Sebastián Alvarado Montero

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Índice

Resumo

A expansão da agricultura é um dos principais propulsores do desmatamento, levando à degradação das comunidades biológicas e aos serviços ecossistêmicos que elas fornecem. No entanto, uma vez que a matriz agrícola permita o uso de recursos e o movimento de espécies, pode reduzir os efeitos negativos da perda de habitat. A remoção de carniça é um dos serviços ecossistêmicos menos estudados, embora seja de suma importância para o ciclo de nutrientes e controle de doenças, e muito menos estudado com uma abordagem de paisagem. Aqui, pretendemos contribuir para essa lacuna de conhecimento avaliando como a comunidade de insetos necrófagos é afetada pela configuração do habitat nativo e tipo de matriz (plantações de café ou pastagens) em 18 locais de amostragem independentes no domínio da Floresta Atlântica Brasileira. Nós estudamos a comunidade de insetos e o serviço de remoção de carcaças usando um modelo de amostragem pareado (dentro da floresta e dentro da matriz agrícola adjacente) através de um gradiente de cobertura florestal. Medimos a riqueza de espécies de insetos, a composição da comunidade e a remoção de carniça, usando iscas de carne colocadas dentro de gaiolas de exclusão e monitoradas ao longo de seis dias. A carniça em cafezais atraiu comunidades mais ricas do que em pastagens para gado, e paisagens com maior fragmentação apresentaram maior riqueza de espécies devido a um componente mais rico de espécies associadas à matriz, enquanto paisagens mais florestadas facilitaram a presença de espécies associadas à floresta. A remoção de carniça foi maior na floresta e nos cafezais do que nas pastagens de gado. A riqueza de espécies apresentou uma relação negativa com a remoção de carniça, sendo as espécies associadas à floresta as principais responsáveis pela prestação do serviço. Assim, paisagens mais florestadas e matrizes menos contrastantes mantêm um alto fornecimento de serviço de remoção de carniça ao conter comunidades compostas por essas espécies mais efetivas no fornecimento deste serviço ecossistêmico.

Palavras chaves

1. Mata Atlântica 2. Composição da comunidade 3. Fragmentação 4. Serviços ecossistêmicos 5. Tipo de matriz

Abstract

Agriculture expansion is one of the main drivers of deforestation, leading to the degradation of biological communities and the ecosystem services they provide. However, once the agricultural matrix allows resource use and species movement, it may reduce the negative effects of habitat loss. Carrion removal is one of the least studied ecosystem services, albeit its paramount importance for nutrient cycling and disease control, and much less studied with a landscape approach. Here we aim to contribute to this knowledge gap by evaluating how the scavenger insect community is affected by the configuration of native habitat and matrix type (coffee plantations or cattle pastures) across 18 independent sampling sites in the Atlantic Brazilian Forest domain. We studied the scavenger insect community and carrion removal service using a paired sampling design (in-forest and within the adjacent agricultural matrix) across a forest cover gradient. We measured insect species richness, community composition and carrion removal using meat baits placed inside exclusion cages and monitored along six days. Carrion in coffee plantations attracted richer communities than in cattle pastures, and landscapes with higher fragmentation presented higher species richness due to a richer component of matrix associated species, while more forested landscapes harbored the presence of forest-associated species. Carrion removal was higher in-forest patches and coffee plantations than in cattle pastures. Species richness presented a negative relationship with carrion removal, with forest-associated species being the main responsible of carrion removal service provision. Thus, more forested landscapes and less contrasting matrices maintain a high provision of carrion removal service by containing communities composed by those species more effective providing this ecosystem service.

Key-words

1. Atlantic Forest 2. Community composition 3. Fragmentation 4. Ecosystem services
5. Matrix type

Introdução Geral

Todo ser vivo produz resíduos na sua existência. Graças aos organismos que processam estes detritos, a matéria orgânica é degradada e os nutrientes são reincorporados no sistema (Poveda *et al*. 2005). Caso contrário, os resíduos produzidos se acumulariam, contaminando os ecossistemas e comprometendo sua sustentabilidade (Dangles *et al*. 2002).

Entre os detritos, carcaças de animais mortos constituem uma significativa parcela de recursos na natureza, o que faz que ela suporte uma alta diversidade de espécies associadas, principalmente de insetos necrófagos (Barton *et al*. 2013). Contudo, a degradação dos ambientes naturais pela atividade humana compromete a viabilidade destas comunidades biológicas, provocando a perda de espécies com as mudanças no uso do solo (Gibbs & Stanton 2001, Markandya *et al*. 2008, Dónazar *et al*. 2016). Isto afeta também a remoção de carniça e resulta em problemas que chegam a ser percebidos pela sociedade (Margalida & Colomer 2012, Beasley *et al*. 2015).

Ferramentas como o conceito de serviços ecossistêmicos (os serviços fornecidos pela natureza e que são percebidos pelos seres humanos como ganho econômico ou aumento no seu bem-estar) facilitam a conscientização da importância da natureza para os seres humanos, incluídos grupos como os animais necrófagos. Eles fornecem o serviço de regulação de remoção de carniça, importante por evitar a acumulação de carcaças, de onde derivam outros serviços ecossistêmicos chave para o bem-estar humano (Barton *et al*. 2013, Cortés-Avizanda *et al*. 2016, Dónazar *et al*. 2016). Entre eles estão a ciclagem de nutrientes, de grande importância para o setor agrícola (Dupont *et al.* 2012, Moleón *et al*. 2014, Beasly *et al*. 2015); a prevenção de surto de doenças (Inger *et al*. 2016, Buechley & Sekercioglu 2017); regulação nas emissões de carbono (Morales-Reyes *et al*. 2015, Morales-Reyes *et al*. 2016); e o fortalecimento das redes tróficas (Dónazar *et al.* 2016, Inger *et al*. 2016). Este último serviço ecossistêmico é de especial importância porque funciona como suporte para outros serviços de interesse para a sociedade.

