD':-28.

Lima, M. M. and E. Mariano-Neto. 2014. Extinction thresholds for Sapotaceae due to forest cover in Atlantic Forest landscapes. Forest Ecology and Management **312**:260-270.

Lira, P. K., R. M. Ewers, C. Banks-Leite, R. Pardini, and J. P. Metzger. 2012. Evaluating the legacy of landscape history: extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic Forest. Journal of Applied Ecology **49**:1325-1333.

Luck, G. W., A. Carter, and L. Smallbone. 2013. Changes in Bird Functional Diversity across Multiple Land Uses: Interpretations of Functional Redundancy Depend on Functional Group Identity. Plos One **8**.

Lynch, J. F. 1995. Effects of point count duration, time-of-day, and aural stimuli on detectability of migratory and resident species in Quintana Roo, Mexico. Pages 1-6 *in* C. J. Ralph, J. R. Sauer, and S. Droege, editors. Monitoring bird population by point counts. USDA Forest Service General Technical Report PSW-GTR-149, Albany, CA.

Maas, B., Y. Clough, and T. Tscharntke. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. Ecology Letters **16**:1480-1487.

Marini, M. A. 2010. Bird movement in a fragmented Atlantic Forest landscape. Studies on Neotropical Fauna and Environment **45**:1-10.

Mason, N. W. H., K. MacGillivray, J. B. Steel, and J. B. Wilson. 2003. An index of functional diversity. Journal of Vegetation Science **14**:571-578.

McKinney, M. L. 1997. Extinction vulnerability and selectivity: Combining ecological and paleontological views. Annual Review of Ecology and Systematics **28**:495-516.

MEA. 2005. Millennium Ecosystem Assessment Synthesis, United Nations.

Mouchet, M., F. Guilhaumon, S. Villeger, N. W. H. Mason, J.-A. Tomasini, and D. Mouillot. 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. Oikos **117**:794-800.

Muggeo, V. M. R., D. C. Atkins, R. J. Gallop, and S. Dimidjian. 2014. Segmented mixed models with random changepoints: a maximum likelihood approach with application to treatment for depression study. Statistical Modelling **14**:293-313.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853-858.

Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The Functions of Biological Diversity in an Age of Extinction. Science **336**:1401-1406.

Neuschulz, E. L., M. Brown, and N. Farwig. 2013. Frequent bird movements across a highly fragmented landscape: the role of species traits and forest matrix. Animal Conservation **16**:170-179.

Ochoa-Quintero, J. M., T. A. Gardner, I. Rosa, S. F. de Barros Ferraz, and W. J. Sutherland. 2015. Thresholds of species loss in Amazonian deforestation frontier landscapes. Conservation Biology **29**:440-451.

Oliveira, A. T. and M. A. L. Fontes. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. Biotropica **32**:793-810.

Oliver, T. H., N. J. B. Isaac, T. A. August, B. A. Woodcock, D. B. Roy, and J. M. Bullock. 2015. Declining resilience of ecosystem functions under biodiversity loss. Nature Communications **6**.

Owens, I. P. F. and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America **97**:12144-12148.

Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life history, sexual selection or ecology? Proceedings of the Royal Society B-Biological Sciences **266**:933-939.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature **401**:877-884.

Pardini, R., A. D. Bueno, T. A. Gardner, P. I. Prado, and J. P. Metzger. 2010. Beyond the Fragmentation Threshold Hypothesis: Regime Shifts in Biodiversity Across Fragmented Landscapes. Plos One **5**.

Pasher, J., S. Mitchell, D. King, L. Fahrig, A. Smith, and K. Lindsay. 2013. Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. Landscape Ecology **28**:371-383.

Pavoine, S. and M. B. Bonsall. 2011. Measuring biodiversity to explain community assembly: a unified approach. Biological Reviews **86**:792-812.

Perovic, D. J., G. M. Gurr, A. Raman, and H. I. Nicol. 2010. Effect of landscape composition and arrangement on biological control agents in a simplified agricultural system: A cost-distance approach. Biological Control **52**:263-270.

Petchey, O. L. and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. Ecology Letters **5**:402-411.

Petchey, O. L. and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecology Letters **9**:741-758.

Phalan, B., M. Onial, A. Balmford, and R. E. Green. 2011. Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. Science **333**:1289-1291.

Pompeu, P., M. Costa, and M. A. Fontes. 2009. Classificação e apresentação dos parâmetros climáticos de Poços de Caldas - MG. III Congresso Latino Americano de Ecologia, São Lourenço, Minas Gerais.

Prevedello J.A. & Vieira M.V. (2010). Does the type of matrix matter? A quantitative review of the evidence. *Biodivers Conserv*, 19, 1205-1223.

Prevedello, J. A., N. Gotelli, and J. P. Metzger. In press. A stochastic model for landscape patterns of biodiversity. Ecological Monographs.

Purvis, A., P. M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. Science **288**:328-330.

R Development Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Renjifo, L. M. 2001. Effect of natural and anthropogenic landscape matrices on the abundance of subandean bird species. Ecological Applications **11**:14-31.

Revell, L. J., L. J. Harmon, and D. C. Collar. 2008. Phylogenetic Signal, Evolutionary Process, and Rate. Systematic Biology **57**:591-601.

Ribeiro, M. C., A. C. Martensen, J. P. Metzger, M. Tabarelli, F. Scarano, and M.-J. Fortin. 2011. The Brazilian Atlantic Forest: a shrinking biodiversity hotspot. Pages 405-434 *in* F. E. Zachos and J. C. Habel, editors. Biodiversity Hotspots: distribution and protection of conservation priority areas. Spring Verlag, Berlin.

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.

Richmond, S., E. Jenkins, A. Couturier, and M. Cadman. 2015. Thresholds in forest bird richness in response to three types of forest cover in Ontario, Canada. Landscape Ecology **30**:1273-1290.

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist **158**:87-99.

Ricotta, C. 2005. A note on functional diversity measures. Basic and Applied Ecology **6**:479-486.

Ruffell, J., C. Mick, and R. K. Didham. 2016. The matrix matters, but how should we manage it? Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented landscapes. Ecography **39**:001-008.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation – a review. Conservation Biology **5**:18-32.

Saura, S., O. 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.

Sekercioglu, C. H., D. G. Wenny, and C. J. Whelan. 2016. Why birds matter: avian ecological function and ecosystem services. The University of Chicago Press, Chicago, London.

Sick, H. 1997. Ornitologia Brasileira. Nova Fronteira, Rio de Janeiro.

Swenson, N. G. 2014. Functional and Phylogenetic Ecology in R. Springer, New York.

Thompson, P. L., T. J. Davies, and A. Gonzalez. 2015. Ecosystem Functions across Trophic Levels Are Linked to Functional and Phylogenetic Diversity. Plos One **10**.

Tilman, D. 2001. Functional diversity. Pages 109-120 *in* S. A. Levin, editor. Encyclopedia of Biodiversity. Academic Press, San Diego.

Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control **43**:294-309.

Tubelis, D. P., D. B. Lindenmayer, and A. Cowling. 2007. Bird populations in native forest patches in south-eastern Australia: the roles of patch width, matrix type (age) and matrix use. Landscape Ecology **22**:1045-1058.

Tucker, C. M., M. W. Cadotte, S. B. Carvalho, T. J. Davies, S. Ferrier, S. A. Fritz, R. Grenyer, M. R. Helmus, L. S. Jin, A. O. Mooers, S. Pavoine, O. Purschke, D. W. Redding, D. F. Rosauer, M. Winter, and F. Mazel. 2016. A guide to phylogenetic metrics for conservation, community ecology and macroecology. Biological Reviews.

Uezu, A., D. D. Beyer, and J. P. Metzger. 2008. Can agroforest woodlots work as stepping stones for birds in the Atlantic Forest region? . Biodiversity and Conservation **17**:1907-1922.

UNICAMP, C. 2016. Clima dos municipios paulistas. Avaiable at: http://www.cpa.unicamp.br/outras-informacoes/clima-dos-municipios-paulistas.html. Access in October 28th 2016.

Villeger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology **89**:2290-2301.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. American Naturalist **156**:145-155.

Webb, C. O., J. B. Losos, and A. A. Agrawal. 2006. Integrating phylogenies into community ecology. Ecology **87**:S1-S2.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. Year in Ecology and Conservation Biology 2008 **1134**:25-60.

Supplementary material

Supplementary Material 1 (SOM1) – Functional traits selection

Trait selection was based on features related to food type, intensity of resources use (body size), and species' reproductive output (i.e. nest type, clutch size; Table 1). These traits are related to both the role performed by birds in ecosystems and species ability to persist and breed in disturbed environments.

Food acquisition: we focused only on diet as trait related to resource use. Diet is related to how birds affect ecosystem function. Differences in diet specialization can provide information on niche width, bird morphology, energetic requirements (Remsen and Robinson 1990), and species function (for instance, seed dispersal, pollination, and insect predation). We assigned six diet categories: insectivorous, frugivorous, nectarivorous, granivorous, herbivorous, and carnivorous (details in Table 2). In addition, for functional traits related to diet, we performed a ranking of use as (De Coster et al. 2015) based on specialized literature (Sick 1997, del Hoyo et al. 2014).

Body size: Body size determines a host of species traits (Owens and Bennett 2000, Woodward et al. 2005). Larger species are often considered more vulnerable to extinction because they have naturally low population densities, slow growth rates, high energetic requirements, and might suffer from anthropogenic overexploitation (Cardillo et al. 2005). Because many life-history traits are correlated with body size, this variation can have potentially profound effects across multiple scales of biological organization, from individual to ecosystem functioning. Measuring body size is an easy way to collapse co-varying traits over a single dimension, with no need to observe these traits directly (Woodward et al. 2005). Species body mass information (weight) was compiled following Ramirez et al. (2008).

Reproductive output: reproductive potential of birds has profound effects upon the patterns of distribution and population abundance in environments (Beissinger 2000). Populations with high reproductive output and rapid population turnover may be able to respond rapidly to environmental changes and exploit new resource opportunities (Owens et al. 1999, Owens and Bennett 2000). On the other

hand, populations with lower reproductive output and slower population turnover rates may be especially stable in suitable biotopes but are relatively sensitive to environmental changes.

1. *Clutch size:* it is the major component of natality rates and is relatively easy to measure (Skutch 1985). We assigned values of minimum and maximum number of eggs per clutch recorded for each species (Sick 1997, del Hoyo et al. 2014). Although it is assumed that there is a strong relationship between body size and clutch size (larges species producing smaller clutch sizes), in a recent global analysis, this assumption was only weakly confirmed (Jetz et al. 2008). Another factor influencing clutch size around world is nest type: cavity nesters (which are naturally exposed to lower rates of nest predation) tend to have smaller clutch sizes than open nesters, and species with half-open nests are in between. Clutch size also varies according to diet (i.e. granivores and omnivore laying larger clutches than frugivores and nectarivores; Jetz et al. 2008).

2. *Nest type:* One of the main factors impacting bird populations in fragmented landscapes is nest predation due the increase on predators and brood parasitism rates (Cavitt and Martin 2002, Tewksbury et al. 2006). Mortality rates are generally greater among field- and marsh-nesting passerines than among tree-nesting species, especially those nesting in cavities (Sibly et al. 2012). We assigned our species to four nest categories: closed, cavity, semi-open, and open (See Table 2 for major details). In addition, the lack of suitable nesting habitat in disturbed environments can have a strong effect on the reproductive success of certain bird species such as those from Picidae and Psittacidae families, which require old or dead trees to build their nests in (Sick 1997).

Table 1. Functional traits selected to calculate functional diversity of bird assemblages. For each trait, the different possible measurements (levels) are listed, along with a description.

Trait	Levels	Description
Body size	Body mass	body mass in grams
Clutch size	Mean number of eggs	minimum and maximum
	Closed	globular or cylindrical nest with entrance
	Cavities	nests built inside wood or soil cavities
	Semi-open	nests as a shallow or deep cup
Nest type	Open	exposed layer of leaves or sticks
	Frugivorous	fruits, berries, fleshy seeds
	Insectivorous	insects, arthropods, caterpillars
	Granivorous	seeds, maize, nuts, spores
Diet	Nectarivorous	nectar
	Carnivorous	vertebrate animals, fledglings, eggs, reptiles
	Herbivorous	flowers, leaves

Table 2. Ranking of intensity of use of diet traits to include in Functional Diversity calculation.

Ranking	Common words to describe use
0	Nothing
1	Also, at times, less commonly, less frequently, occasionally, once, only infrequently, possibly, probably, rarely, readily, regularly, relatively frequently, single records of, small amount, some, sometimes, supplemented by
2	Also considerable, also important, also many, also much, also wide variety of, as well as, just as frequently, often
3	Great majority, mainly, mostly, particularly, usually

*For those species using all resources without preference, was designated **2** for each component

Literature cited

Beissinger, S. R. 2000. Ecological mechanisms of extinction. Proceedings of the National Academy of Sciences of the United States of America **97**:11688-11689.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science **309**:1239-1241.

Cavitt, J. F. and T. E. Martin. 2002. Effects of forest fragmentation on brood parasitism and nest predation in eastern and western landscapes. Studies in Avian Biology:73-80.

De Coster, G., C. Banks-Leite, and J. P. Metzger. 2015. Atlantic forest bird communities provide different but not fewer functions after habitat loss. Proceedings of the Royal Society B-Biological Sciences **282**.

del Hoyo, J., A. Elliott, J. Sargatal, D. A. Christie, and E. Juana. 2014. Handbook of the Birds of the World Alive. Linx Edicions, Barcelons.

Jetz, W., C. H. Sekercioglu, and K. Boehning-Gaese. 2008. The Worldwide Variation in Avian Clutch Size across Species and Space. Plos Biology **6**:2650-2657.

Owens, I. P. F. and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America **97**:12144-12148.

Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life history, sexual selection or ecology? Proceedings of the Royal Society B-Biological Sciences **266**:933-939.

Ramirez, L., J. A. F. Diniz-Filho, and B. A. Hawkins. 2008. Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. Global Ecology and Biogeography **17**:100-110.

Remsen, J. V. J. and S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Morrison, M. L., Et Al. (Ed.). Studies in Avian Biology, No. 13. Avian Foraging: Theory, Methodology, and Applications; International Symposium, Asilomar, California, USA, December 18-19, 1988. X+515p. Cooper Ornithological Society: Los Angeles, California, USA. Illus. Paper:144-160.

Sibly, R. M., C. C. Witt, N. A. Wright, C. Venditti, W. Jetz, and J. H. Brown. 2012. Energetics, lifestyle, and reproduction in birds. Proceedings of the National Academy of Sciences of the United States of America **109**:10937-10941.

Sick, H. 1997. Ornitologia Brasileira. Nova Fronteira, Rio de Janeiro.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithological Monographs:575-594.

Tewksbury, J. J., L. Garner, S. Garner, J. D. Lloyd, V. Saab, and T. E. Martin. 2006. Tests of landscape influence: Nest predation and brood parasitism in fragmented ecosystems. Ecology **87**:759-768.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. Trends in Ecology & Evolution **20**:402-409.

Table S1. Forest-dependent species recorded in the study system. We are given both scientific and common name and if it was recorded in-patches embedded in pasture or in coffee matrices. We also demonstrate functional traits used to measure functional diversity. Body size (in grams), clutch size (mean clutch size – minimum and maximum), net type (open, closed, semi-open, cavity), and diet: I (insectivorous), F (frugivorous), G (granivorous), N (nectarivorous), C (carnivorous), H (herbivorous).

Scientific name	Common name	Pasture	Coffee	Body size	Eggs (Min)	Eggs (Max)	Nest	I	F	G	N	C	H
Accipiter striatus	Sharp-shinned Hawk	X		174	3	5	open	1	0	0	0	3	0
Anabazenops fuscus	White-collared Foliage-gleaner	X	X	39	2	3	open	3	0	0	0	0	0
Arremon flavirostris	Saffron-billed Sparrow		X	28.5	3	3	closed	3	0	1	0	0	0
Arremon semitorquatus	Half-collared Sparrow	X		24.8	1	1	closed	3	0	1	0	0	0
Attila phoenicurus	Rufous-tailed Attila	X		34.5	3	4	cavity	3	1	0	0	0	0
Attila rufus	Grey-hooded Attila	X		43.4	3	4	cavity	3	1	0	0	0	0
Automolus leucophthalmus	White-eyed Foliage gleaner	X	X	35.5	3	4	cavity	3	0	0	0	0	0
Baryphthengus rufucapillus	Rufous-capped Motmot	X	X	175	2	3	cavity	3	1	0	0	3	0
Basileuterus culicivorus	Golden-crowned Warbler	X	X	10.3	2	4	closed	3	1	0	0	0	0
Basileuterus flaveolus	Flavescent Warbler		X	13	3	3	closed	3	0	0	0	0	0
Basileuterus leucoblepharus	White-browed Warbler	X	X	16.3	3	4	closed	3	0	0	0	0	0
Batara cinerea	Giant Antshrike	X		149	2	3	open	3	0	0	0	1	0
Cacicus chrysopterus	Golden-winged Cacique	X	X	32.8	2	4	closed	3	1	0	1	3	0
Campephilus robustus	Robust Woodpecker		X	200	2	3	cavity	3	1	0	0	0	0
Carpornis cucullata	Hooded Barryeater	X		75.7	1	1	open	1	3	0	0	0	0
Celeus flavescens	Blond-crested Woodpecker	X	X	150	2	4	cavity	3	1	0	0	0	0
Chamaeza campanisona	Short-tailed Antthrush		X	91.1	2	3	cavity	3	3	0	0	0	0