A prestação de serviços ecossistêmicos está altamente relacionada com a estrutura da paisagem, tanto assim que a maioria das propostas de manejo para melhorar o fornecimento de serviços são desenvolvidas nesta escala (de Groot *et al*. 2010). Características da paisagem como a quantidade de cobertura de hábitat nativo, o nível de fragmentação e o tipo de matriz estão altamente relacionadas com a riqueza e composição das comunidades biológicas e a sua capacidade de prestar serviços ecossistêmicos (Fahrig 2003, Sweeney *et al*. 2004, Dobson *et al*. 2006, Allan *et al.* 2015, Newbold *et al.* 2015, Rodríguez-San Pedro & Simonetti 2015, Sánchez-de-Jesús *et al*. 2016, Wilson *et al.* 2016). No caso do serviço de remoção de carniça, esta relação da estrutura da paisagem com a comunidade de animais necrófagos e o serviço que eles fornecem ainda não foi estudada diretamente, em particular no componente dos insetos. Este trabalho pretende preencher esta lacuna de conhecimento avaliando a influência da estrutura de paisagens agrícolas no domínio de Mata Atlântica, sobre a comunidade de insetos necrófagos e a prestação do serviço ecossistêmico de remoção da carniça.

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Capítulo Único

Paisagens mais florestadas e matrizes menos contrastantes melhoram a remoção de carniça por insetos em paisagens tropicais

Sebastián Alvarado-Montero, Andrea Larissa Boesing, Rodolfo Jaffé

Higher forest cover and less-contrasting matrices improve carrion removal by insects in tropical landscapes

Abstract

Agriculture expansion is one of the main drivers of deforestation, leading to the degradation of biological communities and the ecosystem services they provide. However, once the agricultural matrix allows resource use and species movement, it may reduce the negative effects of habitat loss. Carrion removal is one of the least studied ecosystem services, albeit its paramount importance for nutrient cycling and disease control, and much less studied with a landscape approach. Here we aim to contribute to this knowledge gap by evaluating how the scavenger insect community is affected by the configuration of native habitat and matrix type (coffee plantations or cattle pastures) across 18 independent sampling sites in the Atlantic Brazilian Forest domain. We studied the scavenger insect community and carrion removal service using a paired sampling design (in-forest and within the adjacent agricultural matrix) across a forest cover gradient. We measured insect species richness, community composition and carrion removal using meat baits placed inside exclusion cages and monitored along six days. Carrion in coffee plantations attracted richer communities than in cattle pastures, and landscapes with higher fragmentation presented higher species richness due to a richer component of matrix associated species, while more forested landscapes harbored the presence of forest-associated species. Carrion removal was higher in-forest patches and coffee plantations than in cattle pastures. Species richness presented a negative relationship with carrion removal, with forest-associated species being the main responsible of carrion service provision. Thus, more forested landscapes and less contrasting matrices maintain a high provision of carrion removal service by containing communities composed by those species more effective providing this ecosystem service.

Key-words

1. Atlantic Forest 2. Community composition 3. Fragmentation 4. Ecosystem services
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Introduction

The conversion of natural forests to agricultural landscapes has increased rapidly in response to a growing human population. This process has been particularly acute in Brazil, reaching 20,000-40,000 km^2/year of forest loss during the last 20 years (Hansen *et al*. 2013). Loss of native habitats generally leads to deleterious and homogenizing effects of biological communities (Allan *et al.* 2015, Newbold *et al.* 2015), since it makes local populations vulnerable to drastic environmental changes and increases intraspecific competition by reducing availability of space and resources, driving species to extinction (Pardini *et al*. 2017). Habitat loss is often tied to habitat fragmentation as well, altering the spatial configuration of native remnants, increasing isolation between patches and decreasing the quality on in-patch habitats due to edge effects (Fahrig 2003, Fischer & Lindenmayer 2007, Wilson *et al.* 2016, Liu *et al.* 2018). These processes consequently impacts the provision of ecosystem services through species loss and their function in ecosystems (Millennium Ecosystem Assessment 2005, Sweeney *et al*. 2004, Dobson *et al*. 2006), resulting in economic loss and decrease of human welfare (Arkema, *et al*. 2015, Diaz *et al.* 2015, Walsh *et al.* 2016, IPBES 2018).

The type of matrix surrounding forest patches also has a strong effect on the viability of biological communities in-patches, and drives species occurrence of biota in agricultural lands (Rodríguez-San Pedro & Simonetti 2015, Sánchez-de-Jesús *et al*. 2016). Less-contrasting matrices can facilitate species movement between habitat remnants and within the matrix (Dunning *et al*. 1992, Blitzer *et al*. 2012, Biz *et al*. 2017), and provide both feeding resources and refuge, allowing species persistence within matrices (Malekian *et al.* 2015, Howell *et al*. 2018). Eventually, the flow of species from forest patches into the matrices can support the provision of ecosystem services in these anthropogenic environments (Tscharntke *et al*. 2012).

Carrion removal is among the ecosystem services that could be affected by landscape structure through changes on scavenger communities. This group regulates carcass accumulation, in turn inhibiting the proliferation of undesirable species (Cortés-Avizanda *et al*. 2016) and preventing outbreaks of dangerous diseases, like rabies and Ebola (Sekercioglu *et al*. 2004, Rouquet *et al.* 2005, Beasley *et al*. 2015). For instance, in the European Union the carrion removal service by natural communities saves between €9.3 thousand to €1.6 million for farmers annually (Margalida & Colomer 2012), while in India, the extinction of scavenger vertebrates provoked an outbreak of rabies that cost $34 billion between 1993 and 2013 (Beasley *et al.* 2015). Therefore, these communities are crucial not only for natural ecosystems functioning, but also for the well-being of human societies.

Vultures, some mammals and insects are the main components of the community associated to this resource, the latter making up for the most diverse and recurrent group (Braack 1987). Despite their size in comparison to the rest of the scavenger animals, insects are highly effective in carrion degradation. They are capable of removing all carcass soft-tissues often within four days, and in well-wooded environments they can find and colonize carcasses easier than vertebrate scavengers (Braack 1987). Some attempts to include the landscape perspective to understand its influence on scavenger communities and the carrion removal service have been done. For example, Amézquita & Favila (2011) evaluated the effect of forest fragment size and time of day over the community of dung beetles and carrion removal. However, their investigation brings only one component of landscape structure, eluding a better understanding of the mechanisms modulated at the landscape level over the community and the carrion removal service. The studies that do relate a proper landscape structure analysis with the scavenger insect community, however, do not include the ecosystem service they provide (Trumbo & Bloch 2000, Gibbs & Stanton 2001, DeVault *et al.* 2004, von Hoermann *et al*. 2018). Thus, understanding the links between biological communities and ecosystem service provision through the mechanisms driven by landscape structure is crucial in order to promote landscape management strategies aiming to safeguard scavenger communities and assure long-term carrion removal service provision.