Chamaeza meruloides	Cryptic Antthrush	X	X	70.9	2	2	cavity	3	0	0	0	0	0
Chiroxiphia caudata	Blue Manakin	X	X	25.6	2	2	semi	2	3	0	0	0	0
Cissopis leverianus	Magpie Tanager	X		71	2	2	semi	1	3	0	0	0	0
Cnemotriccus fuscatus	Fuscous Flycather	X	X	11.9	3	3	semi	3	0	0	0	0	0
Conirostrum speciosum	Chestnut-vented Conebill	X	X	8.4	3	3	semi	3	0	0	3	0	0
Conopophaga lineata	Rufous Gnateater	X	X	22.1	2	2	semi	3	1	0	0	0	0
Corythopis delalandi	Southern Antpipit	X	X	14.9	2	3	closed	3	0	0	0	1	0
Cranioleuca pallida	Pallid Spinetail	X	X	11.5	2	3	closed	3	0	0	0	0	0
Crypturellus obsoletus	Brown Tinamou	X	X	482	4	5	open	3	0	3	0	0	0
Dendrocolaptes platyrostris	Planalto Woodcreeper	X	X	61.9	3	4	cavity	3	0	0	0	1	1
Dromoccoccys pavoninus	Pavonine Cucko	X		54	1	2	open	3	0	0	0	0	0
Drymophia rubricollis	Bertoni's Antbird	X	X	21.4	2	2	semi	3	0	0	0	0	0
Drymophila ferruginea	Ferrugineous Antbird	X	X	10.2	2	2	semi	3	0	0	0	0	0
Drymophila malura	Dusky-tailed Antbird	X	X	12.2	2	2	semi	3	0	0	0	0	0
Drymophila ochropyga	Ochre-rumped Antbird	X	X	16.3	2	2	semi	3	0	0	0	0	0
Drymophila squamata	Scaled Antbird	X		10.8	2	2	semi	3	0	0	0	0	0
Dysithamnus mentalis	Plain Antvireo	X	X	14	2	2	semi	3	1	0	0	0	0
Euphonia chalybea	Green-chinned Euphonia	X		19	3	3	closed	1	3	0	0	0	0
Euphonia pectoralis	Chestnut-bellied Euphonia	X		14.4	3	3	closed	1	3	0	1	0	0
Geotrygon montana	Ruddy Quail-dove	X		135	1	2	open	1	3	3	0	0	0
Geotrygon violacea	Violaceous Quail-dove	X		150	2	2	open	1	3	3	0	0	0
Grallaria varia	Variegated Antpitta	X	X	121.5	2	2	semi	3	0	0	0	0	0
Habia rubica	Red-crowed Ant-tanager	X		35.2	1	4	semi	3	1	0	0	0	0
Herpsilochmus longirostris	Large-billed Antwren		X	10.3	2	2	semi	3	0	0	0	0	0

Herpsilochmus rufimarginatus	Rufous-winged Antwren	X	X	10.4	2	2	semi	3	1	0	0	0	0
Hylophilus poicilotis	Rufous-crownd Greenlet	X	X	10	2	3	semi	3	1	0	0	0	0
Hypoedaleus guttatus	Spot-backed Antshrike	X	X	46	2	2	semi	3	0	0	0	0	0
Lathrotriccus euleri	Euler's Flycatcher	X	X	11	2	3	semi	3	0	0	0	0	0
Lepidocolaptes squamatus	Scaled Woodcreeper	X	X	27	2	2	cavity	3	0	0	0	0	0
Leptopogon amaurocephalus	Sepia-capped Flycatcher	X	X	10.7	2	2	closed	3	1	0	0	0	0
Leptotila rufaxilla	Grey-fronted Dove	X	X	155	1	2	open	1	1	3	0	0	0
Lochmias nematura	Sharp-tailed Streamcreeper	X	X	23	2	2	closed	3	0	0	0	0	0
Mackenziaena leachii	Large-tailed Antshrike	X	X	67.8	2	2	semi	3	0	0	0	1	0
Mackenziaena severa	Tufted Antshrike		X	51.3	2	2	semi	3	0	0	0	1	0
Malacoptila striata	Greater Crescent-chested Puffbird	X		44.1	2	3	cavity	3	0	0	0	1	0
Micrastur ruficapillus	Barred Forest-falcon		X	193.5	2	3	cavity	3	0	0	0	3	0
Micrastur semitorquatus	Collared Forest-falcon		X	643	2	3	cavity	0	0	0	0	1	0
Mionectes rufiventris	Grey-hooded Flycatcher	X	X	13.3	3	3	closed	3	3	0	0	0	0
Myiopagis caniceps	Grey Elaenia	X	X	10.3	2	2	semi	3	1	0	0	0	0
Myiornis auricularis	Eared-Pygmy-tyrant	X	X	5.3	2	3	closed	3	0	0	0	0	0
Myrmeciza squamosa	Squamate Antbird	X		18.5	2	2	semi	3	0	0	0	0	0
Odontophorus capueira	Spot-winged Wood-quail		X	396	3	5	cavity	1	3	3	0	0	0
Pachyramphus castaneus	Chestnut-crowned Becard	X	X	17.3	2	4	closed	3	1	0	0	0	0
Pachyramphus validus	Plain Becard	X		28.8	4	4	closed	3	0	0	0	0	0
Pachyramphus viridis	Green-backed Becard	X	X	21	2	4	closed	3	0	0	0	0	0
Penelope obscura	Dusky-legged Guan	X	X	960	2	3	semi	0	3	1	0	0	1
Philydor rufum	Buff-fronted Foliage-gleaner	X	X	32.5	2	3	cavity	3	0	0	0	0	0
Phyllomyias fasciatus	Planalto Tyrannulet	X	X	10.5	2	2	semi	3	1	0	0	0	0

Phylloscartes ventralis	Mottle-cheeked Tyrannulet	X	X	8.1	3	3	closed	3	0	0	0	0	0
Platyrinchus mystaceus	White-throated Spadebill	X	X	10.2	2	2	semi	3	0	0	0	0	0
Poecilotriccus plumbeiceps	Ochre-faced Tody-flycatcher	X	X	7.4	2	3	closed	3	0	0	0	0	0
Pogonotriccus eximius	Southern Bristle-tyrant	X		6.8	3	3	closed	3	0	0	0	0	0
Psilorhamphus guttatus	Spotted Bamboowren	X		22.5	2	2	open	3	0	0	0	0	0
Pteroglossus bailloni	Saffron Toucanet	X		139	2	3	cavity	0	3	0	0	1	0
Pyriglena leucoptera	White-shouldered Fire-eye	X	X	28.8	2	2	closed	3	0	0	0	0	0
Pyroderus scutatus	Red-ruffed Fruitcrow	X	X	372.5	1	1	semi	1	3	0	0	0	0
Pyrrhocoma ruficeps	Chestnut-headed Tanager	X	X	15	2	3	semi	3	0	0	0	0	0
Saltator fuliginosus	Black-throated Grosbeak		X	50.8	2	3	semi	1	1	0	0	0	3
Saltator maxillosus	Thick-billed Saltator		X	59.9	3	3	semi	0	3	3	0	0	0
Schiffornis virescens	Greenish Mourner	X	X	24.8	2	2	semi	3	1	0	0	0	0
Sclerurus scansor	Rufous-breasted Leaftosser	X	X	37.4	2	3	cavity	3	0	0	0	0	0
Sirystes sibilator	Sirystes	X	X	32	2	4	cavity	3	1	0	0	0	0
Sittasomus griseicapillus	Olivaceous Woodcreeper	X	X	13.5	3	3	cavity	3	1	0	0	0	0
Sporophila frontalis	Buffy-fronted Seedater	X		14.3	2	3	semi	1	0	3	0	0	0
Synallaxis cinerascens	Grey-bellied Spinetail	X	X	13.2	3	3	closed	3	0	0	0	0	0
Synallaxis ruficapilla	Rufous-capped Spinetail	X	X	13.9	1	2	closed	3	0	0	0	0	0
Syndactyla rufosuperciliata	Buff-browed Foliage-gleaner	X	X	27.7	2	4	cavity	3	0	0	0	0	0
Tangara cyanoventris	Gilt-edged Tanager	X	X	16.5	2	2	semi	3	3	0	0	0	0
Tangara desmaresti	Brassy-breasted Tanager	X		19.8	2	2	semi	1	3	0	0	0	0
Terenura maculata	Streak-capped Antwren	X		6.5	2	2	semi	3	0	0	0	0	0
Thamnophilus caerulescens	Variable Antshrike	X	X	21.4	2	3	semi	3	1	1	0	0	0
Tolmomyias sulphurescens	Yellow-olive Flycatcher	X	X	14.8	2	3	closed	3	1	0	0	0	0

Trichothraupis melanops	Black-goggled Tanager	X	X	24.3	3	3	semi	3	1	0	0	0	0
Trogon rufus	Black-throated Trogon	X		55.5	2	2	cavity	3	1	0	0	0	1
Trogon surrucura	Southern Surucua Trogon	X	X	73.3	2	4	cavity	3	1	0	0	0	1
Turdus albicollis	White-throated Thrush	X	X	50	2	3	semi	3	1	0	0	0	0
Turdus flavipes	Yellow-legged Thrush	X		51.2	2	2	semi	1	3	0	0	0	0
Xenops rutilans	Streaked Xenops	X	X	12.8	2	3	cavity	3	0	0	0	0	0
Xyphorhynchus fuscus	Lesser Woodcreeper	X	X	21.8	2	3	cavity	3	0	0	0	0	0

Table S2: Phylogenetic signal (λ) measured for all functional traits used to calculate functional richness. It ranges from 0 to 1, with values closer to 1 indicating higher phylogenetic signal. Log likelihood of estimates (logL) and respective p-values are also shown.

Functional trait	λ	logL	*p-value*
Low-permeability matrix			
Body size	1.006	- 461.9	< 0.05*
Number of eggs (Min)	0.56	- 75.67	> 0.05
Number of eggs (Max)	0.82	- 101.12	< 0.001*
Insectivorous	0.78	- 88.15	< 0.001*
Frugivorous	0.97	- 111.65	< 0.001*
Granivorous	0.84	- 67.74	< 0.001*
Nectarivorous	0.02	- 32.65	> 0.05
Carnivorous	1	- 66.73	< 0.001*
Herbivorous	0.87	27.33	< 0.001*
Nest type	-	-	< 0.05*
Higher-permeability matrix			
Body size	1.004	- 415.53	< 0.05*
Number of eggs (Min)	0.42	- 51.92	> 0.05
Number of eggs (Max)	0.82	- 76.71	< 0.001*
Insectivorous	0.76	- 72.45	< 0.001*
Frugivorous	0.67	- 93.85	< 0.01*
Granivorous	1.004	- 56.87	< 0.01*
Nectarivorous	0.0005	- 30.35	> 0.05
Carnivorous	0.79	- 65.02	< 0.05*
Herbivorous	0.0006	- 36.1	> 0.05
Nest type	-	-	< 0.05*

Table S3. Diversity indexes calculated for each sampling point in both types of matrix composition: P (pasture matrices), C (coffee matrices). Taxonomic diversity (TD), Functional diversity (FD), Phylogenetic diversity (PD), Phylogenetic diversity standard effect size (PD$_{ses}$).

Landscape id	Sample Id	Matrix	Forest cover	TD	FD	PD	PD$_{ses}$
P148	10	P	9.3477	12	0.08758	423.8329	-1.34942
P148	13	P	37.989	24	0.683532	791.2936	-1.22117
P148	17	P	33.5624	26	0.391556	889.0463	-0.84752
P148	18	P	73.9473	31	0.531186	1183.413	0.600347
P215	1	P	15.4375	12	0.758342	592.6722	0.386128
P215	4	P	47.0613	6	0.072987	297.1179	-0.61391
P215	30	P	39.5115	19	0.724278	865.6926	1.074608
P215	35	P	37.8839	16	0.873541	711.3956	0.530675
P220	0	P	48.3349	30	0.784038	1086.072	-0.10009
P220	7	P	15.0401	12	0.671803	511.8779	-0.56818
P220	8	P	27.1422	17	0.760976	702.1461	-0.29161
P220	19	P	33.6789	27	0.813966	1058.016	0.499638
P263	0	P	7.6464	13	0.112096	521.2697	-0.89694
P263	2	P	3.5751	5	0.07792	276.3014	-0.15352
P263	5	P	7.4995	12	0.095568	449.2117	-1.38865
P263	9	P	22.8289	18	0.703791	799.401	0.424935
P266	1	P	7.7327	15	0.495167	693.1343	0.296333
P266	12	P	12.7421	12	0.084	485.3885	-0.94628
P266	22	P	53.569	31	0.506595	1059.34	-0.55955
P266	28	P	37.6157	24	0.738019	891.3725	-0.25953
P282	9	P	28.4045	13	0.116982	557.0635	-0.43867
P282	13	P	18.3364	13	0.677352	580.623	-0.19828
P282	19	P	19.6823	14	0.29908	579.7223	-0.56964
P282	38	P	8.9832	5	0.077472	265.0476	-0.40372
P291	1	P	43.4559	27	0.764604	1102.885	0.981935
P291	11	P	26.8632	34	0.815742	1326.859	-1.14862
P291	17	P	61.8058	28	0.478021	1162.321	1.261586
P291	24	P	39.7145	31	0.799539	1194.742	0.4571
P317	0	P	48.4034	35	0.796249	1466.428	0.428682
P317	20	P	37.8239	33	0.840493	1153.48	-0.17685
P317	22	P	63.4434	20	0.490288	734.822	-0.55378

P317	24	P	64.767	29	0.888481	962.3952	-1.02453
P329	0	P	14.1903	7	0.436073	444.6526	1.105888
P329	1	P	23.2632	14	0.123947	487.9376	-1.25454
P329	7	P	17.9752	9	0.446554	461.7902	0.099962
P329	10	P	35.9127	10	0.099351	386.4565	-1.33615
P333	2	P	22.4375	8	0.264949	421.2528	0.077191
P333	3	P	4.6893	4	0.050682	228.5567	-0.18853
P333	4	P	10.0153	10	0.085224	358.1529	-1.7795
P333	8	P	21.3022	13	0.70361	571.2279	-0.32499
P335	1	P	28.8896	25	0.31166	806.6443	-1.42766
P335	2G	P	60.7647	27	0.662228	1042.367	0.32597
P335	2P	P	9.1559	12	0.503169	553.6834	-0.16131
P335	20	P	26.6026	22	0.459062	935.5569	0.826638
P359	2	P	12.0913	16	0.492966	715.8758	0.167607
P359	4	P	12.1113	17	0.513336	766.1737	0.731784
P359	13	P	25.2469	15	0.423237	694.4524	0.319859
P359	20	P	32.9214	24	0.790836	922.5029	0.026524
P399	0	P	43.8317	18	0.145859	664.066	-1.02143
P399	9	P	20.1038	17	0.894842	730.2237	-0.00766
P399	11	P	50.2616	10	0.411276	547.3801	0.785441
P399	18	P	20.206	14	0.744706	600.4185	-0.35029
P02	0	C	57.51	24	0.729168	846.3368	-0.16705
P02	1	C	43.33	24	0.183187	715.3724	-1.55905
P02	2	C	51.41	21	0.384616	833.1117	0.519503
P02	3	C	51.59	32	0.408441	967.5554	-0.76206
P09	0	C	16.76	20	0.117311	625.4373	-1.45899
P09	1	C	14.03	15	0.119752	463.5406	-1.74476
P09	2	C	19.02	16	0.33346	449.6709	-2.20368
P09	3	C	12.65	17	0.123521	573.6657	-1.16744
P10	0	C	26.33	25	0.718258	831.1365	-0.64192
P10	1	C	21.69	25	0.754309	806.5829	-0.90568
P10	2	C	28.62	37	0.776842	1061.041	-1.31199
P10	3	C	44.39	24	0.733878	810.2877	-0.58864
P11	0	C	51.8634	27	0.748132	890.4791	-0.62033
P11	1	C	54.2145	29	0.421998	735.6826	-2.68516
P11	2	C	33.3042	23	0.285159	660.2209	-1.871
P11	3	C	7.33	13	0.599304	516.6151	-0.49569
P12	0	C	35.95	24	0.637079	814.3311	-0.5849
P12	1	C	35.63	15	0.111686	452.4793	-1.91868

P12	2	C	57.7797	22	0.278981	667.8609	-1.57284
P12	3	C	52.91	23	0.638526	814.9062	-0.28909
P19	0	C	37.5803	22	0.149392	554.0372	-2.75587
P19	1	C	72.82	30	0.573062	962.04	-0.58318
P19	2	C	50.0458	30	0.677276	1040.757	0.196698
P19	3	C	62.23	29	0.498648	1077.807	0.819842
P26	0	C	18.9986	25	0.355611	861.7666	-0.40358
P26	1	C	16.1737	34	0.385641	808.0214	-3.18068
P26	2	C	21.3872	28	0.73358	913.5376	-0.60991
P26	3	C	36.6065	36	0.59899	1144.407	-0.2471
P27	0	C	36.8156	30	0.643808	981.4384	-0.43713
P27	1	C	30.0334	28	0.68425	861.835	-1.13973
P27	2	C	40.8874	23	0.60696	820.3381	-0.18831
P27	3	C	43.6138	27	0.500844	743.176	-2.02309
P28	0	C	25.1072	40	0.737573	1056.336	-2.20797
P28	1	C	15.19	27	0.356413	726.7271	-2.28816
P28	2	C	34.7123	25	0.585223	954.2387	0.650307
P28	3	C	40.1279	29	0.333075	925.3192	-0.79667
P30	0	C	26.21	21	0.592802	698.4994	-0.60193
P30	1	C	29.9278	22	0.198978	716.3047	-1.01627
P30	2	C	8.8915	12	0.088008	444.2675	-0.9942
P30	3	C	34.02	31	0.724812	913.3035	-1.32133