Using a paired sampling design encompassing forest patches and the adjacent agricultural matrix differing in terms of contrast with native habitat (coffee plantations as less contrasting matrix and cattle pastures as more contrasting matrix) and spanning a gradient of forest cover, we assessed the effect of landscape structure on scavenger insect communities and the provision of carrion removal ecosystem service. To our knowledge, this is the first study explicitly evaluating landscape effects on both scavenger insect community and carrion removal ecosystem service. We tested two hypotheses. First, that more forested landscapes and less contrasting matrices harbor richer communities of scavenger insects; and second, that communities of scavenger insects found in more forested landscapes and less contrasting matrices promote a higher provision of the carrion removal ecosystem service.

We expect that landscapes with higher forest cover, less fragmentation and with less contrasting matrices (i.e. coffee plantations) will sustain higher diversity of scavenger insects, since this landscape structure is related to higher diversity of supplementary resources (Banks-Leite *et al.* 2014, Fletcher *et al.* 2018). Also, given that agricultural matrices might work as ecological filter for a large number of native species (Ansell *et al.* 2016, Ferrante *et al.* 2017), we expect that matrix type will alter the composition of the scavenger insect community outside of forest patches, with a large number of forest associated species in less contrasting matrices due to spillover (movement of organisms between different habitats for dispersal and foraging activities). Moreover, given that high biodiversity levels are often related to higher ecosystem service provision (Gamfeldt *et al.* 2013, Balvanera *et al.* 2014), we expect that carrion removal will be higher in the most forested landscapes and the less contrasting matrix containing richer communities. In addition to species richness, the presence of specific groups within a community is essential for the provision of ecosystem services (Kremen 2005, Diaz *et al.* 2007), so we expect carrion removal to be higher when key groups, undertaking the bulk of the service, are present in the environment.

Methods

Study region: We conducted our study in three focal landscapes (3 km radius, 2,828 ha) within the South Minas and Mogiana regions, in Southeastern Brazil (Fig. 1). The region is in the range of the Brazilian Atlantic Forest domain, one of the most biodiverse and endangered ecosystems in the world (Myers *et al.* 2000). Currently it is reduced to 12% of its original vegetation cover, and mostly composed of small second growth patches (<50 ha) (Ribeiro et al. 2009, 2011). The agricultural matrix in this region consists mainly of sun coffee plantations with manual harvesting, as well as unmanaged cattle pastures mostly owned by small holders. The region presents a subtropical climate with mild summers and winter drought. Rainy season extends from October to March, with an average annual rainfall of 1482 mm. Temperature ranges from -6°C to 31.7°C, for an annual average of 19.9°C (Guimarães *et al*. 2008).

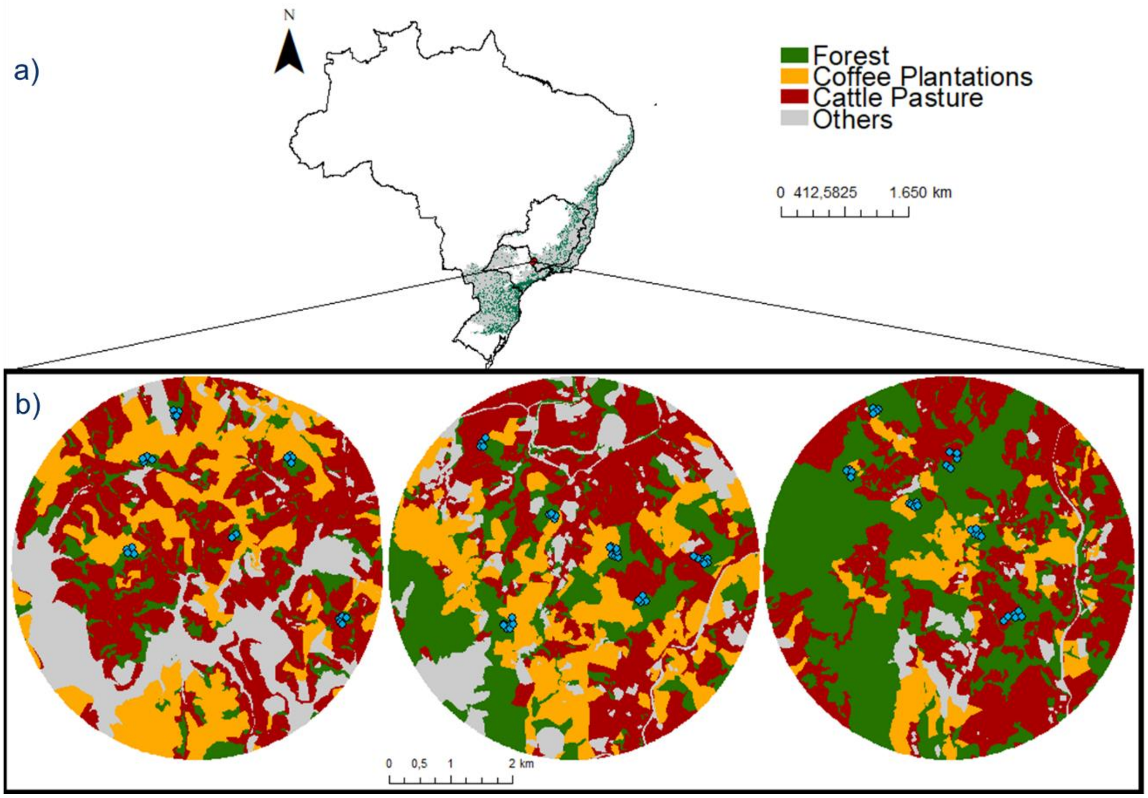

Figure 1. a) Original distribution (grey) and actual cover (green) of the Brazilian Atlantic Forest biome. **b)** The three focal landscapes and their location at the South Minas and Morgiana regions, with the three cover types studied in this study. The grey area in **b)** include all the other cover types not included in our analysis.

Sampling site selection: Within each focal landscape, we selected six forest patches, controlling for forest quality (i.e. similar succession stage, well-established canopy and no human disturbance in the understory) and assuring that the distance between all the edges and the interior of the forest was higher than 100 m. Three of the forest patches were adjacent to coffee plantations (less-contrasting matrix), and three to cattle pastures (more-contrasting matrix), forming paired sampling locations (Fig. S1). Each interface was spaced at a minimum of 800 m (2,170.98 ± 935.57 m) from each other in order to guarantee spatial independence. In each forest-matrix interface we applied a distance treatment to allocate our sampling points, locating one sampling point at 50 m and at 100 m from forest edges in both directions: towards the forest and the matrix interior (N = 4 sampling points per interface, N = 24 sampling points per focal landscape). To avoid interference in recruitment of insects between the two sampling points in the same environment, we located them in parallel and separated them by a minimum of 50 m (Fig. 2).