Figure S1. Illustration of matrix composition in studied areas. **A**: coffee matrix; **B**: pasture matrix.
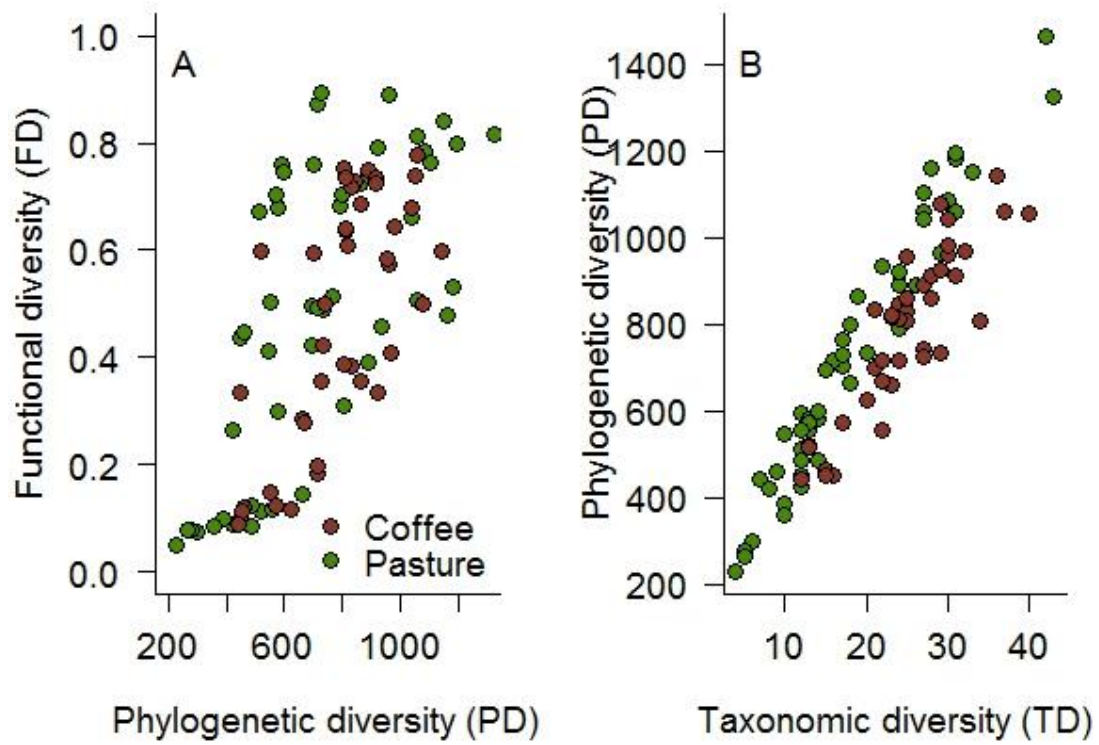
Figure S2. (**A**) Correlation between phylogenetic (PD) and functional diversity (FD) and between taxonomic (TD) and phylogenetic diversity (**B**) in both contexts of matrix permeability (pasture and coffee plantations).
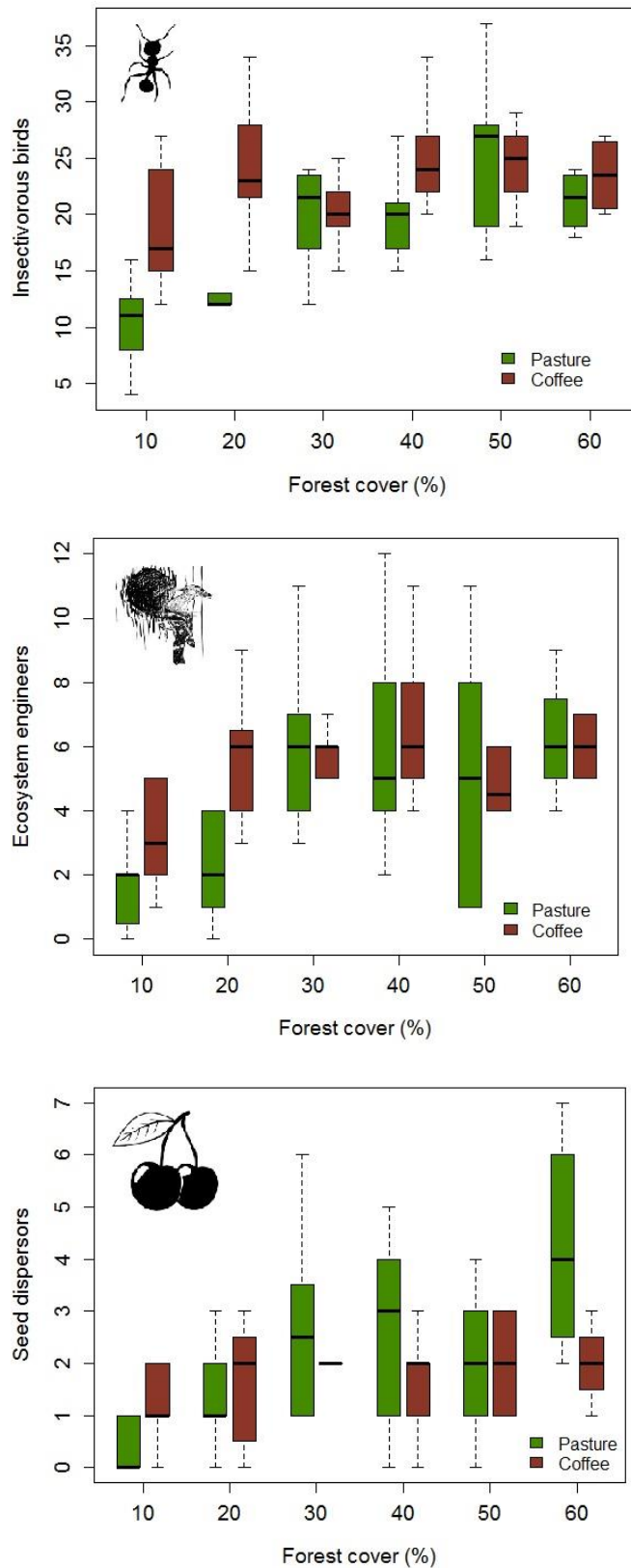
Figure S3: Loss of bird functions along the forest cover gradient. Avian insectivores, ecosystem engineers, and seed dispersers are shown.
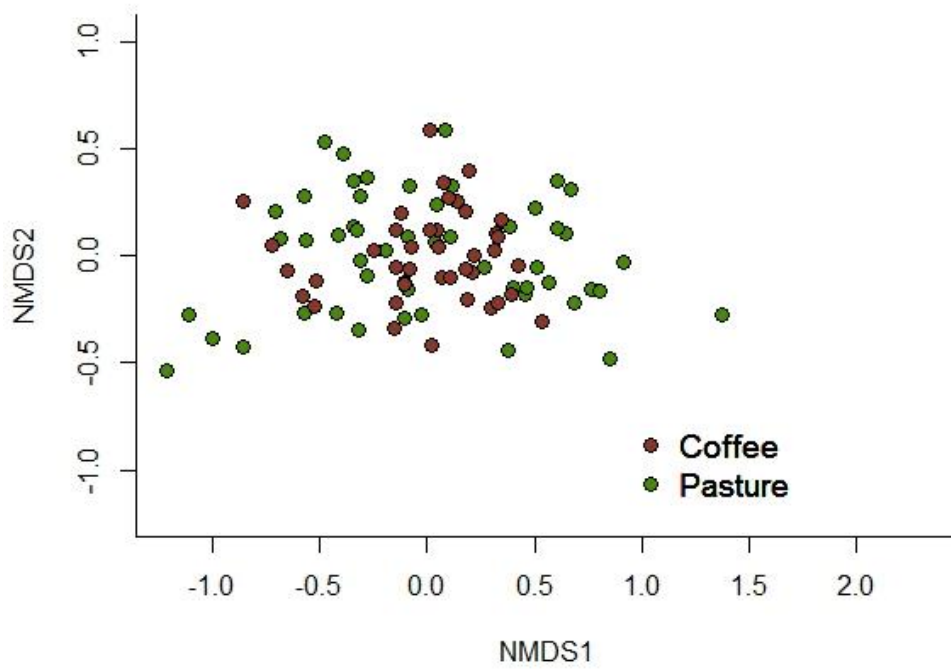
Figure S4. Bray-Curtis dissimilarity between bird assemblages in forest patches embedded in both coffee and pasture matrices.

Chapter 3

How does landscape structure modulate avian cross-habitat spillover?

Andrea Larissa Boesing, Elizabeth Nichols, Jean Paul Metzger

Abstract

Natural habitats adjacent to crop fields are often considered source habitats of species that provide beneficial regulating ecosystem services through cross-habitat spillover, such as pest control and pollination. Both matrix composition and landscape configuration should influence spillover by controlling organismal ability to disperse through landscapes, influencing species functional connectivity, and affecting the provision of additional or supplementary resources that impact organism survival. Using a well-replicated study design across 23 independent landscapes (2 km radius), we sampled avian communities in both forest patches and adjacent agricultural matrices across a landscape-level forest cover gradient (9-54%) and in two contexts of matrix permeability: lower-permeability (cattle pastures, N= 13) and higher-permeability (sun coffee plantations; N = 10). We expected that spillover would be intensified in coffee matrices and at intermediated amounts of forest cover, as landscape-level edge density peaks at intermediate forest cover. We found that 24% of the forest-dependent species pool was capable of spilling over into coffee matrices, while spillover was nearly non-existent in pasture matrices. The number of forest-dependent bird individuals spilling over into coffee matrices is intensified in landscapes with high edge density, however this effect was heightened in landscapes with low forest cover. This unexpected result may be due to higher resource competition at smaller native habitat amounts, compelling individuals to move to areas of lower density or because edge density increases functional connectivity and provides better access to different resources types. The few records of birds travelling among patches through pasture matrices occurred exclusively in highly forested landscapes. We present strong evidence that matrix permeability is a key factor facilitating species spillover into agricultural matrices, and that a combination of edge density and habitat amount is especially important facilitating species spilling over into matrices. These results should be considered in efforts to plan or manage sustainable agricultural landscapes.

Key-words: Agricultural systems; Dispersal; Edge density; Forest cover; Landscape complementation; Landscape supplementation; Matrix composition.

Introduction

Cross-habitat spillover is defined as the exchange of materials or movement of organisms among different habitats, and encompasses both organismal dispersal and foraging that takes them from one distinct habitat type to another (Blitzer *et al.* 2012; Tscharntke *et al.* 2012). Cross-habitat spillover may have important impacts on ecosystem processes (McCoy *et al.* 2009), especially on food web dynamics through ecological coupling of consumers and resources (Holt 1996).

Cross-habitat spillover may occur in both directions, from native habitats to matrix (i.e. areas of non-habitat or less suitable habitat; Villard & Metzger 2014), and from matrix to native habitats (Rand *et al.* 2006; Lucey & Hill 2012; Frost *et al.* 2015; Schneider *et al.* 2016). In recent years, spillover from native habitat to matrix habitat has attracted particular scientific attention, as species that spill over into crop fields might provide beneficial regulating ecosystem services, such as pest control and crop pollination (Bianchi *et al.* 2006; Kremen *et al.* 2007). Spillover from native to agricultural patches has frequently been documented for native-habitat specialist pollinators (Ricketts *et al.* 2006; Livingston *et al.* 2013), invertebrates (Thies *et al.* 2005; Lucey & Hill 2012), avian predators (Bianchi *et al.* 2006; Maas *et al.* 2015; Boesing *et al.* in review), and small mammals (Estavillo *et al.* 2013). Given that spillover may provide key ecological services in agricultural fields, understanding the role of landscape structure on spillover regulation is an important component of efforts to design and manage multifunctional agricultural landscapes.

Spillover can be considered a connectivity process, acting at edges between different habitats (Rand *et al.* 2006). As both connectivity and edge effects are affected by landscape structure (Taylor *et al.* 1993; Fahrig 2002), and particularly by the composition of the surrounding matrix, it is expected that both landscape structure and matrix composition should affect cross-habitat spillover (Blitzer *et al.* 2012). More habitat cover is associated with increased species richness and abundance inside habitat patches (Martensen *et al.* 2012) and decreased isolation among patches (Fahrig 2003), which should favor cross-habitat spillover both due to the higher density of organisms in "source" habitat patches (Brudvig *et al.* 2009) as well as lower isolation, which should favor movement among habitat patches (Baguette *et al.* 2012). In addition, lower isolation facilitates supplementation

processes, defined as the capacity of the landscape to provide the same kind of resource in different neighboring patches in order to supplement the lack of sufficiently abundant resources in only one patch (Dunning *et al.* 1992). In this case, species needing a specific resource cannot be limited to one patch, and should thus move among several patches to obtain the necessary amount of resources (Villard & Metzger 2014).

Spillover should also be intensified in more complex or heterogeneous mosaics, where contact between native habitat and matrix is more frequent. Increased areas of contact between matrix and native habitat can enhance functional connectivity among different habitats (Perovic *et al.* 2010) and may also increase the propensity of individuals to leave their source habitat. Following this reasoning, spillover should be particularly favored at intermediate amounts of forest cover, when edge density usually reaches its peak (Fahrig 2003; Villard & Metzger 2014). However, spillover might be attenuated to some extent when edge contrasts between habitat and matrix reduce animal movement (Rand & Louda 2006).

Finally, spillover might be a function of the permeability of the matrix surrounding habitat patches. Empirical evidence suggests that dung beetles (Collinge & Palmer 2002), mammals (Estavillo *et al.* 2013), and birds (Boesing *et al.* In prep) are more likely to move into a low-contrast (high permeability) matrix (Gray *et al.* 2016). In addition to facilitating inter-patch movement of organisms, different kind of land uses in the matrix might provide additional or alternative foraging and nesting resources, contributing to landscape complementation processes, i.e. the capacity of a landscape to provide different kind of resources, usually located in different landscape units (Dunning *et al.* 1992). This means that not only a particular landscape composition, but also adequate spatial arrangement and heterogeneity are necessary in order to make the different types of resources functionally available (Villard & Metzger 2014).

Birds are an especially interesting group of organisms to test ideas about how landscape structure influences cross-habitat spillover from native habitats into agricultural matrices. As vagile organisms, birds can easily move between habitat patches and might benefit from resources pulses, moving from patches in which resources are no longer sufficient to other areas where resources are

available or even to establish new territories (Whelan *et al.* 2008). In addition, birds have a diverse range of functional traits, which allows them to use a variety of resources (Sekercioglu *et al.* 2016) and provide an associated diversity of ecosystem services (Whelan *et al.* 2008). While our understanding of the influence of landscape structure bird species composition inside native habitat patches (Banks-Leite *et al.* 2012; Martensen *et al.* 2012) and in different matrix types (Karp *et al.* 2013; Maas *et al.* 2015) is growing, how landscape structure and matrix composition influence avian-cross habitat spillover has not yet been rigorously tested.

We tested these ideas by relating three key aspects of landscape structure (native habitat cover, edge density, and matrix composition) to measures of avian-cross-habitat spillover, using a well-replicated and landscape-level study design. We collected data across 23 independent landscapes, spanning a gradient of tropical forest cover (6-54%), where forest patches were embedded in either low-permeability matrix habitat (i.e. cattle pasture), or high-permeability matrix (i.e. sun coffee plantations). We tested three related hypotheses: (1) that high-permeability matrices are associated with higher avian cross-habitat spillover; (2) that avian-cross habitat spillover is intensified at intermediate amounts of native habitat cover; and (3) avian cross-habitat spillover is intensified in landscapes with higher edge density.

Methods

Study region: Field data were collected in the northeast São Paulo Atlantic Plateau and in the South Minas Gerais Mogiana region in southeastern Brazil (Fig. 1). The study region has a subtropical climate (UNICAMP 2016), with annual mean temperature varying from 11.3°C (minimum, in the colder season April-September) to 27.7°C (maximum, in the warmer season October-March), and annual rainfall varying between 1,350 and 2,000 mm (Pompeu *et al.* 2009). The relief is hilly to mountainous, with elevation between 700-1700 m.a.s.l (Oliveira & Fontes 2000). The whole region was once covered by Atlantic Forest, a tropical forest domain with one of the highest rates of species diversity and endemism in the world (Myers *et al.* 2000; Brooks *et al.* 2002). However, after five centuries of human expansion (Joly *et al.* 2014), much of the region has been reduced to

fragments in early to medium stages of succession (Lira *et al.* 2012), and more than 80% of forest remnants are smaller than 50 ha (Ribeiro *et al.* 2009).

Landscape selection: Field sites were located in 23 1,256 ha (2 km radius) landscapes varying between 6 and 54% native forest cover (Fig. 1). All landscapes were constrained to be between 800 and 1,300 m.a.s.l on ferric red latosol or argisol soil, and to exclude major interstate highways and water reservoirs in order to control these potential confounding factors (Pasher *et al.* 2013). A minimum distance of 6 km between landscape centroids was maintained to guarantee spatial independence between landscapes. Land use and land cover in each 2 km focal landscape was mapped using high-resolution images (ArcGis 10.3 basemap imagery, DigitalGlobe satellites 2010-2011; scale of 1:5,000). Ten studied landscapes are located in a major traditional area for coffee production in Brazil, responsible for about one third of the whole Brazilian production (EMBRAPA 2016). The matrix in this region is composed mostly of sun coffee plantations, considered as a "high-permeability matrix" (Fig. S1A). The remaining 13 landscapes are situated in the Cantareira region, where the matrix is composed mostly of unmanaged cattle pastures (Fig. S1B), considered a "low-permeability matrix". The agricultural matrices within focal landscapes also contained other land use types (sugar cane, eucalyptus plantations, urban settlements), but in much smaller proportions than the main land use type.

Study sites and bird sampling: We selected four forest patches within each of the 23 focal landscapes (N = 92 forest patches) using a stratified random proportional selection process based on the largest fragment size, using Sampling Design tool in ArcGIS 10.1. We calculated the percentage of total forest cover represented by the largest forest fragment in each landscape and allocated that proportion of sampling sites to that fragment. For instance, if the largest fragment contained 50% of the landscape forest cover, 50% of sampling sites (N = 2) were located at this fragment, and 50% were randomly distributed across the remaining forest fragments larger than 2.5 ha. In each one of the 92 selected forest patches (varying from 2.5 to 571.9 ha), we randomly selected a sampling site along the forest-matrix interface and placed a sampling point to bird counting 100 m inwards forest from

the edge (100.92 ± 12.97 m) and another sampling point 100 m from the edge in the adjacent matrix (109.30 ± 30.37 m), creating a paired design with two sampling points per sampling site (Fig. 2). Each sampling site was spaced at minimum 800 m apart (1,591 ± 621 m).
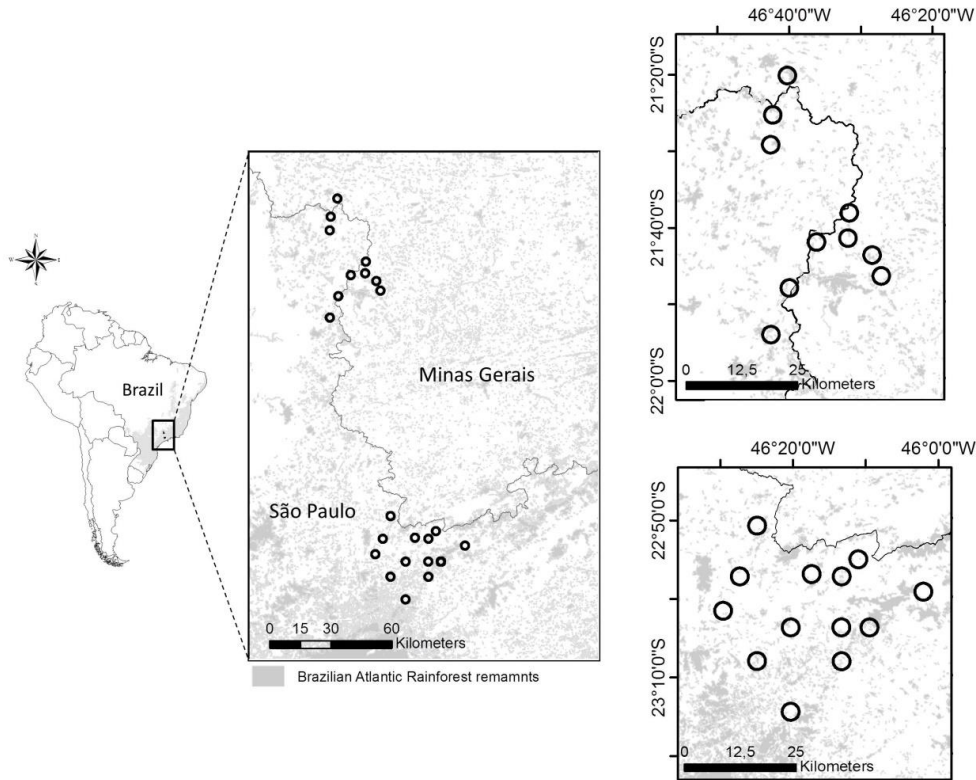

Figure 1. Study areas in the Brazilian Atlantic Forest domain between states of São Paulo and Minas Gerais. Ten 2-km radius landscapes within coffee matrices are shown in the top right-hand panel, and thirteen 2-km radius landscapes within pasture matrices are shown in the bottom right-hand panel.

Birds were counted using 15 min 50 m fixed-radius point counts (Blondel *et al.* 1970; Bibby *et al.* 2002), the most recognized method for sampling birds in Neotropical regions (Blake 2007). This method consists of counting all birds detected visually or aurally within a given radius from a sampling point within a period of 15 min. Species flying above the canopy or flying through the sample area were not recorded (Bibby *et al.* 2002). A total of 184 sampling points (92 inside forest patches; 92 in the adjacent matrix) were sampled, replicated four times within one year (between January-April and August-November 2014; N = 736 point counts). Studies using point counts in the Brazilian Atlantic Rainforest

indicate that four replicates is enough to record 80 – 90 % of bird species, including rare and inconspicuous species (Anjos 2003; Anjos *et al.* 2011). All point counts were performed within the periods that birds are more active: in the four hours after sunrise and the last hour before sunset (Lynch 1995; Esquivel & Peris 2008). In addition, each point count was sampled in different times (early in the morning and end of the afternoon), giving the same chance of detection for all species. All point counts were performed by the same observer (A.L.B.).
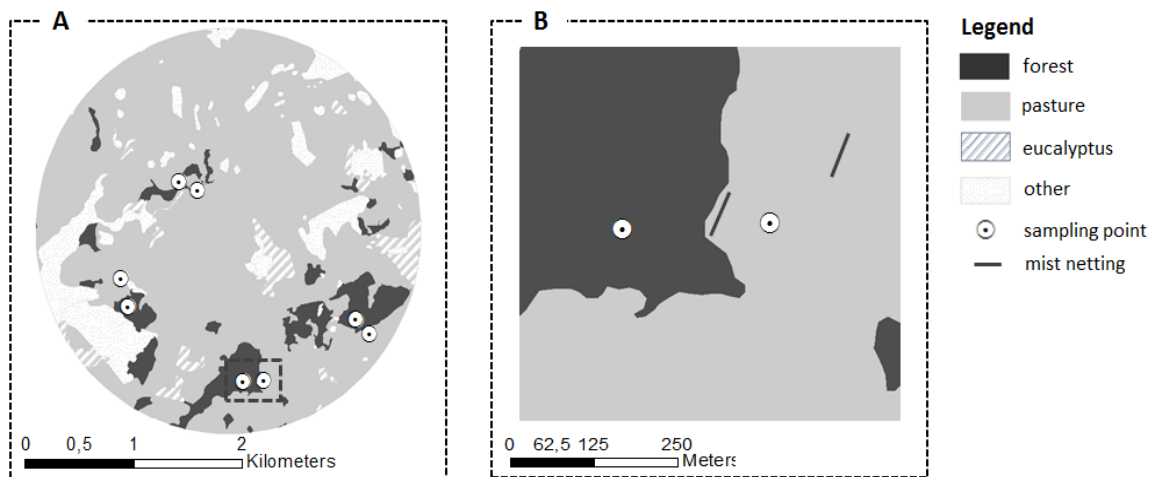
Figure 2. An example of sampling sites distribution in one of the study landscapes (low permeability matrix) with 30 % forest cover. In each landscape we placed four sampling sites with paired sampling points (**A**). A closer view of one sampling site (**B**) showing the spatial arrangement of two sampling points used for bird point counts, and two lines of mist nets used for catching birds.

We complemented bird point counts by performing captures using mist nets in pasture matrices in three 2 km focal landscapes (10, 30, and 50% of forest cover) in order to detect species potentially missed in point counts (Dunn & Ralph 2004). We performed this additional sampling only in pasture matrices, as very few birds were detected using point counts in this matrix, and mist netting could potentially determine whether species were traveling through pasture matrices, even if they were not spending time there. Mist nets were placed in 3 of the 4 sampling site locations within each landscape (i.e. using the same forest-matrix interface as for point counts; Fig. 2). We placed a line of seven mist nets (12 m length, 3 m high, 29 mm mesh) parallel to the edge of the sampled forest patch (~5 m from the edge, outside the forest), and another line ~150 m from the edge in the

137

pasture matrix. A total of 18 mist net lines (6 lines per landscape; 3 at edges; 3 in the matrix) were monitored for a period of six hours in the morning for two consecutive days, totaling 12,096 net-hours per sampling site (36,288 net-hours per landscape). Permission for data collection was obtained from the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA) under SISBIO number 46697-1.

Data analysis: We restricted all analyses to forest-dependent species (i.e. those species dependent of forest environments to breeding and survive; Sick 1997; del Hoyo *et al.* 2014). We defined 'spillover species' as those forest-dependent species that were recorded in both forest and the adjacent matrix in at least one sampling site. We quantified three measures of spillover, at both the community and species levels. First, we defined *spillover abundance* as the overall abundance of forest-dependent species in the matrix in relation to the adjacent forest patch. Second, we defined *spillover richness* as the overall number of forest-dependent species in the matrix in relation to the adjacent forest patch. Third, for the most abundant spillover species, we defined an *individual spillover abundance* as the proportion of a given species' abundance in the matrix habitat in relation to its abundance in the adjacent forest patch.

To test our first hypothesis that high-permeability matrices are associated with increased spillover of forest-dependent birds, we used a paired t-test comparing spillover richness and abundance between matrices (coffee plantations and cattle pastures) using data from the paired point counts. In order to test the relationship between spillover and native habitat cover and edge-density (second and third hypothesis), we modeled spillover richness, spillover abundance, and individual spillover as a function of forest cover and edge density in a series of generalized linear mixed models with Binomial error distributions, and incorporating focal landscape identity as random factor. We used forest cover as the percentage of forest cover around each sampling site within a 800 m radius buffer and edge density (m/ha), given by the sum of the lengths (m) of all edge segments of forest-non-forest divided by the total landscape area (using 800 m radius buffer) and multiplied by 10,000 to convert to hectares. We used 800 m as our definition of landscape spatial scale, as a series of evidence suggests that 800

m adequately reflects forest-dependent species' response to landscape processes in the Brazilian Atlantic Forest (Boscolo & Metzger 2009; Banks-Leite *et al.* 2011). For example, data on bird movement suggests that most movements are limited to under 400 m, with a small portion up to 1000 m (Marini 2010). In addition, most species in the study region are Passeriformes, a group with relatively reduced dispersal ability and smaller territories (Lira *et al.* 2012). In total, we built five predictive models (including a null model), incorporating the individual, additive, and interactive effects of forest cover and edge density, then performed model selection (AICc), to identify the best predictive model, considering models with ΔAICc ≤ 2 as equiprobable (Burnham & Anderson 2002).

To assess the differences in pasture captures in mist nets according to the three levels of forest cover (10%, 30%, 50%) we performed a one-way analysis of variance (ANOVA) using square root transformed spillover richness and abundance as a function of forest cover Homogeneity of variance was tested using the Barlett test.

All analyses were conducted in the R environment, version 3.3.1 (R Development Core Team 2016), using the packages "bbmle" (Bolker 2016), "lme4" (Bates *et al.* 2016), and "car" (Fox *et al.* 2016).

Results

We found 71 forest-dependent species in forest patches embedded in coffee matrices and 85 species in forest patches in pasture matrices (Table S1). In coffee matrices, we recorded 17 species spilling over, corresponding to 24% of the forest-dependent species pool. Over 83% of all these individuals (113 individuals in total; Table 1) were represented by only six species. In contrast, we observed only five individuals from five different species spilling over into pasture matrices (Table 1). Both spillover richness (t = -10.72, df = 42.11, p < 0.001; Fig. 3) and abundance (t = -9.76, df = 40.22, p < 0.001; Fig. 3) were significantly higher in coffee matrices.

Mist netting data confirmed that forest-dependent species rarely move into pasture matrices, as no species were caught in the nets placed deep (e.g. ≤ 150 m) within pastures. Of the 11 species and 28 individuals captured in mist nets at forest edges, around 60% of both species and individuals were caught in the most-forested landscapes (richness: $F_{1,7}$ = 6.87, p = 0.03; abundance: $F_{1,7}$ = 7.84 p = 0.02;

Fig. SM2). The majority of individuals caught in more forested landscapes were recorded leaving (as opposed to entering) the forest (n = 12). As native habitat cover decreased, the number of captures also decreased substantially, to only four captures in intermediate forest cover (in either direction), and three catches of a single species (Golden-crowned Warbler) entering the forest in the landscape with the least forest cover (Fig. 4).
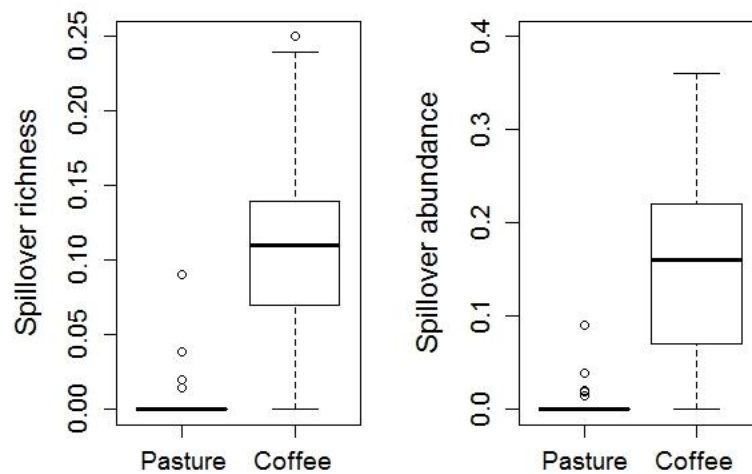
Figure 3. Boxplots of both spillover richness and abundance into coffee and pasture matrices. The median spillover richness was 0.11 (IQR = 0.07-0.14) in coffee matrices and 0 in pasture matrices. Median spillover abundance was 0.16 (IQR = 0.07-0.22) in coffee matrices and 0 in pasture matrices.

As bird occurrence in pasture matrices was practically non-existent (only five unique occurrences recorded in point counts), we tested our second and third hypotheses only in coffee matrices. There was no clear predictor of spillover richness into coffee matrices (Table 2). However, best predictive model of spillover abundance into coffee matrices was the interactive model of forest cover and edge density (Table 2; Fig. 5). Spillover abundance was intensified when edge density is higher, particularly when forest cover is low. There was no clear predictor of individual spillover abundance into coffee matrices for the six most abundant forest-dependent species (Table S2).

Discussion

We found strong evidence that matrix composition plays a key role in facilitating avian cross-habitat spillover into agricultural matrices. About 24% of the forest-dependent species pool could spill over into coffee matrices, while spillover was an exceptionally rare occurrence in pasture matrices, and occurred nearly exclusively in highly forested landscapes. Furthermore, we observed that edge density might positively affect spillover when matrix permeability is high, especially in less-forested landscapes. These findings highlight the importance of increasing the permeability of matrices surrounding native habitat patches in order to ensure species movement, and the importance of maintaining native habitat patches adjacent to crop fields to ensure the provision of ecosystem services.

Matrix permeability is a key factor influencing avian cross-habitat spillover, facilitating species movement into coffee matrices and acting as a barrier to spill over into pasture matrices. The structure of coffee plantations leads to a less-contrasting edge with native patches, which favors bird movement through the matrix, especially for understory insectivorous birds that compose the totality of birds spilling over to these plantations (see Table 1). Edge effects might be less pronounced when the matrix is structurally similar to the original habitat (Renjifo 2001), allowing some species (or subset of species) to cross this edge (Renjifo 2001; Perfecto *et al.* 2004; Hernandez *et al.* 2013), which is perceived as a soft edge (Duelli *et al.* 1990; Gascon *et al.* 1999).

On the other hand, pasture matrices present a very contrasting edge, which should discourage the movement of birds from forest to pasture. In addition to this barrier effect associated with their physical structure (Ries *et al.* 2004), pasture habitats may be higher risk for predation attempts on forest-dependent species (Silva 2012). Translocation experiments using a forest-dependent species (White-shouldered Fire-eye *Pyriglena leucoptera*) demonstrated higher predation risk in pastures relative to eucalyptus or corn matrices, linked to high predator density (Silva 2012). Nearly all of the bird movement we recorded through pasture patches occurred in short gap-crossing events, in highly-forested landscapes. While this corroborates the findings of other studies that have found that spillover intensifies with forest cover (e.g. Estavillo *et al.* 2013; Gonzalez *et al.* 2016), more

Table 1. Total abundance (number of individuals) of forest-dependent bird species spilling over into coffee matrices (using point counts*) and into pasture matrices (using both point counts* and mist nets**). Total abundance in-matrices and in-forest patches are given for both matrices. Diet: Ins (predominantly insectivorous), Fru (predominantly frugivorous); Foraging stratum: U (understory), M (midstory), C (canopy); Foraging behavior: Gle (Gleaning: gathering food items from a nearby substrate that can be reached without extension of legs or neck; no acrobatic movement involved); Pec (Pecking: driving the bill against the substrate to remove some of the exterior of the substrate); Pro (Probing: inserting the bill into cracks or holes in firm substrate or directly into softer substrates to capture hidden food); Han (Hanging: using legs and toes to suspend the body below the feet to reach food that cannot be reached from any other perched position); Lun (Lunging: those maneuvers in which food item is beyond the range of 'reach', but rapid leg movements rather than flight are used to approach and capture the prey); Fla (Flaking: brushing aside loose substrate with sideways, sweeping motions of the bill); Fly (Flycatching: attacking in a fluid movement without gliding, hovering or landing); Hov (Hovering: the bird hovers at the target substrate at the end of the sally); Sal (Sally-pouncing: landing briefly at the end of the flight to take food from a substrate). In-matrix (total abundance of forest-dependent species inside matrices), In-patch (total abundance of forest-dependent species in the adjacent forest patch), **B** (total abundance in the matrix in relation to the adjacent forest patch). Bird nomenclature follows del Hoyo *et al.* (2014).

| | | | | | | Total abundance | | | | | | |
| | | | | | | ------------Coffee--------------- | | | ------------------Pasture--------------- | | | |
Common name	Scientific name	Diet	Foraging stratum	Foraging behavior	Body size (grams)	In-matrix	In-Patch*	*B*	In-matrix	In-patch*	*B*	In-matrix**
Golden-crowned Warbler	*Basileuterus culicivorus*	Ins	U/M	Gle/Fly/Pro	10.3	21	252	0.083	1	326	0.003	7
White-shouldered Fire-eye	*Pyriglena leucoptera*	Ins	U	Gle/Sal/Lun	28.8	19	126	0.151	0	56	0.000	0
Plain Antvireo	*Dysithamnus mentalis*	Ins	U	Gle/Hov/Sal	14	17	166	0.102	1	163	0.006	0
Variable Antshrike	*Thamnophilus caerulescens*	Ins	U	Gle/Hov/Sal/Lun	21.4	16	95	0.168	0	82	0.000	0
Flavescent Warbler	*Basileuterus flaveolus*	Ins	U	Gle/Lun/Fla	13	13	62	0.210	0	0	-	0
Ochre-faced Tody-flycatcher	*Poecilotriccus plumbeiceps*	Ins	U	Hov/Sal	7.4	8	79	0.101	0	25	0.000	0
Rufous-crowned Greenlet	*Hylophilus poicilotis*	Ins	M/C	Gle/Han	10	3	10	0.300	0	3	0.000	0
Buff-browed Foliage-gleaner	*Syndactyla rufosuperciliata*	Ins	U	Gle	27.7	3	24	0.125	0	5	0.000	0

Common name	Scientific name											
Rufous Gnateater	*Conopophaga lineata*	Ins	U	Gle/Fla	22.1	2	98	0.020	0	106	0.000	1
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	Ins	M	Gle/Hov/Sal	14.8	2	101	0.020	1	99	0.010	1
Tufted Antshrike	*Mackenziaena severa*	Ins	U	Gle/Sal	51.3	2	16	0.125	0	0	-	0
Black-goggled Tanager	*Thricothraupis melanops*	Ins	U	Gle/Sal	24.3	2	75	0.027	0	46	0.000	4
Rufous-winged Antwren	*Herpsilochmus rufimarginatus*	Ins	M	Gle/Sal/Lun	10.4	1	34	0.029	0	4	0.000	0
Golden-winged Cacique	*Cacicus chrysopterus*	Ins	C	Pec/Pro/Han	32.8	1	1	1.000	0	2	0.000	0
Large-tailed Antshrike	*Mackenziaena leachii*	Ins	U	Gle/Fla	67.8	1	5	0.200	0	1	0.000	0
Euler's Flycatcher	*Lathrotriccus euleri*	Ins	U	Hov/Sal	11	1	77	0.013	0	53	0.000	0
Sharp-tailed Streamcreeper	*Lochmias nematura*	Ins	U	Gle/Pro/Fla	23	1	8	0.125	0	19	0.000	0
Streaked Xenops	*Xenops rutilans*	Ins	M	Pec/G/Han/Fla	12.8	0	67	0.000	1	51	0.020	0
Brassy-breasted Tanager	*Tangara desmaresti*	Fru	C	Gle/Sal/Han	19.8	0	0	-	1	15	0.067	3
Olivaceous Woodcreeper	*Sitassomus griseicapillus*	Ins	U/M	Gle/Pec	13.5	0	65	0.000	0	61	0.000	4
Swallow-tailed Manakin	*Chriroxiphia caudata*	Fru	U	Sal/Han	25.6	0	59	0.000	0	105	0.000	4
Sepia-capped Flycatcher	*Leptopogon amaurocephalus*	Ins	U	Hov/Sal	10.7	0	29	0.000	0	54	0.000	1
Serra do Mar Tyrant-Manakin	*Neopelma chrysolophum*	Fru	U	Sal/Han	14	0	0	-	0	0	-	1
White-necked Thrush	*Turdus albicollis*	Ins	U/M	Gle/Sal/Han/Fla/Lun	50	0	3	0.000	0	16	0.000	1
Yellow-legged Thrush	*Turdus flavipes*	Fru	M/C	Gle/Sal/Han/Lun	51.2	0	0	-	0	11	0	1

Table 2. Model selection for spillover richness and abundance in coffee matrices. *B* corresponds to spillover richness or abundance, AICc corresponds to the Akaike information criteria corrected for small samples, ΔAICc is the difference from the AICc of the best ranked model (ΔAICc), df is the degrees of freedom, and AICc ωi is the evidence weight. Coefficients and standard errors (se) of each model are given. Var 1 corresponds to the first predictor variable in the model, Var 2 corresponds to the second predictor variable, and Interaction represents the interaction between the two. Forest cover corresponds the percentage of forest cover within a 800 m radius buffer around each sampling site (7.33 – 72.8 %, min-max), and edge density corresponds to the total density (m/ha) of forest-non-forest edge within the same 800 m buffer (30.8 – 120.7 m/ha, min-max).