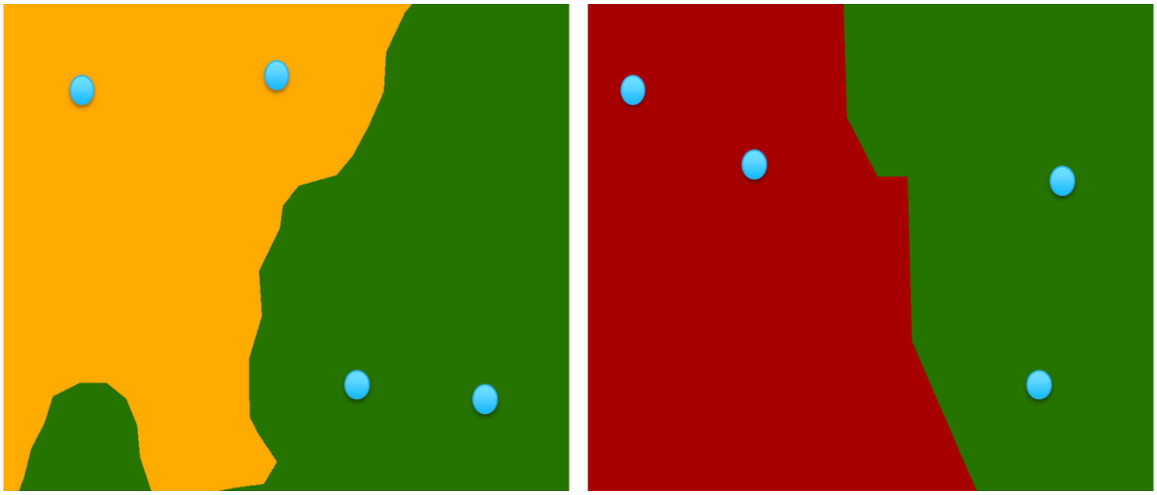

Figure 2. Experimental sampling design: paired sampling points at 50m and 100m from forest edge at coffee plantations (yellow) and cattle pastures (red).

In order to homogenize other possible sources of variation across our study (Pasher *et al*. 2013), we constrained the focal landscapes to elevations ranging from 800 to 1,300 masl, ferric red latosol or argisol soil, and a predominant matrix land-use type of coffee plantations (20.93 ± 7.33%) and cattle pastures (35.14 ± 1.09%). To map the land uses in the three landscapes we used high resolution images (Quantum GIS 2.18.13, Google Maps Satellite Imagery 2017), with a reference scale of 1:5,000.

Insect sampling: In each sampling point we established a vertebrate-exclusion experiment, exposing baits composed of 150.0 ± 0.4 g of fresh chuck steak during six continuous days to obtain data from both scavenger insect community composition and the carrion removal service. We determined exposure time through previous experiments, which indicated that most of the baits were totally removed at the sixth day. Bait exclusion consisted of iron cages for trapping mice, protecting the bait from vertebrates and allowing access only to insects (Fig. S2-a).

We sampled each interface in random order to avoid temporal dependency on sampling effort. Due to logistics limitations, we conducted surveys in half of the interfaces of two different focal landscapes per campaign. We also chose the interfaces randomly, making sure that the three interfaces per landscape were not all of the same matrix type. We collected the adult stages of scavenger insects every two days after placing the bait, from 0800h to 1400h. Thus, we visited each sampling point a total of three times. Since communities of scavenger insects experience species succession as carrion decomposes, this method allowed getting a more complete sample of the community. We collected the crawling insects manually and used an entomological net to capture the flying ones. Sampling at each point took approximately 10 minutes. We preserved the samples in 70% alcohol and separated the samples to pin the insects and identify them to the highest possible taxonomic level.

Carrion removal assessment: To measure the carrion removal ecosystem service, we determined the amount of carrion removed by scavenger insects at the sixth day of sampling. We controlled for mass loss due to dehydration by placing three additional control baits in each type of environment (N = 9), using distant locations to avoid any interference in scavenger insect attraction. We put the control baits inside of iron cages and isolated them with fine mesh to prevent access to insects (Fig. S2-b). These controls also stood for six days, with mass measurements at the beginning and at the end of this period. We averaged this weight difference for each environment type (forest patches = 16.4 ± 13.6 g, coffee plantation = 23.4 ± 17.5 g, cattle pasture = 49.0 ± 13.7 g) and subtracted these values to the weight differences obtained from the baits used for insect collection. Using this approach we thus controlled for dehydration and any non-biotic carrion losses.

Landscape metrics: We used an Atlantic Forest raster from MapBiomas (2013) to calculate four landscape metrics using each sampling point as reference: forest cover amount (percentage of landscape occupied by native forest habitat), number of forest patches, forest edge density (sum of the lengths in meters of all edge segments, divided by the total landscape area in square meters and then converted to hectares) and an aggregation index (the number of adjacent patches of forest habitat, divided by the maximum possible number of adjacencies). We chose these metrics since they give a notion of the structure of forest habitat in the landscape (Uuemaa *et al.* 2009). We calculated these metrics using the 'ClassStat' function from the 'SDMTools' R package (VanDerWal *et al.* 2014).

Species richness and community composition: We used two diversity measures to describe the scavenger insect community: species richness and community composition. Species richness was given by the overall species accumulation per sampling point. While some specimens were identified as morpho-species (hereafter species), the following groups were identified up to species level by specialized taxonomists: Formicidae (Rony Peterson Santos de Almeida, Museu Paraense Emílio Goeldi), Scarabaeidae and Trogidae (Marcely Valois, Universidade Federal do Pará), Vespidae (Orlando Tobias Silveira, Museu Paraense Emílio Goeldi), Muscidae (Lucas Roberto Pereira Gomes), and Calliphoridae and Sarcophagidae (Caroline Costa de Souza e Fernando da Silva Carvalho Filho, Museu Paraense Emílio Goeldi) (Table S1). We also computed Chao estimate of species richness, representing a sample-size corrected richness.