Spillover richness					Coefficients			
Model	AICc	ΔAICc	df	AICc ωi	Intercept (se)	Var 1 (se)	Var 2 (se)	Interaction (se)
B ~ Null	138.6	0	2	0.493	-2.185 (0.099)	-	-	-
B ~ Forest cover	140.4	1.8	3	0.198	-2.189 (0.099)	0.043 (0.103)	-	-
B ~ Edge density	140.6	2	3	0.181	-2.185 (0.099)	-0.002 (0.103)	-	-
B ~ Forest cover + Edge density	142.4	3.8	4	0.073	-2.189 (0.099)	0.043 (0.103)	-0.003 (0.102)	-
B ~ Forest cover* Edge density	143	4.4	5	0.055	-2.187 (0.100)	-0.002 (0.109)	0.099 (0.138)	-0.130 (0.110)

| Spillover abundance					Coefficients			
Model	AICc	ΔAICc	df	AICc ωi	Intercept (se)	Var 1 (se)	Var 2 (se)	Interaction (se)
B ~ Forest cover* Edge density	214.2	0	5	0.956	-1.980 (0.111)	0.010 (0.111)	0.481 (0.126)	-0.327 (0.115)
B ~ Edge density	221.4	7.2	3	0.026	-1.944 (0.088)	0.247 (0.083)	-	-
B ~ Forest cover + Edge density	222.3	8.1	4	0.017	-1.943 (0.084)	0.093 (0.086)	0.232 (0.081)	-
B ~ Null	228.2	14	2	<0.001	-1.924 (0.091)	-	-	-
B ~ Forest cover	228.4	14.2	3	<0.001	-1.927 (0.088)	0.117 (0.086)	-	-

work will be required to understand the biotic and abiotic challenges that bird species face when moving through high-contrasting matrices.
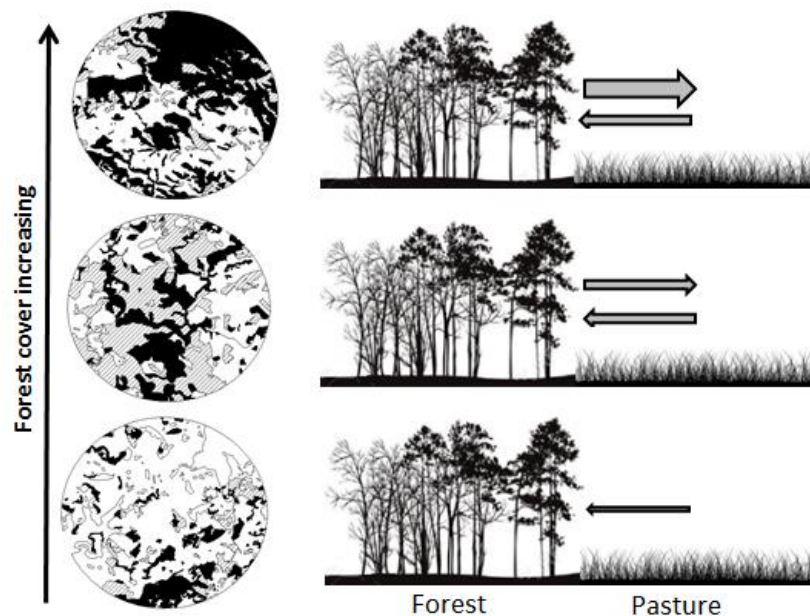
Figure 4. Number of birds caught at forest edges either leaving or entering (indicated by arrow direction) forest patches embedded in pasture matrices. The width of the arrow represents the intensity of the movement - the larger the width, the more species that were captured moving in that direction.

Spillover abundance into coffee matrices was explained by the interaction between forest cover and edge density. Under optimal conditions almost 30% of birds found in forest patches could spill over into coffee matrices, and spillover was maximized at high edge density, particularly in small amounts of habitat cover- an unexpected result. Since highest edge density occurs around 50% of habitat amount (Fig. S6), we expected intensified spillover at this point of the forest cover gradient. However, spillover was intensified in very deforested landscapes, composed by fewer small and isolated forest patches, with a relatively high remaining edge density. We posit that a combination of two processes is driving this pattern. First, at lower amounts of habitat cover, habitat patches do not have enough resources to maintain in-patch bird populations and some individuals need to leave and search for complementary resources in other habitat patches (landscape supplementation) or in the matrix (landscape complementation) in

order to fulfill their needs. This might suggest an in-patch density-dependent process occurring, which seems to be sustained by a positive correlation between abundance in-patch and the abundance inside coffee matrices (r = 0.18; Fig. SM3). As organisms' density accumulates inside forest patches, increased local competition for resources and interference between conspecifics may compel individuals to move to areas of lower density (Dunning *et al.* 1992).
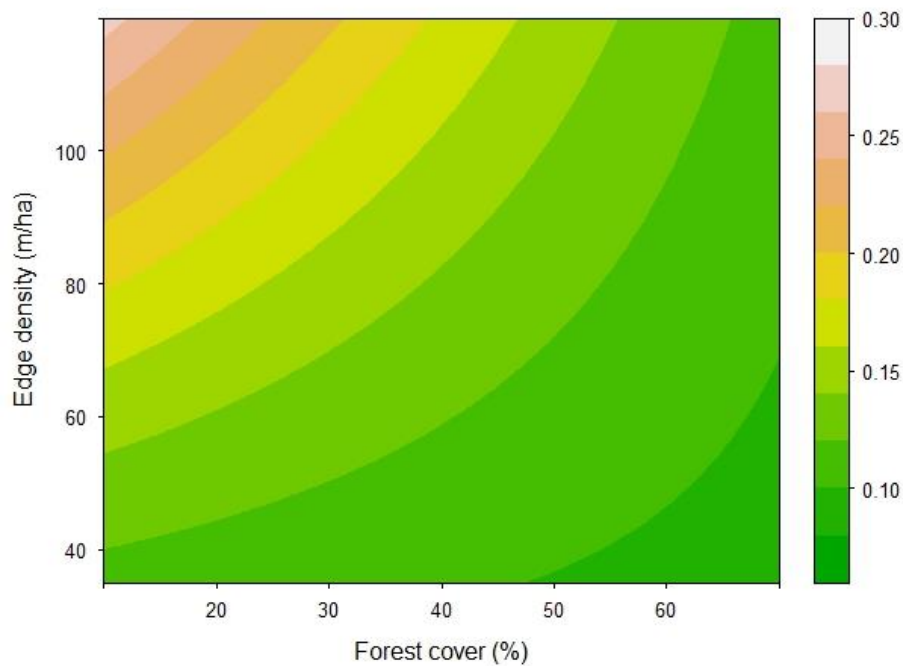
Figure 5. Predicted spillover abundance in coffee matrices, using the best ranked AICc model, which included an interaction between forest cover and edge density. The color scale bar to the right indicates the proportion of birds spilling over (from 0 to 0.30; spillover abundance).

Second, a higher edge density might facilitate species movement by increasing functional connectivity for those species that move through edges (Ries *et al.* 2004) or that use habitat edges more frequently (Metzger 2000), or by providing better access to different resource types (Dunning *et al.* 1992). A higher spillover to agricultural matrices was already observed for carabidae beetles in situations where edge density was high and edges presented low contrast (Duflot *et al.* 2016), suggesting that this process occur for different group of species. The original and unexpected result observed in our study sites is that edge density could be particularly important when habitat cover is low, combining thus a situation where birds are compiled to leave their original patches with a landscape

146

configuration that can favor the movement of more generalist species through the landscape.

We also found no evidence that landscape structure influenced neither spillover richness nor individual spillover. There are two potential explanations for this pattern. First, given the diversity of species-specific responses to landscape structure documented for tropical Passerines (Gascon *et al.* 1999; Renjifo 2001), the use of a composite metric like spillover richness may not capture opposing responses of different species. Second, other unmeasured landscape factors may influence spillover, especially as we also failed to find a relationship between our landscape variables and individual spillover. An exploration of the variation in individual spillover of the two most abundant species found in coffee matrices suggests that when habitat cover is high, both the Golden-crowned Warbler (*Basileuterus culicivorus*) and the Variable Antshrike (*Thamnophilus caerulescens*) are observed deeper inside the coffee matrix (Table S4, Fig. S4, S5), maybe as a result of decreased isolation among habitat patches which motivate its movement further its source patch.

Implications for provision of ecosystem services and landscape management

Understanding the role that habitat configuration and composition play in the movements of service-providing organisms is a key applied management concern in the face of current agricultural expansion. In a recent review, Boesing and colleagues (*in* review) compiled evidence that over 226 avian predators provide insect control services in agricultural landscapes across both temperate and tropical regions. Of these, over 35% of overall avian predators in tropical systems are dependent on native tropical forest habitat, clearly linking native habitat conservation and the maintenance of pest control services. In our study, most forest-dependent species spilling over into coffee matrices are small passerines and all the species are insectivores (see Table 1), which might have a substantial impact on the suppression of coffee pests. For example, the majority of spillover species were gleaning feeders that actively target prey on leaves, sticks, or ground - a feeding strategy that might target the coffee-borer beetle (*Hypothenemus hampei*). Another significant proportion of spillover species instead have a *sally-pouncing* foraging behavior, in which species strike their prey in the air - a foraging

147

strategy that might facilitate capture of the coffee-leaf miner (*Leucoptera coffeella*). Despite the remarkable lack of information regarding the identity of bird predators feeding on crop pests in Brazilian coffee plantations, two bird species (Golden-crowned Warbler *B. culicivorus* and Flavescent Warbler *B. flaveolus*) that were often recorded in our study system using coffee matrices, are congeners with an important predator of coffee-borer beetle in Central America (Rufous-capped Warbler, *B. rufifrons*; Karp *et al.* 2013), suggesting that spillover into coffee plantations can have an important effect in coffee pest control.

The observed pattern of spillover suggests that landscape configuration and matrix composition should be considered when planning agricultural landscapes in order to ensure ecosystem services provision. First, maintaining native habitat patches adjacent to crop fields preserves the source of individuals and increases landscape connectivity. There is evidence that habitat patches might provide many benefits in agricultural systems, providing not only avian-predators (Kellermann *et al.* 2008; Koh 2008), but also other natural enemies of insect pests (Lucey & Hill 2012; Gray *et al.* 2016), and different pollinators (Ricketts 2004; Monasterolo *et al.* 2015; Saturni *et al.* 2016). Second, increasing matrix permeability is key facilitating avian cross-habitat spillover. Even though large-scale conversion to high-quality matrices might not be a realistic option, even small changes to part of the matrix may be a feasible and effective action especially in terms of ecosystem service provision. Matrix permeability might also be increased through enhancement of crop diversity, and decreased land management intensity (Perfecto & Vandermeer 2010). Third, increasing landscape heterogeneity could be a key management strategy to facilitate cross-habitat spillover of habitat-dependent species and provide ecosystem services. Increasing elements' diversity in agricultural landscapes, such as stepping stones, strips, or even hedgerows, may be very beneficial for many forest-dependent species that can use these elements to move through matrices (Uezu *et al.* 2008).

Finally, it is important to highlight that avian predator-mediated ecosystem service provision will be influenced by both functional traits that shape bird dietary preferences, but also traits that influence a species' propensity for movement and willingness to cross gaps (Awade & Metzger 2008; Boscolo *et al.* 2008; Brudvig *et al.* 2009; Tscharntke *et al.* 2012). For instance, the Golden-crowned

Warbler, which often uses coffee plantations and is occasionally caught at the edges of pastures, might easily cross gaps smaller than 55 m (Awade & Metzger 2008). However, the White-shouldered Fire-eye, which has not been recorded in pasture matrices, does not cross gaps larger than 25 m (Awade 2008), reflecting different abilities to move across matrices. Moreover, species spilling over into coffee matrices are not the same ones travelling across pastures (with few exceptions of four shared species; see Table 1), demonstrating that the matrix can act as a semi-permeable filter. For instance, most spilling over species into coffee matrices are understory insectivores, while species traveling through pastures are often midstory or canopy fruit-eating species. Collecting and integrating information which species cross and use which matrix habitats and the functional traits associated with foraging will permit a more generalized understanding of the overall implications of matrix composition and landscape structure on avian-mediated ecosystem service provision in changing working landscapes.

Meaningful advancement towards the design and management of multifunctional landscapes capable of maintaining both biodiversity and agricultural production is a fundamental pillar of sustainable agricultural production systems (Balmford *et al.* 2012). This will critically require that we understand how the composition and configuration of working landscapes influence biodiversity. Here we contribute with evidence that (i) matrix composition plays a key role in facilitating bird movements into agricultural matrices, (ii) that edge density has important effects on spillover in more permeable matrices, especially in lower amounts of habitat, and (iii) habitat amount is important promoting spillover when matrix and native habitats have high-contrast. Highly-connected crop-noncrop mosaics may be best for long-term conservation of ecosystem services (Tscharntke *et al.* 2007). Continued efforts are necessary to more fully understand how and why landscape configuration and composition influence forest-dependent mobile organisms and biodiversity-mediated-ecosystem services especially in fragmented tropical landscapes.

Acknowledgments

Literature cited

Anjos L. (2003). A eficiência do método de amostragem por pontos de escuta na avaliação da riqueza de aves. *Revista Brasileira de Ornitologia*, 15, 239-243.

Anjos L., Collins C.D., Holt R.D., Volpato G.H., Mendonca L.B., Lopes E.V., Bocon R., Bisheimer M.V., Serafini P.P. & Carvalho J. (2011). Bird species abundance-occupancy patterns and sensitivity to forest fragmentation: Implications for conservation in the Brazilian Atlantic forest. *Biol Conserv*, 144, 2213-2222.

Awade M. (2008). A importância de uma visão probabilística da conectividade funcional na predição da incidência de uma espécie de ave em paisagens fragmentadas. In: *Departamento de Ecologia*. Universidade de São Paulo, p. 84.

Awade M. & Metzger J.P. (2008). Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral Ecol*, 33, 863-871.

Baguette M., Blanchet S., Legrand D., Stevens V.M. & Turlure C. (2012). Individual dispersal, landscape connectivity and ecological networks. *Biol Rev*, 1-17.

Balmford A., Green R. & Phalan B. (2012). What conservationists need to know about farming. *P Roy Soc B-Biol Sci*, 279, 2714-2724.

Banks-Leite C., Ewers R.M., Kapos V., Martensen A.C. & Metzger J.P. (2011). Comparing species and measures of landscape structure as indicators of conservation importance. *J Appl Ecol*, 48, 706-714.

Banks-Leite C., Ewers R.M. & Metzger J.P. (2012). Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology*, 93, 2560-2569.

Bates D., Maechler M., Bolker B., Walker S., Christensen R.H.B., Singmann H., Dai B., Grothendieck G. & Green P. (2016). lme4: Linear Mixed-Effects Models using

'Eigen' and S4. R package version 1.1-12. URL https://cran.r-project.org/web/packages/lme4/index.html

Bianchi F.J.J.A., Booij C.J.H. & Tscharntke T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *P Roy Soc B-Biol Sci*, 273, 1715-1727.

Bibby C.J., Burgess N.D., Hill D.A. & Mustoe S.H. (2002). *Bird Census Techniques*. Second Edition edn. Academic Press, London, UK.

Blake J.G. (2007). Neotropical forest bird communities: A comparison of species richness and composition at local and regional scales. *Condor*, 109, 237-255.

Blitzer E.J., Dormann C.F., Holzschuh A., Klein A.-M., Rand T.A. & Tscharntke T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agr Ecosyst Environ*, 146, 34-43.

Blondel J., Ferry C. & Frochot B. (1970). [The point count method to recording bird from hearing spots]. *Alauda*, 38, 55-71.

Boesing A.L., Nichols E. & Metzger J.P. (In prep). The role of matrix composition determining extinction thresholds of tropical avian communities

Boesing L., Nichols E. & Metzger J.P. (in review). Landscape structure and avian-mediated pest control.

Bolker B. (2016). bbmle: tools for general maximum likelihood estimation. R package version 1.0.18. Available at: https://cran.r-project.org/web/packages/bbmle/index.html. Accessed on October 26th 2016.

Boscolo D., Candia-Gallardo C., Awade M. & Metzger J.P. (2008). Importance of interhabitat gaps and stepping-stones for lesser woodcreepers (Xiphorhynchus fuscus) in the Atlantic forest, Brazil. *Biotropica*, 40, 273-276.

Boscolo D. & Metzger J.P. (2009). Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? *Landscape Ecol*, 24, 907-918.

Brooks T.M., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B., Rylands A.B., Konstant W.R., Flick P., Pilgrim J., Oldfield S., Magin G. & Hilton-Taylor C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conserv Biol*, 16, 909-923.

Brudvig L.A., Damschen E.I., Tewksbury J.J., Haddad N.M. & Levey D.J. (2009). Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *P Natl Acad Sci USA*, 106, 9328-9332.

Burnham K.P. & Anderson D.R. (2002). *Model selection and multimodel inference. A practical information-theoritical approach*. Springer, New York.

Collinge S.K. & Palmer T.M. (2002). The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. *Landscape Ecol*, 17, 647-656.

del Hoyo J., Elliott A., Sargatal J., Christie D.A. & Juana E. (2014). Handbook of the Birds of the World Alive. In. Linx Edicions Barcelons.

Duflot R., Ernoult A., Burel F. & Aviron S. (2016). Landscape level processes driving carabid crop assemblage in dynamic farmlands. *Popul Ecol*, 58, 265-275.

Dunn E.H. & Ralph C.J. (2004). The use of mist nets as a tool for bird population monitoring. *Studies in Avian Biology*, 29, 1-6.

Dunning J.B., Danielson B.J. & Pulliam H.R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, 65, 169-175.

EMBRAPA (2016). Available at: https://www.embrapa.br/. Accessed on October 26th 2016.

Esquivel M.A. & Peris S. (2008). Influence of time of day, duration and number of counts in point count sampling of birds in an Atlantic forest of Paraguay. *Ornitologia Neotropical*, 19, 229-242.

Estavillo C., Pardini R. & Bernardo da Rocha P.L. (2013). Forest Loss and the Biodiversity Threshold: An Evaluation Considering Species Habitat Requirements and the Use of Matrix Habitats. *Plos One*, 8.

Fahrig L. (2002). Effect of habitat fragmentation on the extinction threshold: A synthesis. *Ecol Appl*, 12, 346-353.

Fahrig L. (2003). Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol S*, 34, 487-515.

Fox J., Weisberg S., Adler D., Bates D., Baud-Bovy G., Ellison S., Firth D., Friendly M., Gorjanc G., Graves S., Heiberger R., Laboissieri R., Monette G., Murdoch D., Nilsson H., Ogle D., Ripley E., Venables W., Winsemius D. & Zeleis A. (2016). car: Companion to Applied Regression. R package version 2.1-3. Available at: https://cran.r-project.org/web/packages/car/index.html. Accessed in October 28th 2016.

Frost C.M., Didham R.K., Rand T.A., Peralta G. & Tylianakis J.M. (2015). Community-level net spillover of natural enemies from managed to natural forest. *Ecology*, 96, 193-202.

Gascon C., Lovejoy T.E., Bierregaard R.O., Malcolm J.R., Stouffer P.C., Vasconcelos H.L., Laurance W.F., Zimmerman B., Tocher M. & Borges S. (1999). Matrix habitat and species richness in tropical forest remnants. *Biol Conserv*, 91, 223-229.

Gonzalez E., Salvo A., Defago M.T. & Valladares G. (2016). A Moveable Feast: Insects Moving at the Forest-Crop Interface Are Affected by Crop Phenology and the Amount of Forest in the Landscape. *Plos One*, 11.

Gray C.L., Simmons B.I., Fayle T.M., Mann D.J. & Slade E.M. (2016). Are riparian forest reserves sources of invertebrate biodiversity spillover and associated ecosystem functions in oil palm landscapes? *Biol Conserv*, 194, 176-183.

Holt R.D. (1996). Food webs in space: an island biogeographic perspective. In: *Food webs: contemporary perspectives* (eds. Polis GA & Winemiller K). Chapman and Hall, pp. 313-323.

Joly C.A., Metzger J.P. & Tabarelli M. (2014). Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. *New Phytologist*, 204, 459-473.

Karp D.S., Mendenhall C.D., Sandi R.F., Chaumont N., Ehrlich P.R., Hadly E.A. & Daily G.C. (2013). Forest bolsters bird abundance, pest control and coffee yield. *Ecol Lett*, 16, 1339-1347.

Kellermann J.L., Johnson M.D., Stercho A.M. & Hackett S.C. (2008). Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms. *Conserv Biol*, 22, 1177-1185.

Koh L.P. (2008). Birds defend oil palms from herbivorous insects. *Ecol Appl*, 18, 821-825.

Kremen C., Williams N.M., Aizen M.A., Gemmill-Herren B., LeBuhn G., Minckley R., Packer L., Potts S.G., Roulston T.a., Steffan-Dewenter I., Vazquez D.P., Winfree R., Adams L., Crone E.E., Greenleaf S.S., Keitt T.H., Klein A.-M., Regetz J. & Ricketts T.H. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol Lett*, 10, 299-314.

Lira P.K., Ewers R.M., Banks-Leite C., Pardini R. & Metzger J.P. (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.

Livingston G., Jha S., Vega A. & Gilbert L. (2013). Conservation Value and Permeability of Neotropical Oil Palm Landscapes for Orchid Bees. *Plos One*, 8.

Lucey J.M. & Hill J.K. (2012). Spillover of Insects from Rain Forest into Adjacent Oil Palm Plantations. *Biotropica*, 44, 368-377.

Lynch J.F. (1995). Effects of point count duration, time-of-day, and aural stimuli on detectability of migratory and resident species in Quintana Roo, Mexico. In: *Monitoring bird population by point counts* (eds. Ralph CJ, Sauer JR & Droege S). USDA Forest Service General Technical Report PSW-GTR-149 Albany, CA, pp. 1-6.

Maas B., Tscharntke T., Saleh S., Putra D.D. & Clough Y. (2015). Avian species identity drives predation success in tropical cacao agroforestry. *J Appl Ecol*, 52, 735-743.

Marini M.A. (2010). Bird movement in a fragmented Atlantic Forest landscape. *Studies on Neotropical Fauna and Environment*, 45, 1-10.

Martensen A.C., Ribeiro M.C., Banks-Leite C., Prado P.I. & Metzger J.P. (2012). Associations of Forest Cover, Fragment Area, and Connectivity with Neotropical Understory Bird Species Richness and Abundance. *Conserv Biol*, 26, 1100-1111.

McCoy M.W., Barfield M. & Holt R.D. (2009). Predator shadows: complex life histories as generators of spatially patterned indirect interactions across ecosystems. *Oikos*, 118, 87-100.

Monasterolo M., Musicante M.L., Valladares G.R. & Salvo A. (2015). Soybean crops may benefit from forest pollinators. *Agr Ecosyst Environ*, 202, 217-222.

Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Oliveira A.T. & Fontes M.A.L. (2000). Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *Biotropica*, 32, 793-810.

Pasher J., Mitchell S.W., King D.J., Fahrig L., Smith A.C. & Lindsay K.E. (2013). Optimizing landscape selection for estimating relative effects of landscape variables on ecological responses. *Landscape Ecol*, 28, 371-383.

Perfecto I. & Vandermeer J. (2010). The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *P Natl Acad Sci USA*, 107, 5786-5791.

Perovic D.J., Gurr G.M., Raman A. & Nicol H.I. (2010). Effect of landscape composition and arrangement on biological control agents in a simplified agricultural system: A cost-distance approach. *Biol Control*, 52, 263-270.

Pompeu P., Costa M. & Fontes M.A. (2009). Classificação e apresentação dos parâmetros climáticos de Poços de Caldas - MG. In: *III Congresso Latino Americano de Ecologia* São Lourenço, Minas Gerais.

R Development Core Team (2016). R: A Language and Environment for Statistical Computing. In. R Foundation for Statistical Computing Vienna, Austria.

Rand T.A. & Louda S.A. (2006). Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. *Conserv Biol*, 20, 1720-1729.

Rand T.A., Tylianakis J.M. & Tscharntke T. (2006). Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol Lett*, 9, 603-614.

Renjifo L.M. (2001). Effect of natural and anthropogenic landscape matrices on the abundance of subandean bird species. *Ecol Appl*, 11, 14-31.

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.

Ricketts T.H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv Biol*, 18, 1262-1271.

Ricketts T.H., Williams N.M. & Mayfield M.M. (2006). Connectivity and ecosystem services: crop pollination in agricultural landscapes. In: *Connectivity for Conservation* (eds. Sanjayan M & Crooks K). Cambridge University Press Cambridge, UK, pp. 255–289.

Ries L., Fletcher R.J., Battin J. & Sisk T.D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annu Rev Ecol Evol S*, 35, 491-522.

Saturni F.T., Jaffé R. & Metzger J.P. (2016). Landscape structure influences bee community and coffee pollination at different spatial scales. *Agriculture, Ecosystems, and Environment*, 235, 1-12.

Schneider G., Krauss J., Boetzl F.A., Fritze M.A. & Steffan-Dewenter I. (2016). Spillover from adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural grasslands. *Oecologia*, In press.

Sekercioglu C.H., Wenny D.G. & Whelan C.J. (2016). *Why birds matter: avian ecological function and ecosystem services*. The University of Chicago Press, Chicago, London.

Sick H. (1997). *Ornitologia Brasileira*. Nova Fronteira, Rio de Janeiro.

Silva M.R.B. (2012). Efeitos de diferentes matrizes no risco de predação e na movimentação de uma ave florestal. In: *Departamento de Ecologia*. Universidade de São Paulo São Paulo, p. 64.

Taylor P.D., Fahrig L., Henein K. & Merriam G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 68, 571-573.

Thies C., Roschewitz I. & Tscharntke T. (2005). The landscape context of cereal aphid-parasitoid interactions. *P Roy Soc B-Biol Sci*, 272, 203-210.

Tscharntke T., Bommarco R., Clough Y., Crist T.O., Kleijn D., Rand T.A., Tylianakis J.M., van Nouhuys S. & Vidal S. (2007). Conservation biological control and enemy diversity on a landscape scale. *Biol Control*, 43, 294-309.

Tscharntke T., Tylianakis J.M., Rand T.A., Didham R.K., Fahrig L., Batary P., Bengtsson J., Clough Y., Crist T.O., Dormann C.F., Ewers R.M., Frund J., Holt R.D., Holzschuh A., Klein A.M., Kleijn D., Kremen C., Landis D.A., Laurance W., Lindenmayer D., Scherber C., Sodhi N., Steffan-Dewenter I., Thies C., van der Putten W.H. & Westphal C. (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol Rev*, 87, 661-685.

Uezu A., Beyer D.D. & Metzger J.P. (2008). Can agroforest woodlots work as stepping stones for birds in the Atlantic Forest region? . *Biodivers Conserv*, 17, 1907-1922.

UNICAMP C. (2016). Clima dos municipios paulistas. Available at: http://www.cpa.unicamp.br/outras-informacoes/clima-dos-municipios-paulistas.html. Accessed in October 28th 2016.

Villard M.-A. & Metzger J.P. (2014). Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. *J Appl Ecol*, 51, 309-318.

Whelan C.J., Wenny D.G. & Marquis R.J. (2008). Ecosystem services provided by birds. *Year in Ecology and Conservation Biology 2008*, 1134, 25-60.

Supplementary material

Table S1. Forest-dependent species recorded in the whole study region in forest patches embedded in both pasture and coffee matrices. Nomenclature follows del Hoyo *et al.* (2014).

Scientific name	Common name	Pasture	Coffee
Accipiter striatus	Sharp-shinned Hawk	X	
Anabazenops fuscus	White-collared Foliage-gleaner	X	X
Arremon flavirostris	Saffron-billed Sparrow		X
Arremon semitorquatus	Half-collared Sparrow	X	
Attila phoenicurus	Rufous-tailed Attila	X	
Attila rufus	Grey-hooded Attila	X	
Automolus leucophthalmus	White-eyed Foliage gleaner	X	X
Baryphthengus rufucapillus	Rufous-capped Motmot	X	X
Basileuterus culicivorus	Golden-crowned Warbler	X	X
Basileuterus flaveolus	Flavescent Warbler		X
Basileuterus leucoblepharus	White-browed Warbler	X	X
Batara cinerea	Giant Antshrike	X	
Cacicus chrysopterus	Golden-winged Cacique	X	X
Campephilus robustus	Robust Woodpecker		X
Carpornis cucullata	Hooded Barryeater	X	
Celeus flavescens	Blond-crested Woodpecker	X	X
Chamaeza campanisona	Short-tailed Antthrush		X
Chamaeza meruloides	Cryptic Antthrush	X	X
Chiroxiphia caudata	Blue Manakin	X	X
Cissopis leverianus	Magpie Tanager	X	
Cnemotriccus fuscatus	Fuscous Flycather	X	X
Conirostrum speciosum	Chestnut-vented Conebill	X	X
Conopophaga lineata	Rufous Gnateater	X	X
Corythopis delalandi	Southern Antpipit	X	X
Cranioleuca pallida	Pallid Spinetail	X	X
Crypturellus obsoletus	Brown Tinamou	X	X
Dendrocolaptes platyrostris	Planalto Woodpcreeper	X	X
Dromoccoccys pavoninus	Pavonine Cucko	X	
Drymophia rubricollis	Bertoni's Antbird	X	X
Drymophila ferruginea	Ferrugineous Antbird	X	X
Drymophila malura	Dusky-tailed Antbird	X	X
Drymophila ochropyga	Ochre-rumped Antbird	X	X
Drymophila squamata	Scaled Antbird	X	
Dysithamnus mentalis	Plain Antvireo	X	X
Euphonia chalybea	Green-chinned Euphonia	X	
Euphonia pectoralis	Chestnut-bellied Euphonia	X	
Geotrygon montana	Ruddy Quail-dove	X	
Geotrygon violacea	Violaceous Quail-dove	X	
Grallaria varia	Variegated Antpitta	X	X

Habia rubica	Red-crowed Ant-tanager	X	
Herpsilochmus longirostris	Large-billed Antwren		X
Herpsilochmus rufimarginatus	Rufous-winged Antwren	X	X
Hylophilus poicilotis	Rufous-crownd Greenlet	X	X
Hypoedaleus guttatus	Spot-backed Antshrike	X	X
Lathrotriccus euleri	Euler's Flycatcher	X	X
Lepidocolaptes squamatus	Scaled Woodcreeper	X	X
Leptopogon amaurocephalus	Sepia-capped Flycatcher	X	X
Leptotila rufaxilla	Grey-fronted Dove	X	X
Lochmias nematura	Sharp-tailed Streamcreeper	X	X
Mackenziaena leachii	Large-tailed Antshrike	X	X
Mackenziaena severa	Tufted Antshrike		X
Malacoptila striata	Greater Crescent-chested Puffbird	X	
Micrastur ruficapillus	Barred Forest-falcon		X
Micrastur semitorquatus	Collared Forest-falcon		X
Mionectes rufiventris	Grey-hooded Flycatcher	X	X
Myiopagis caniceps	Grey Elaenia	X	X
Myiornis auricularis	Eared-Pygmy-tyrant	X	X
Myrmeciza squamosa	Squamate Antbird	X	
Odontophorus capueira	Spot-winged Wood-quail		X
Pachyramphus castaneus	Chestnut-crowned Becard	X	X
Pachyramphus validus	Plain Becard	X	
Pachyramphus viridis	Green-backed Becard	X	X
Penelope obscura	Dusky-legged Guan	X	X
Philydor rufum	Buff-fronted Foliage-gleaner	X	X
Phyllomyias fasciatus	Planalto Tyrannulet	X	X
Phylloscartes ventralis	Mottle-cheeked Tyrannulet	X	X
Platyrinchus mystaceus	White-throated Spadebill	X	X
Poecilotriccus plumbeiceps	Ochre-faced Tody-flycatcher	X	X
Pogonotriccus eximius	Southern Bristle-tyrant	X	
Psilorhamphus guttatus	Spotted Bamboowren	X	
Pteroglossus bailloni	Saffron Toucanet	X	
Pyriglena leucoptera	White-shouldered Fire-eye	X	X
Pyroderus scutatus	Red-ruffed Fruitcrow	X	X
Pyrrhocoma ruficeps	Chestnut-headed Tanager	X	X
Saltator fuliginosus	Black-throated Grosbeak		X
Saltator maxillosus	Thick-billed Saltator		X
Schiffornis virescens	Greenish Mourner	X	X
Sclerurus scansor	Rufous-breasted Leaftosser	X	X
Sirystes sibilator	Sirystes	X	X
Sittasomus griseicapillus	Olivaceous Woodcreeper	X	X
Sporophila frontalis	Buffy-fronted Seedater	X	
Synallaxis cinerascens	Grey-bellied Spinetail	X	X
Synallaxis ruficapilla	Rufous-capped Spinetail	X	X
Syndactyla rufosuperciliata	Buff-browed Foliage-gleaner	X	X
Tangara cyanoventris	Gilt-edged Tanager	X	X

Tangara desmaresti	Brassy-breasted Tanager	X	
Terenura maculata	Streak-capped Antwren	X	
Thamnophilus caerulescens	Variable Antshrike	X	X
Tolmomyias sulphurescens	Yellow-olive Flycatcher	X	X
Trichothraupis melanops	Black-goggled Tanager	X	X
Trogon rufus	Black-throated Trogon	X	
Trogon surrucura	Southern Surucua Trogon	X	X
Turdus albicollis	White-throated Thrush	X	X
Turdus flavipes	Yellow-legged Thrush	X	
Xenops rutilans	Streaked Xenops	X	X
Xyphorhynchus fuscus	Lesser Woodcreeper	X	X

Table S2. Model selection for individual spillover abundance for the six most abundant species that spill over into coffee matrices. *B* corresponds to individual spillover, AICc corresponds to the Akaike Information Criteria corrected to small samples, ΔAICc is the difference between AICc from the best ranked model (ΔAICc), df is the degrees of freedom, and AICc ωi is the evidence weight. Coefficients and standard errors (se) of each model are given. Var 1 corresponds to the first predictor variable in the model, Var 2 corresponds to the second predictor variable, and Interaction represents the interaction between the two. Forest cover corresponds to the percentage of forest cover around each sampling site within 800 m radius buffer (7.33 – 72.8%, min-max), and edge density corresponds to the total area in hectares of forest-non-forest edge / area within the same 800 m buffer (30.8 – 120.7 m/ha, min-max).