To assess community composition we ran a Principal Coordinates Analysis (PCoA) using the Jaccard dissimilarity index with the ‘vegan’ R package (Oksanen *et al.* 2018, R Core Team 2018), employing presence-absence of species. Since the first two axes of this PCoA were only able to explain 16.14% of total variance, we decided to run another analysis grouping species into families. This grouping improved the amount of total variance explained by the first two axes (MDS1= 18.91%, MDS2= 13.87%, accumulated variance= 32.78%), which were thus used as proxies of community composition in subsequent analysis. MDS1 described the scavenger insect community according to colonization strategies: ants (positive values) vs. the rest of the scavenger insect families (negative values). MDS2 described the scavenger insect community according to the environments where they predominated, separating the community in forest-associated families (negative values) and matrix-associated families (positive values) (Fig. S3). To corroborate this environment preference separation we calculated the occurrence frequency of each family of scavenger insects in forest patches or in both matrices, using 70% of occurrence as a threshold to determine predominance for either environment type. We classified those families that did not reach this threshold as habitat generalists, since they did not predominate in any particular environment. Our categorization matched the MDS2 separation, with generalist groups occupying values around zero.

Statistical analysis: Given that different taxonomic groups respond to landscape structure at different spatial scales (Miguet *et al.* 2016), we tested the response of the community of scavenger insects to landscape structure at different scales of analysis (from 200 - 1200 m, every 200 m). We ran seven linear mixed-effect models (one for each scale and the seventh corresponding to a null model) for each landscape metric (forest cover amount, number of forest patches, forest edge density and aggregation index), using each paired interface as random factor. In the case of species richness models, we fitted generalized mixed-effect models with Poisson distribution error and controlled for overdispersion adding an individual-level random effect (sampling points; Harrison *et al.* 2018), while linear mixed effect models were employed to analyze community composition (using the first two PCoA axes as response variable). We then chose the best spatial scale for each landscape metric through a model selection procedure (see below), determining that 200 m was the scale at which species richness and community composition of scavenger insects better respond to landscape structure (Table S2).

To determine the effect of landscape structure on the community of scavenger insects, we performed a two-step procedure. First, to test the effect of matrix type on species richness and community composition, we used the two predictor variables measured at the focal landscape level: environment type (forest patches, coffee plantations or cattle pastures) and distance from forest edge (50 m and 100 m). Since the focal landscapes lacked the required number of levels ($N > 5$) to be included in the model as a random effect (Bolker 2015), we included it as a fixed effect to consider other possible sources of unaccounted variation. We ran a set of models (GLMM with a Poisson error distribution to model species richness, and LMM to model community composition) using the most logical combinations of these three variables in unique, additive and double interaction models, as well as a null model. We used the paired interfaces as a random effect in all models. To control for overdispersion in Poisson GLMMs we added an individual-level random effect (sampling points). In a second step, we tested the effect of landscape structure on species richness using the four landscape metrics measured at the 200 m scale: forest cover amount (0.08 - 0.89; min-max), number of forest patches (1 - 4), forest edge density (0.004 - 0.02) and aggregation index (67.69 - 98.51). We ran another set of models (GLMM with a Poisson error distribution to model species richness, and LMM to model community composition) using unique and additive variations of these four variables, as well as a null model. We excluded those models containing correlated predictor variables ($r > 0.6$) and included the paired interfaces as a random effect in all models. To control for overdispersion in Poisson GLMMs we added an individual-level random effect (sampling points).

To test the effect of species richness and composition of the scavenger insect community on carrion removal service, we first used species richness and environment type as predictor variables, and the proportion of carrion removed as the response variable. We ran a set of generalized linear mixed-effect models with a binomial error distribution using the proportion of removed carrion as the response variable in unique, additive and double interaction variations of the two predictive variables, as well as a null model. We also included the paired interfaces as a random effect and controlled for overdispersion adding an individual-level random effect (sampling points). To test the effect of community composition over carrion removal, we also applied generalized linear mixed-effect models with binomial error distribution, but using the first two PCoA components and environment type as predictor variables instead. All models were implemented using the 'lme4' R package (Bates *et al.* 2015), and model selection was performed employing the 'MuMIn' R package (Barton 2018) and based on the Akaike Information Criterion (AIC) (Burnham & Anderson 2002), using ∆AIC<2 as reference.

Results

We recorded a total of 167 species, distributed in 35 families and five orders (Table S1). The most representative families were Sarcophagidae (Diptera), Muscidae (Diptera) and Formicidae (Hymenoptera), with 20, 13 and 12 species, respectively. The most frequent families were Sarcophagidae, Muscidae, Ulidiidae, Chloropidae, Formicidae and Drosophilidae. The scavenger insect community was mostly composed of matrix-associated species (N = 81), followed by forest-associated species (N = 54) and generalists species (N = 32). Overall, total species richness was higher in native forest patches (N = 107), followed closely by coffee plantations (N = 105). Cattle pastures presented the lower total species richness (N = 74, Table 1). According to the Chao estimate of species richness, we were able to sample around 65 - 70% of the scavenger insect community (Table S3).

Table 1. Total species richness of scavenger insects according to focal landscape, matrix type and distance from forest edge.

	Edge Distance	**Focal Landscape**			**Total**	
		1 (13%)	**2 (28%)**	**3 (48%)**		
Forest	50 m	32	43	41	76	107
	100 m	38	41	40	77	
Coffee	50 m	24	55	35	72	105
	100 m	38	43	29	81	
Pasture	50 m	26	34	17	47	74
	100 m	31	21	20	52	
Total		93	119	97	169	

Table 2. Summary statistics for the best models explaining scavenger species richness and community composition according to matrix type, landscape structure, and parameter estimates with standard error for the selected models.

Focal Landscape Scale							
Response Variable	Predictor Variable(s)	AIC	ΔAIC	ωAIC	Parameter	Estimate (SE)	Pr(>|t|)
Sp. Richness	Matrix Type***	465.8	0.00	0.73	Intercept	2.10 (0.13)	<0.001
					Coffee	0.65 (0.15)	<0.001
					Pasture	0.00 (0.16)	0.99
Community Composition (MDS1)	~Matrix Type*	153.8	0.00	0.54	Intercept	0.04 (0.13)	0.78
					Coffee	-0.36 (018)	0.05
					Pasture	0.21 (0.18)	0.24
Community Composition (MDS2)	~Matrix Type*	74.8	0.00	0.54	Intercept	-0.60 (0.08)	<0.001
					Coffee	1.01 (0.10)	<0.001
					Pasture	1.39 (0.10)	<0.001
200 m Scale							
Response Variable	Predictor Variable(s)	AIC	ΔAIC	ωAIC	Parameter	Estimate (SE)	Pr(>|t|)
Sp. Richness	~N. Patches**	471.1	0.00	0.52	Intercept	2.26 (0.11)	<0.001
					N. Patches	0.21 (0.07)	0.002
Community Composition (MDS2)	~Forest Cover*** + N. Patches*	136.3	0.00	0.54	Intercept	0.00 (0.10)	1.00
					N. Patches	0.16 (0.08)	0.05
					Forest Cover	-0.45 (0.09)	<0.001