Spilling over species	AICc	ΔAICc	df	AICc ωi	Intercept (se)	Var 1 (se)	Var 2 (se)	Interaction (se)
Basileuterus culicivorus								
B ~ **Null**	101.5	0	2	0.37	-1.061 (0.173)	-	-	-
B ~ **Forest cover**	102.4	0.8	3	0.24	-1.077 (0.171)	0.183 (0.169)	-	-
B ~ **Edge density**	103.1	1.6	3	0.17	-1.064 (0.173)	0.106 (0.170)	-	-
B ~ Forest cover* Edge density	103.9	2.3	5	0.12	-1.084 (0.178)	0.322 (0.246)	0.072 (0.185)	-0.267 (0.190)
B ~ Forest cover + Edge density	104	2.5	4	0.11	-1.080 (0.175)	0.094 (0.166)	0.180 (0.171)	-
Thamnophilus caerulescens								
B ~ **Forest cover**	68.2	0	3	0.36	-1.131 (0.232)	0.362 (0.207)	-	-
B ~ **Null**	69.3	1.1	2	0.2	-1.049 (0.219)	-	-	-
B ~ **Forest cover + Edge density**	69.7	1.5	4	0.17	-1.149 (0.236)	0.127 (0.188)	0.360 (0.210)	-
B ~ **Forest cover* Edge density**	69.8	1.6	5	0.16	-1.182 (0.248)	0.462 (0.336)	0.260 (0.221)	-0.313 (0.239)
B ~ Edge density	70.7	2.5	3	0.1	-1.070 (0.222)	0.152 (0.194)	-	-
Pyriglena leucoptera								

B ~ **Null**	73.7	0	2	0.35	-0.860 (0.231)	-	-	-
B ~ **Forest cover**	73.8	0.1	3	0.33	-0.853 (0.230)	-0.326 (0. 250)	-	-
B ~ **Forest cover + Edge density**	75.6	1.9	4	0.13	-0.865 (0.236)	-0.349 (0.262)	0.109 (0.252)	-
B ~ **Edge density**	75.6	1.9	3	0.13	-0.865 (0.234)	0.055 (0.234)	-	-
B ~ Forest cover* Edge density	77.2	3.5	5	0.06	-0.862 (0.242)	-0.411 (0.284)	0.198 (0.293)	0.164 (0.259)

Basileuterus flaveolos

B ~ **Null**	52	0	2	0.327	-1.080 (0.265)	-	-	-
B ~ **Edge density**	52	0	3	0.319	-1.130 (0.275)	-0.352 (0.257)	-	-
B ~ **Forest cover**	53.3	1.4	3	0.165	-1.171 (0.296)	0.213 (0.271)	-	-
B ~ **Forest cover + Edge density**	53.7	1.7	4	0.138	-1.187 (0.297)	0.150 (0.268)	0.324 (0.259)	-
B ~ Forest cover* Edge density	55.7	3.7	5	0.051	-1.193 (0.301)	0.172 (0.320)	-0.346 (0.308)	0.030 (0.244)

Poecilotriccus plumbeiceps

B ~ **Null**	39.8	0	2	0.493	-1.729 (0.327)	-	-	-
B ~ **Forest cover**	41.6	1.8	3	0.198	-1.707 (0.329)	0.128 (0.306)	-	-
B ~ **Edge density**	41.8	2	3	0.183	-1.730 (0.327)	0.049 (0.375)	-	-
B ~ Forest cover + Edge density	43.6	3.8	4	0.074	-1.707 (0.329)	0.133 (0.310)	0.058 (0.364)	-
B ~ Forest cover* Edge density	44.3	4.5	5	0.052	-1.818 (0.362)	-0.027 (0.349)	0.324 (0.486)	-0.355 (0.322)

Dysithamnus mentalis

B ~ **Null**	68	0	2	0.37	-1.553 (0.234)	-	-	-
B ~ **Edge**	68.5	0.5	3	0.29	-1.628 (0.250)	0.337 (0.277)	-	-
B ~ **Forest cover**	69.9	2	3	0.139	-1.553 (0.234)	-0.056 (0.269)	-	-
B ~ Forest cover + Edge density	70.4	2.4	4	0.113	-1.633 (0.252)	-0.096 (0.281)	0.354 (0.287)	-
B ~ Forest cover* Edge density	70.9	2.9	5	0.088	-1.689 (0.264)	-0.045 (0.274)	0.604 (0.371)	-0.373 (0.306)

Table S3. Spillover richness and abundance into coffee matrices per sampling site. Forest cover corresponds to the percentage of forest cover around each sampling site within 800 m radius buffer (7.33 – 72.8%, min-max), and edge density corresponds to the total area in hectares of forest-non-forest edge / area within the same 800 m buffer (30.8 – 120.7 m/ha, min-max). In-patch richness: total number of species inside forest patches; In-matrix richness: total number of species recorded inside coffee matrices; Spillover richness: as the overall number of forest-dependent species in the matrix in relation to the adjacent forest patch. In-patch abundance: total number of individuals inside forest patches; In-matrix abundance: total number of individuals recorded inside coffee matrices; Spillover abundance: the overall abundance of forest-dependent species in the matrix in relation to the adjacent forest patch.

Sampling site	Edge density	Forest cover	-------------Richness----------			------------Abundance-------		
			In-patch	In-matrix	Spillover Richness	In-patch	In-matrix	Spillover Abundance
P02a	81.18	57.51	24	2	0.08	55	6	0.11
P02b	80.13	43.33	24	6	0.25	61	14	0.23
P02d	77.79	51.59	32	3	0.09	46	12	0.26
P02c	30.89	51.41	21	3	0.14	63	6	0.1
P09c	88.19	19.02	16	0	0	54	0	0
P09a	77.1	16.76	20	4	0.2	34	5	0.15
P09b	73.23	14.03	15	2	0.13	36	4	0.11
P09d	65.35	12.65	17	1	0.06	40	1	0.03
P10d	93.36	44.39	24	2	0.08	67	5	0.07
P10a	79.1	26.33	25	2	0.08	61	2	0.03
P10b	64.46	21.69	25	3	0.12	77	6	0.08
P10c	56.88	28.62	37	2	0.05	46	4	0.09
P11a	120.79	51.86	27	3	0.11	62	7	0.11
P11b	97.72	54.21	29	3	0.1	73	4	0.05

|								
P11c	61.12	33.3	23	3	0.13	59	9	0.15
P11d	34.4	7.33	13	1	0.08	26	1	0.04
P12a	70.6	35.95	24	3	0.13	59	5	0.08
P12b	69.83	35.63	15	0	0	30	0	0
P12c	67.77	57.78	22	2	0.09	56	2	0.04
P12d	35.86	52.91	23	4	0.17	42	4	0.1
P19a	80.58	37.58	22	1	0.05	46	3	0.07
P19d	69.14	62.23	29	2	0.07	71	4	0.06
P19c	52.72	50.05	30	4	0.13	74	7	0.09
P19b	33.35	72.82	30	5	0.17	57	11	0.19
P26c	67.31	21.39	28	3	0.11	50	10	0.2
P26b	63.35	16.17	34	4	0.12	81	10	0.12
P26a	62.1	19	25	5	0.2	78	5	0.06
P26d	57.05	36.61	36	5	0.14	81	6	0.07
P27a	77.03	36.82	30	6	0.2	69	11	0.16
P27d	74.53	43.61	27	3	0.11	73	3	0.04
P27c	71.26	40.89	23	5	0.22	58	4	0.07
P27b	62.84	30.03	28	1	0.04	82	2	0.02
P28c	81.8	34.71	25	3	0.12	84	4	0.05
P28b	64.94	15.19	27	2	0.07	61	4	0.07
P28a	61.14	25.11	40	6	0.15	55	4	0.07
P28d	46.74	40.13	29	1	0.03	80	2	0.03
P30a	77.66	26.21	21	5	0.24	50	15	0.2
P30b	66.72	29.93	22	1	0.05	52	1	0.02
P30d	50.64	34.02	31	1	0.03	34	2	0.06
P30c	32.52	8.89	12	1	0.08	81	1	0.01

Table S4. Model selection for individual spillover abundance of Golden-crowned Warbler (*Basileuterus culicivorus*) and Variable Antshrike (*Thamnophilus caerulescens*) spilling over into coffee matrices. *B* corresponds to individual spillover, AICc corresponds to the Akaike Information Criteria corrected to small samples, ΔAICc is the difference between AICc from the best ranked model (ΔAICc), df is the degrees of freedom, and AICc ωi is the evidence weight. Coefficients and standard errors (se) of each model are given. Var 1 corresponds to the first predictor variable in the model, Var 2 corresponds to the second predictor variable, and Interaction represents the interaction between the two. Forest cover corresponds to the percentage of forest cover around each sampling site within 800 m radius buffer (7.33 – 72.8%, min-max), and edge density corresponds to the total area in hectares of forest-non-forest edge / area within the same 800 m buffer (30.8 – 120.7 m/ha, min-max). Distance from sampling point inside matrix to the nearest forest patch (50.3 – 159 m, min-max).

Model	AICc	ΔAICc	df	AICc ωi	Intercept (se)	Var 1 (se)	Var 2 (se)	Interaction (se)
								Coefficients
Basileuterus culicivorus								
***B* - Distance**	99.2	0	3	0.265	-1.115 (0.180)	-0.410 (0.208)	-	-
***B* - Distance*Forest cover**	100.5	1.3	5	0.136	-1.060 (0.188)	-0.277 (0.238)	0.185 (0.190)	0.403 (0.284)
***B* - Distance + Forest cover**	100.9	1.6	4	0.117	-1.123 (0.182)	-0.387 (0.214)	0.106 (0.177)	-
***B* - Distance* Edge density**	101.1	1.9	5	0.105	-1.049 (0.185)	-0.377 (0.255)	0.025 (0.187)	0.425 (0.321)
***B* - Distance + Edge density**	101.2	2	4	0.098	-1.114 (0.180)	-0.405 (0.213)	0.018 (0.181)	-
B - Null	101.5	2.3	2	0.083	-1.06 (0.173)	-	-	-
B - Fc	102.4	3.1	3	0.055	-1.077 (0.175)	0.183 (0.169)	-	-
B - Edge	103.1	3.9	3	0.037	-1.064 (0.173)	0.106 (0.170)	-	-
B - Edge density*Forest cover	103.9	4.6	5	0.026	-1.084 (0.178)	0.322 (0.246)	0.072 (0.185)	-0.267 (0.190)
B - Edge density+ Forest cover	104	4.8	4	0.023	-1.080 (0.175)	0.094 (0.166)	0.180 (0.171)	-

|	AICc	ΔAICc	df	AICc ωi	Intercept (se)	Var 1 (se)	Var 2 (se)	Interaction (se)
							Coefficients	
Thamnophilus caerulescens								
B - Distance*Forest cover	66.1	0	5	0.393	-1.072 (0.245)	0.724 (0.351)	0.516 (0.233)	0.734 (0.392)
B – Fc	68.2	2	3	0.141	-1.131 (0.232)	0.362 (0.207)	-	-
B - Distance+ Forest cover	68.7	2.5	4	0.11	-1.183 (0.242)	0.356 (0.291)	0.455 (0.225)	-
B - Null	69.3	3.2	2	0.08	-1.049 (0.219)	-	-	-
B - Edge density+ Forest cover	69.7	3.6	4	0.065	-1.149 (0.236)	0.127 (0.188)	0.360 (0.210)	-
B - Edge density*Forest cover	69.8	3.6	5	0.064	-1.182 (0.248)	0.462 (0.336)	0.260 (0.221)	-0.313 (0.239)
B - Distance*Edge distance	70.2	4.1	5	0.051	-1.005 (0.230)	0.390 (0.300)	0.181 (0.214)	0.522 (0.331)
B - Edge density	70.7	4.6	3	0.04	-1.070 (0.222)	0.152 (0.194)	-	-
B - Distance	71	4.8	3	0.035	-1.060 (0.221)	0.147 (0.251)	-	-
B - Distance + Edge density	72	5.9	4	0.021	-1.094 (0.227)	0.229 (0.268)	0.202 (0.203)	-

Figure S1. Illustration of matrix composition in studied areas. (**A**) coffee matrix; (**B**) pasture matrix.
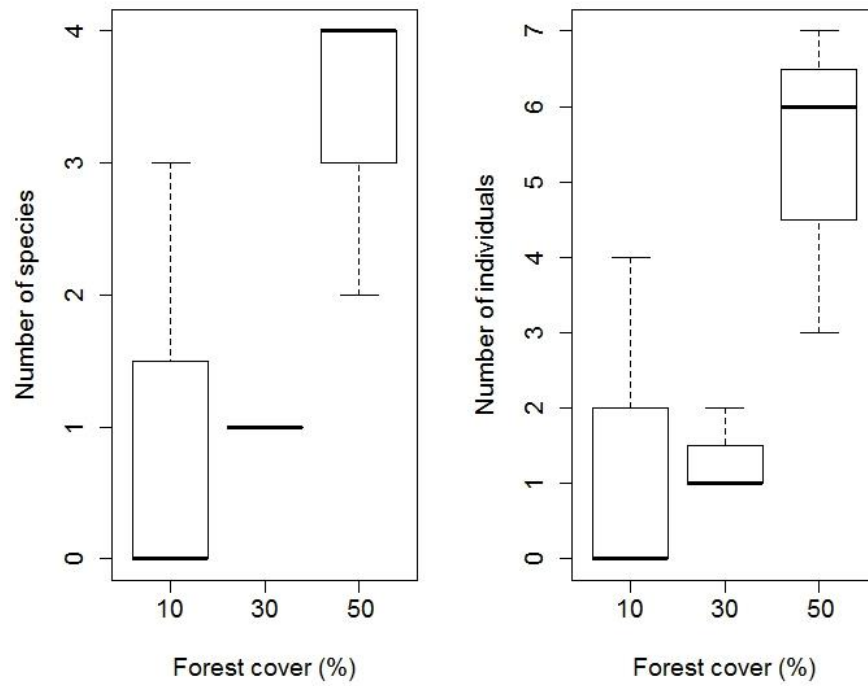
Figure S2. Median and respective 25% and 75% quartiles of both number of species and number of individuals caught spilling over at forest edges embedded in three landscapes with low (10%), intermediate (30%) and high (50%) forest cover.
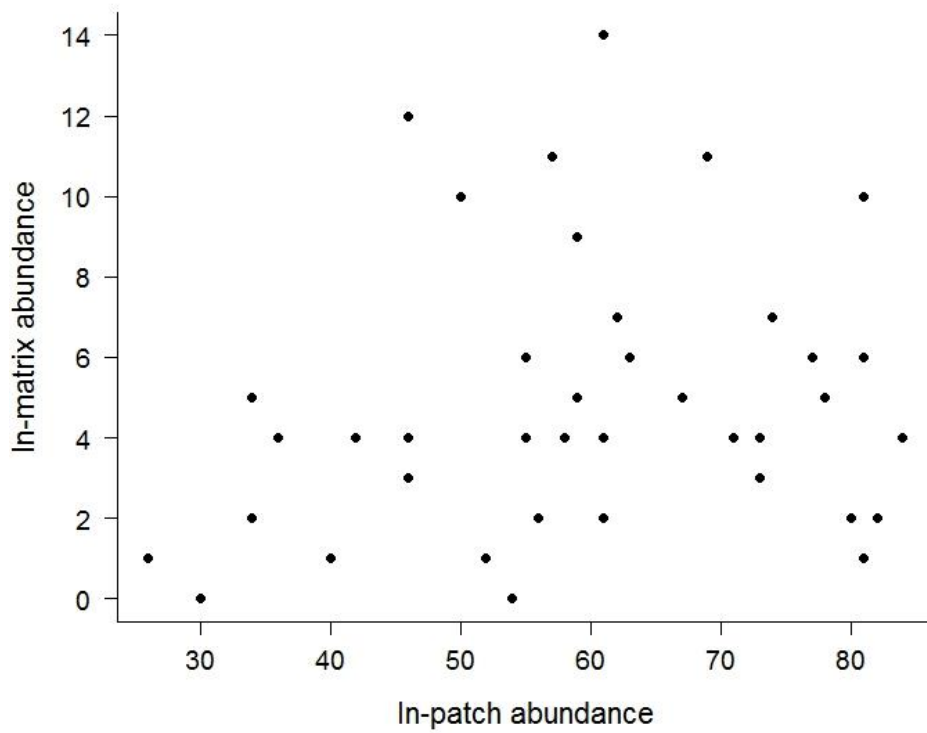
Figure S3. Pearson-correlation between in-patch bird abundance and spillover bird abundance (total of individuals) in coffee matrices (r= 0.18, p = 0.487).
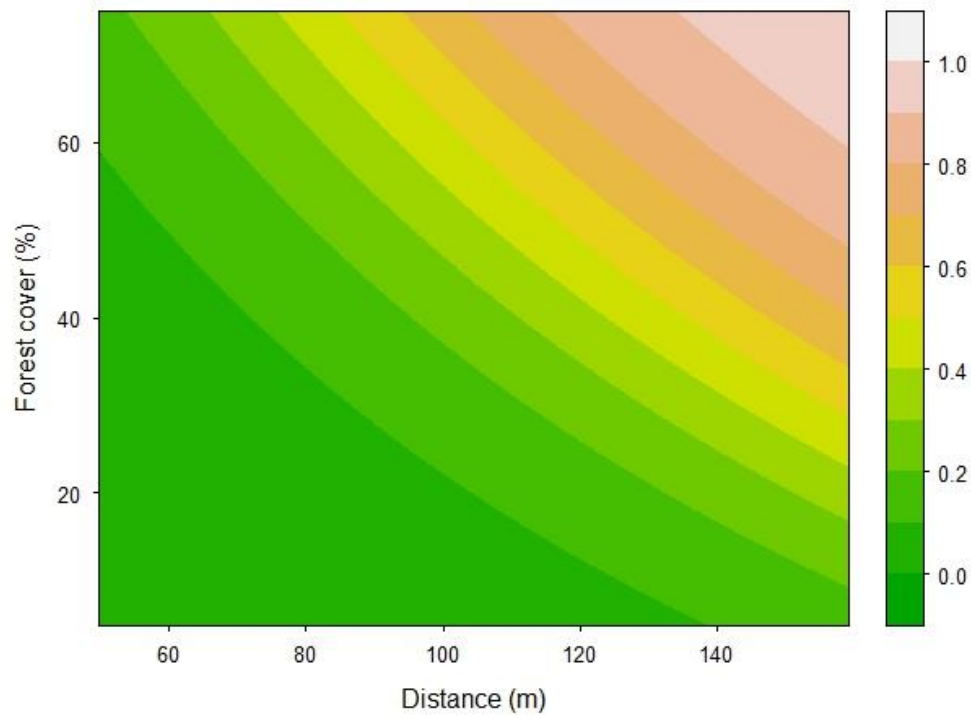
Figure S4. Predicted individual spillover abundance of the Variable Antshrike *Thamnophilus caerulescens* in coffee matrices using the top-ranked AICc model, including the interaction between forest cover and distance from nearest habitat patch.
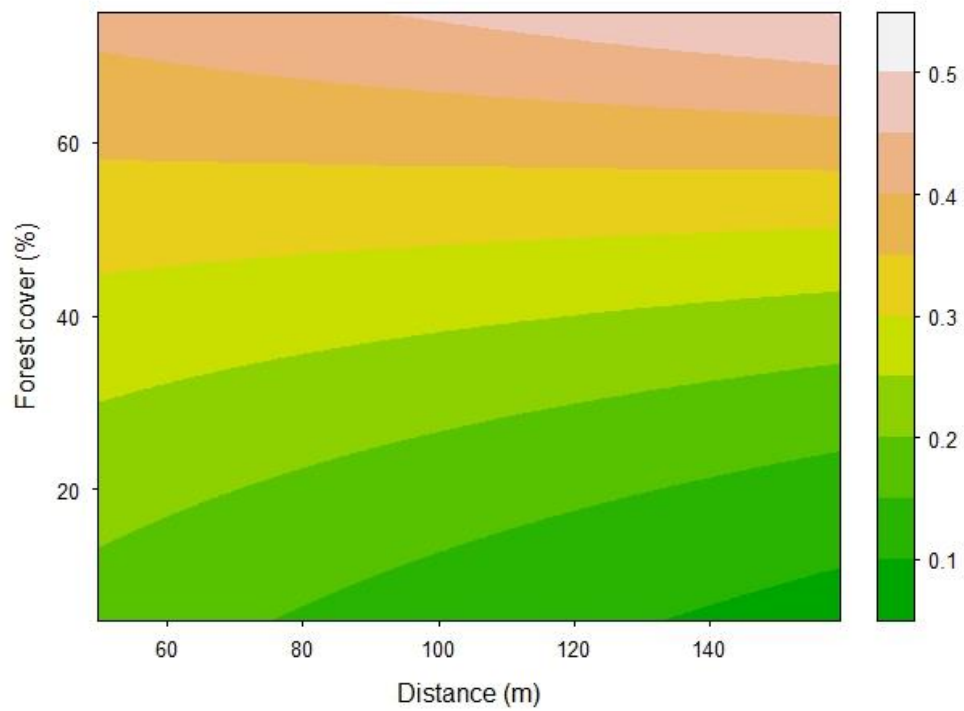
Figure S5. Predicted individual spillover abundance of the Golden-crowned Warbler *Basileuterus culicivorus* in coffee matrices using the second top-ranked AICc model, including the interaction between forest cover and distance from nearest habitat patch.
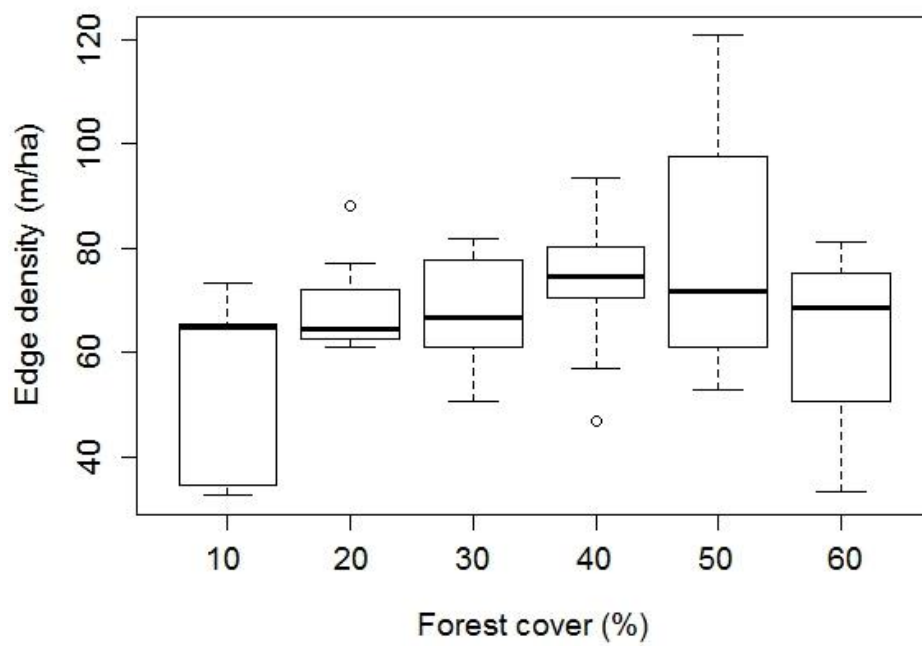
Figure S6. Edge density distributed according forest cover gradient in coffee matrices.

General Discussion

Agricultural intensification, along with other environmental changes such as climate change, pollution, and species invasion, has currently degraded biodiversity to such an extent that many ecosystem services contributing to human well-being are becoming increasingly eroded (Hooper et al. 2005, MEA 2005, Bommarco et al. 2013). To minimize this degradation process, a current challenge is to plan multifunctional landscapes that, in addition to support crop production, are able to maintain biological diversity and its ecological functions (Foley et al. 2005). Despite the growing knowledge base on ecosystem services provision (Albert et al. 2014), current implementing of ecosystem services science in practical planning and decision-making at landscape scale is in its infancy (Daily et al. 2009).

In chapter one, we demonstrate that a large number of bird species may provide pest control services in agricultural systems worldwide, and that a substantial proportion of avian predators are native habitat-dependent species in tropical systems, suggesting a link between native habitat management and the maintenance of pest control services. We have found 226 bird species that provide pest regulation worldwide, and a substantial proportion of those are native habitat-dependent species in tropical systems. Moreover, more heterogeneous landscapes, increased habitat amount, and decreased isolation among patches are positively associated with increased avian-mediated pest control rates. We highlight that highly-connected crop-noncrop mosaics may be best for long-term conservation of pest control services (Tscharntke et al. 2007). Based on our findings, we propose a conceptual model that highlights the role of landscape-level processes affecting the main mechanisms related to avian-mediated pest control, including (i) the persistence of avian predators in agricultural habitats, (ii) the dispersal ability of avian predators into and through crop fields, and (iii) trophic interactions between assemblages of natural enemies and pests.

In the second chapter we move forward investigating the processes modulating bird persistence in agricultural landscapes and demonstrate that matrix composition strongly affects the dynamics of biodiversity thresholds not only for the taxonomic diversity, but also for the functional and phylogenetic

diversity of bird assemblages. Even though we demonstrate that more permeable matrices might postpone species loss in fragmented landscapes, when deforestation reaches 20% remaining habitat, not only species richness, but also important aspects of functional and phylogenetic structure of bird assemblages collapse. These changes may have important implications in terms of ecosystem functioning and ecosystem resilience, since a large proportion of the original functions performed by bird species, such as insectivory and frugivory, are lost below this threshold, and some specific branches of the phylogeny are lost as well. Since the historical context plays an important role in assembling phylogenetic structure of studied bird assemblages, we highlight the importance of maintaining preserved tracks of native forest as source of individuals that can colonize new patches in order to maintain more heterogeneous communities. In addition, increasing matrix permeability is key in enhancing landscape connectivity, and allowing species movement and persistence in these highly fragmented landscapes. For practical purposes, taxonomic diversity seems to be the best predictor index of biodiversity loss in fragmented landscapes, since it is the first index to be affected - especially in high-contrasting matrices - and therefore detecting a minimal habitat cover threshold for taxonomic diversity can prevent subsequent functional and phylogenetic loss.

Finally, in chapter three, we demonstrated the importance of matrix permeability and landscape heterogeneity in regulating species movement among patches and facilitating avian cross-habitat spillover of forest-dependent species into agricultural matrices. We have found that (1) matrix composition plays a key role in facilitating bird movement into agricultural matrices, where very contrasting matrices act as a barrier to species movement and less contrasting matrices act as a semi-permeable filter, facilitating bird movement into managed areas; (2) that edge density has important effects on spillover in more permeable matrices, especially in lower amounts of habitat, which might be due both complementation and supplementation processes at landscape scale and an increased landscape connectivity, and (3) habitat amount is important in promoting spillover when matrix and native habitats are high-contrast, because although most species avoid high-contrast matrices, some species travel short distances across them to reach other habitat patches. Increasing the structural

174

similarity between matrix and native patches will promote species movement, ensuring species persistence and avian-mediated ecosystem services. Matrix management matters, as matrix land cover dominates the world's terrestrial ecosystems (Vitousek et al. 1997, MEA 2005). Although large-scale conversion to high-quality matrix might not be a realistic option, even small punctual changes in matrix making it more heterogeneous or permeable may be a feasible and effective conservation strategy (Ruffell et al. 2016).

Our results suggest that landscape configuration and matrix composition should be considered when planning agricultural landscapes in order to ensure long-term persistence and ecosystem services provision in highly fragmented landscapes. Increasing matrix permeability through land uses that provide substantial resources, facilitate dispersal, and create lower-edge contrast (Kupfer et al. 2006) might reduce the impacts of habitat loss on bird communities and also guarantee avian-mediated ecosystem services provisioning. Increasing spatial heterogeneity in agricultural landscapes, for example by adding stepping stones, strips, or even hedgerows, may be beneficial for many forest-dependent species that can use these elements to move through matrices (Uezu et al. 2008). Matrix permeability might also be increased through enhancement of crop diversity and decreased land management intensity (Perfecto and Vandermeer 2010). Continued efforts are necessary to more fully understand how and why landscape configuration and composition influence forest-dependent mobile organisms and biodiversity-mediated-ecosystem services, especially in fragmented tropical landscapes.

This study is part of Project Interface[1], a research project that aims to contribute to the understanding and planning of multifunctional landscapes capable of sustaining both biodiversity and the ecosystem services essential for human well-being.

Conserving biodiversity in agricultural landscapes no longer implies a focus solely on species richness, but also on ecological functions performed by species and on evolutionary history supported by lineages (Diniz-Filho et al. 2013). An integrative approach would seek the mechanistic underpinning of ecosystem

---

[1] http://ecologia.ib.usp.br/projetointerface/en/

responses to species loss by focusing on the relationships among species, traits, phylogeny, biotic and abiotic factors affecting these relationships, and how they ultimately affect ecosystem functioning (Naeem et al. 2012, Monnet et al. 2014). The general pattern that has arisen in our study it that increasing both landscape heterogeneity and matrix permeability, in addition to native habitat conservation, is a key management action to implement in order to guarantee bird persistence in anthropogenic landscapes and the provisioning of ecosystem services.

Literature cited

Albert, C., J. Aronson, C. Furst, and P. Opdam. 2014. Integrating ecosystem services in landscape planning: requirements, approaches, and impacts. Landscape Ecology **29**:1277-1285.

Bommarco, R., D. Kleijn, and S. G. Potts. 2013. Ecological intensification: harnessing ecosystem services for food security. Trends in Ecology & Evolution **28**:230-238.

Daily, G. C., S. Polasky, J. Goldstein, P. M. Kareiva, H. A. Mooney, L. Pejchar, T. H. Ricketts, J. Salzman, and R. Shallenberger. 2009. Ecosystem services in decision making: time to deliver. Frontiers in Ecology and the Environment **7**:21-28.

Diniz-Filho, J. A. F., R. D. Loyola, P. Raia, A. O. Mooers, and L. M. Bini. 2013. Darwinian shortfalls in biodiversity conservation. Trends in Ecology & Evolution **28**:689-695.

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.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs **75**:3-35.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 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.

MEA. 2005. Millennium Ecosystem Assessment Synthesis, United Nations.

Monnet, A.-C., F. Jiguet, C. N. Meynard, D. Mouillot, N. Mouquet, W. Thuiller, and V. Devictor. 2014. Asynchrony of taxonomic, functional and phylogenetic diversity in birds. Global Ecology and Biogeography **23**:780-788.

Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The Functions of Biological Diversity in an Age of Extinction. Science **336**:1401-1406.

Perfecto, I. and J. Vandermeer. 2010. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. Proceedings of the National Academy of Sciences of the United States of America **107**:5786-5791.

Ruffell, J., C. Mick, and R. K. Didham. 2016. The matrix matters, but how should we manage it? Estimating the amount of high-quality matrix required to maintain biodiversity in fragmented landscapes. Ecography **39**:001-008.

Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control **43**:294-309.

Uezu, A., D. D. Beyer, and J. P. Metzger. 2008. Can agroforest woodlots work as stepping stones for birds in the Atlantic Forest region? . Biodiversity and Conservation **17**:1907-1922.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melilli. 1997. Human domination of Earth's ecosystems. Science **277**:494-499.

Abstract

The influence of habitat loss on biodiversity is related to a set of non-linear processes, which strongly affect isolation and connectivity and determine both extinction and colonization rates. Landscape changes due anthropogenic disturbances are driving not only species loss *per se*, but also loss of functions performed by those species, which could have important impacts on the provision of ecosystem services and ecosystem function. The objective of this dissertation is to move beyond our current understanding about landscape processes underpinning bird persistence and avian-mediated pest control in fragmented landscapes. In chapter 1, we systematically review the empirical evidence of landscape structure effects on avian-mediated pest control in agricultural systems worldwide in order to point out the main landscape processes underpinning ecosystem service provision and gaps in knowledge where research efforts should be focused. We have found 226 bird species that provide pest regulation worldwide, and a substantial proportion of those are native habitat-dependent species in tropical systems. Moreover, more heterogeneous landscapes, increased habitat amount, and decreased isolation among patches are positively associated with increased avian-mediated pest control rates. Then, using bird data collected in fragmented landscapes in the Brazilian Atlantic forest, in chapter 2 we test for community-level extinction thresholds across a range of biodiversity indices (taxonomic, functional, and phylogenetic diversity) in order to evaluate how much habitat is need to maintain sustainable ecosystem functioning and ecosystem resilience, and how matrix composition might affect these thresholds. In general, we have found that more permeable matrices are able to postpone species loss in fragmented landscapes. However, since habitat loss reaches 20% of habitat remaining, all aspects of biodiversity are compromised. Finally, in chapter 3 we investigate the cross-habitat spillover process - one of the main processes regulating avian-mediated pest control in tropical regions. Matrix composition is a key factor in facilitating species movement into matrices, as 24% of the species pool can spill over into coffee plantations, while spillover into pasture is nearly non-existent. Moreover, the interaction between forest cover and edge density is

an important predictor of spillover when habitat amount is low. Our results suggest that landscape configuration and matrix composition should be considered when planning agricultural landscapes in order to ensure long-term persistence of biodiversity and ecosystem services provision.

Resumo

O efeito da perda de habitat sobre a biodiversidade está ligado a um conjunto de processos não-lineares que fortemente afetam a conectividade e o isolamento da paisagem, e determinam taxas de extinção e colonização. Mudanças na estrutura da paisagem desencadeadas por distúrbios antropogênicos levam não somente à perda de espécies *per se*, mas também a perda de funções que estas espécies desempenham no ecossistema, com importantes implicações em termos de funcionalidade e provisão de serviços ecossistêmicos. O objetivo geral desta tese é elucidar os processos, que ocorrem no nível da paisagem, que modulam a persistência de aves e, consequentemente, as funções destas aves na provisão do controle de pragas em paisagens fragmentadas. No primeiro capítulo da tese, nós revisamos sistematicamente as evidências empíricas dos efeitos da estrutura da paisagem sobre o controle de pragas provido por aves em sistemas agrícolas ao redor do mundo, identificando os processos, no nível da paisagem, subjacentes a este controle e as lacunas de conhecimento onde futuros esforços devem ser concentrados. Identificamos 226 espécies de aves provendo controle de pragas em sistemas agrícolas, sendo que uma porção substancial destas espécies em sistemas tropicais são dependentes de habitats nativos. Em geral, paisagens mais heterogêneas, com elevada cobertura de habitat nativo e menor isolamento entre fragmentos estão positivamente relacionados com elevadas taxas de controle de pragas provido por aves. Por conseguinte, no segundo capítulo, usamos dados de aves em paisagens fragmentadas emersas em diferentes contextos de matriz agrícola na Mata Atlântica brasileira, para testar limiares de extinção ao nível de comunidade. Foram usadas diferentes métricas de diversidade biológica (taxonômica, funcional e filogenética), com o intuito de avaliar o quanto de habitat é necessário para garantir o funcionamento e resiliência do ecossistema. Nós encontramos que matrizes mais permeáveis são capazes de postergar a perda de espécies em paisagens fragmentadas, no entanto, quando a perda de habitat alcança o limiar crítico de 20%, todos os aspectos da biodiversidade estão comprometidos, independentemente do tipo de matriz. Por fim, no capítulo 3, nós investigamos o processo de 'transbordamento' (i.e. *spillover*), um dos principais processos reguladores da provisão do serviço de controle de pragas pela biota dependente de habitats nativos. Nós demonstramos que a composição da matriz é um fator determinante facilitando o movimento de espécies para as matrizes agrícolas,

sendo que 24% do *pool* de espécies consegue utilizar matrizes de cafezal, enquanto este movimento é quase inexistente em matrizes de pastagem. Ademais, em paisagens com pouca cobertura florestal, a interação entre cobertura florestal e densidade de borda é um importante preditivo do *spillover*. Nossos resultados sugerem que a configuração da paisagem e a composição da matriz devem ser consideradas no planejamento de paisagens agrícolas para garantir a persistência em longo prazo da biodiversidade e a provisão de serviços ecossistêmicos.