Likelihood Ratio Tests significance levels: * p =0.05; ** p < 0.01; *** p< 0.001

Environment type was the best predictor of both scavenger insect species richness and community composition at the focal landscape level (Table 2). Average species richness of scavenger insects per sampling point (mean ± sd) was higher in coffee plantations (19.89 ± 11.82) compared to forest patches (11.06 ± 8.27) and cattle pastures

(10.94 ± 7.95, Fig. 3). Ants were a stronger component of the scavenger community in cattle pastures and forest patches, while in coffee plantations the community was mainly composed of the other scavenger insect groups, such as beetles and flies. There was also a clear separation between groups associated with forest patches and those associated with matrices (Fig. S1). The best 200m scale landscape metric describing species richness was the number of forest patches, which is positively associated with number of species (Table 2, Fig. 4). From our proxies of community composition (the two PCoA axes) only the second one was significantly affected by landscape structure at the 200 m scale (Table S2). The occurrence of forest associated scavenger insects was associated with higher forest cover and lower number of forest patches (Fig. 4).

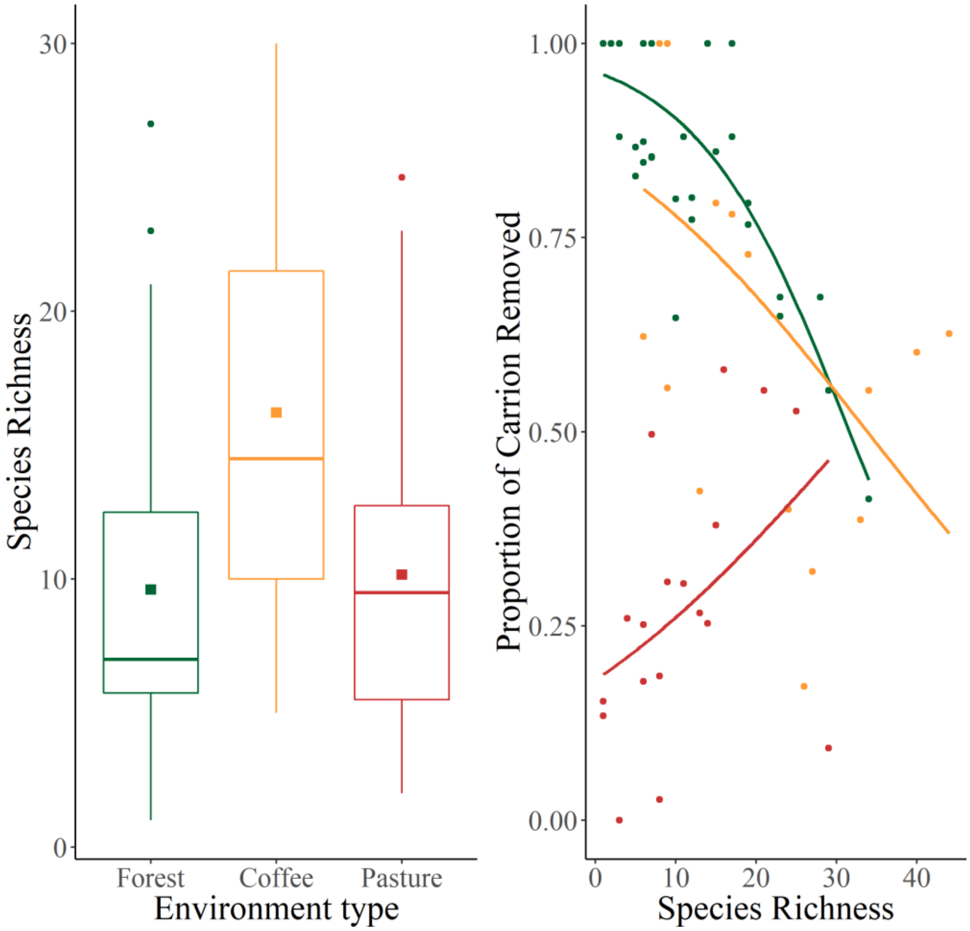

Figure 3. a) Boxplots showing the average species richness of scavenger insects for each environment. **b)** Proportion of carrion removed in relation to species richness of scavenger insects in the same three environments.

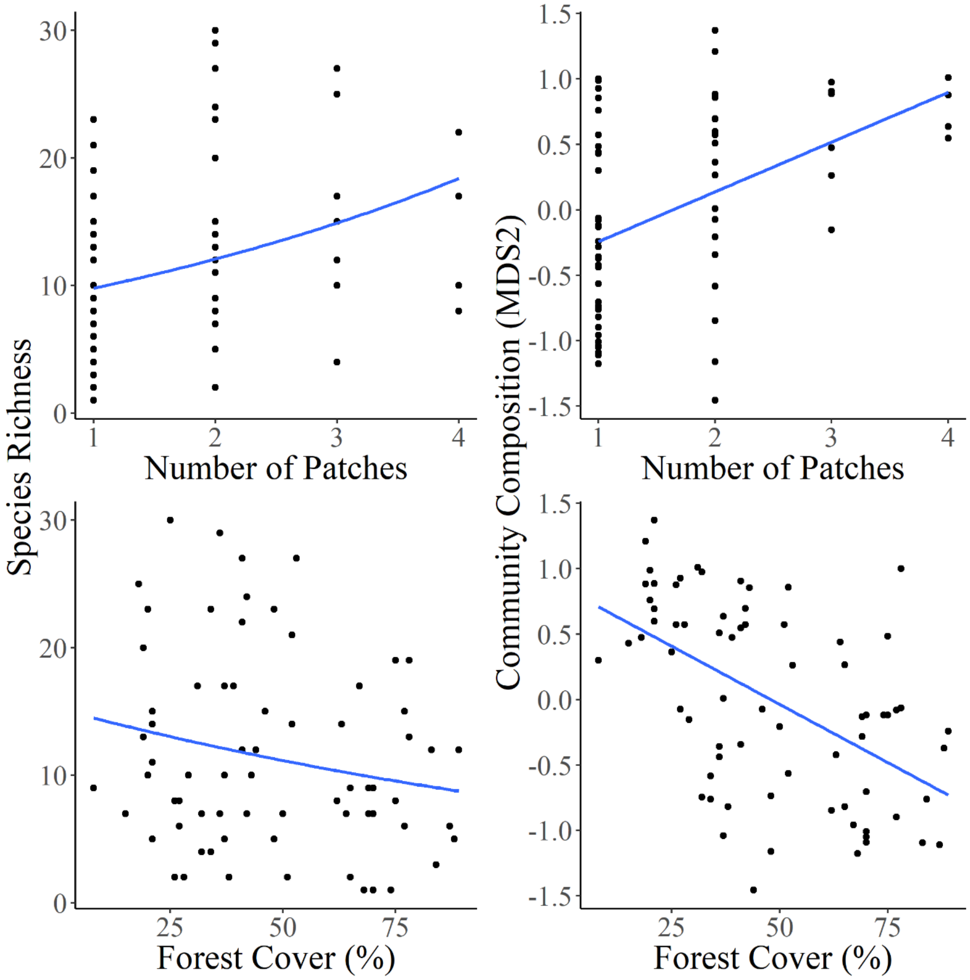

Figure 4. Species richness and community composition (MDS2) of scavenger insects in relation to the number of forest patches and forest cover measured at the 200m scale.

Environment type was also a key predictor of carrion removal ecosystem service (Table 3). The amount of carrion removed was higher in forest patches (123.4 ± 17.0 g), followed by coffee plantations (93.6 ± 31.9 g), and lastly by cattle pastures (41.3 ± 26.3 g). In general, there was a negative significant relationship between carrion removal and species richness, especially in forest patches and coffee plantations. However, in cattle pastures this relationship was positive (Table 3, Fig. 3). Regarding community composition, carrion removal was generally higher when only ants colonized the bait, but in cattle pastures the ensembles composed by the rest of the families were the ones providing a higher carrion removal (Table 3, Fig. 5). Forest-associated scavenger insects were more efficient on carrion removal compared to the matrix-associated species (Table 3, Fig. 6). In forest patches, the main families associated with a higher carrion removal were the beetle families Scarabaeidae and Silphidae, and the fly family Mesembrinellidae. Higher carrion removal in coffee plantations was associated to species from Muscidae and Sarcophagidae families, as well as forest-associated groups like the two beetle families mentioned above, which also occurred in this environment. Finally, carrion removal in cattle pastures was mainly associated with families more frequent in matrix, like Sarcophagidae, Ulidiidae, Faniidae and Calliphoridae, lacking the forest species component.

Table 3. Summary statistics for the best models explaining carrion removal according to species richness or community composition and matrix type, and the parameter estimates with standard error for the selected models.

Response Variable	Predictor Variable(s)	AIC	ΔAIC	ωAIC	Parameter	Estimate (SE)	Pr(>|t|)
Carrion Removal	~Sp. Richness : Matrix Type**	614.0	0.00	0.98	Intercept	5.72 (0.74)	<0.001
					Sp. Richness	-0.23 (0.06)	<0.001
					Coffee	-1.04 (1.44)	0.47
					Pasture	-8.01 (1.21)	<0.001
					Sp. Richness:Coffee	0.05 (0.09)	0.55
					Sp. Richness:Pasture	0.33 (0.10)	<0.001
	~ Community Composition (MDS1) : Matrix Type**	624.6	0.00	0.94	Intercept	3.49 (0.44)	<0.001
					MDS1	1.82 (0.58)	0.002
					Coffee	-1.32 (0.85)	0.12
					Pasture	-4.56 (0.73)	<0.001
					MDS1:Coffee	-0.59 (1.47)	0.69
					MDS1:Pasture	-2.89 (0.94)	0.002
	~Community Composition (MDS2) + Matrix Type**	633.0	0.00	0.77	Intercept	3.35 (0.67)	<0.001
					MDS2	-0.31 (0.80)	0.70
					Coffee	-1.42 (1.13)	0.21
					Pasture	-4.47 (1.33)	<0.001

Likelihood Ratio Tests significance levels: * p =0.05; ** p < 0.01; *** p< 0.001

Discussion

Our results bring novel evidence of landscape structure affecting scavenger insect communities and the carrion removal service they provide. First, species richness increased with forest fragmentation, favoring the expansion of both generalists and matrix associated-species, while the predominance of forest-associated species was related to landscapes with higher forest amount and lower fragmentation. We found matrix type to be a key factor determining the composition of scavenger insect community, with ensembles of scavenger insects in coffee plantations (less-contrasting matrix) being richer than in cattle pastures (more-contrasting matrix) and forest patches. There also was a clear separation in community composition between forest and both matrices, the latter showing a greater component of matrix-associated species, but with some forest-associated species also found in coffee plantations. Lastly, carrion removal service was more efficient in both forest patches and coffee plantations than in cattle pastures. In general, the ensembles with lower species richness removed more carrion than the richer ones, since the presence of certain groups of forest-associated species was found to be more important for the carrion removal provision than number of species.

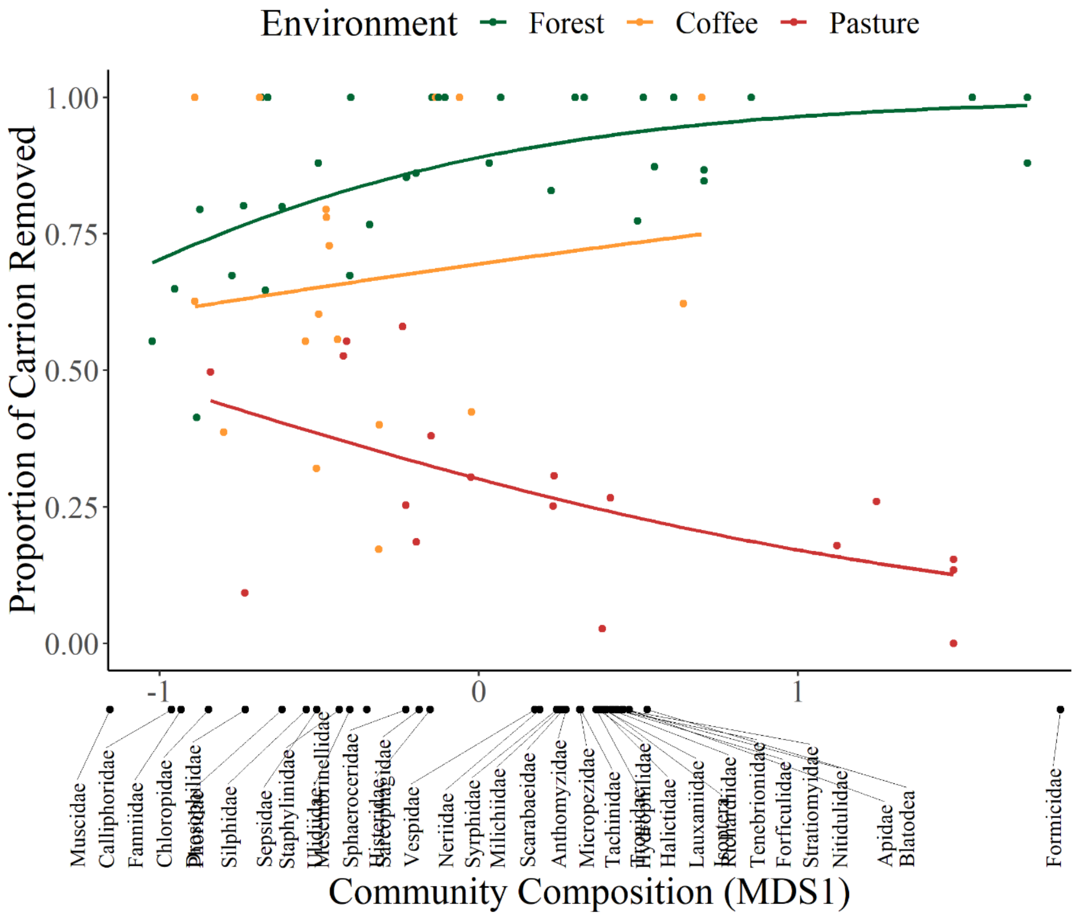

Figure 5. Proportion of carrion removed according to community composition (MDS1) in each environment. The families associated to the MDS1 axis are shown below.

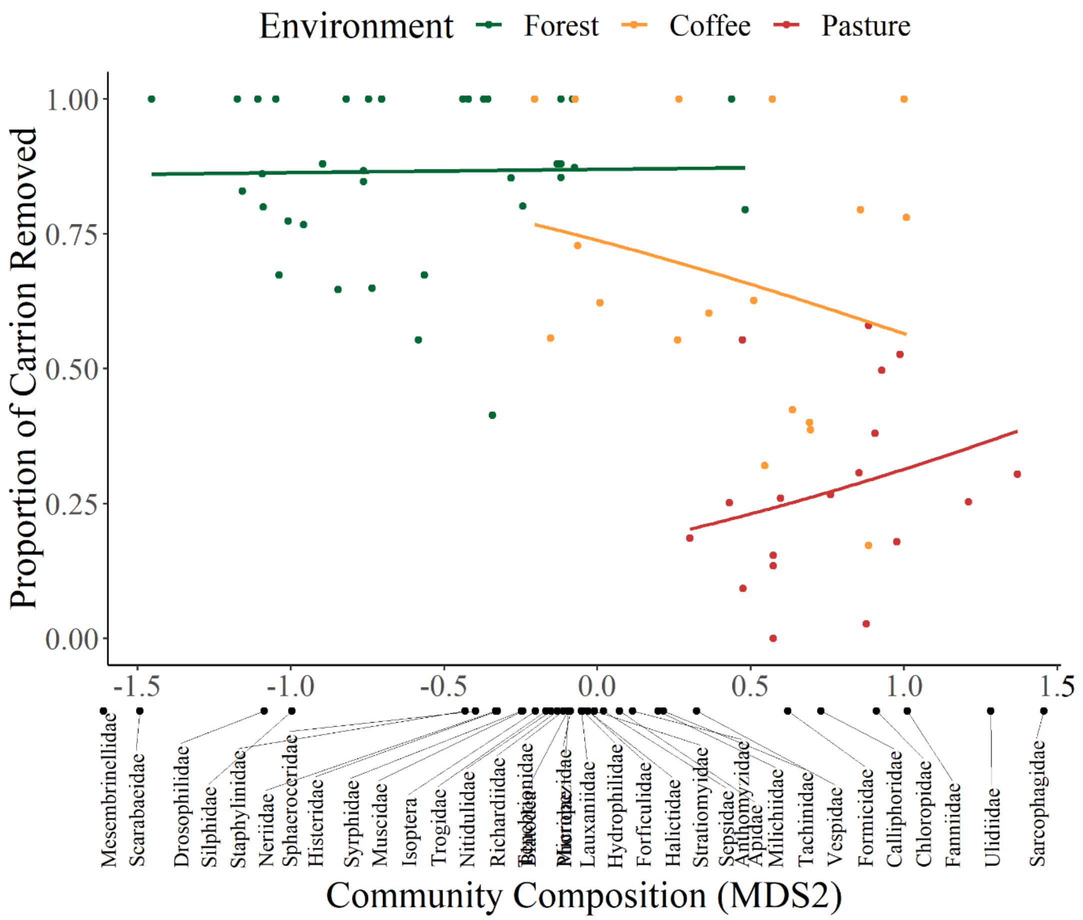

Figure 6. Proportion of carrion removed according to community composition (MDS2) in each environment. The families associated to the MDS2 axis are shown below.

As predicted, environment type was a key factor affecting the community of scavenger insects attracted by carrion, with richer communities found in coffee plantations compared to cattle pastures. The shrubby structure of coffee plantations resembles the structure of forest patches more than cattle pastures, increasing matrix suitability and propensity of use for forest-associated species (Prevedello & Vieira 2010). Given the nature of carrion as an ephemeral and patchy resource, an important component of the scavenger insect community utilize other resources available in their environment when carrion is absent (Braack 1987, Wilson & Wolkovich 2011). Thus, less contrasting agroecosystems might present higher productivity and food availability (fruits, detritus, prey) compared to cattle pastures (Tscharntke *et al.* 2008, Campbell *et al.* 2011). However, species richness in coffee plantations was unexpectedly higher than in forest patches. This result might be influenced by the complexity of the environmental structure, which interferes in the carrion signal, obstructing the perception of the resource and its eventual colonization (Braack 1987). Carrion perception might be easier in both coffee plantations and cattle pastures. In the latter, however, the absence of protective vegetation also implies a lack of protection against predators and solar radiation. As arthropods are very sensitive to temperature, their physiological performance, and their reproductive and survival capacity are compromised in this type of environment (Estay *et al.* 2014). Thus, these open and less structured environments may actually hinder the colonization of carrion, in spite of facilitating its perception.

Unexpectedly, we found a positive effect of fragmentation (number of patches) on scavenger insect richness. Many studies have demonstrated that habitat fragmentation can positively affect biodiversity (see Fahrig 2017). While our results support these findings, the richer communities of scavenger insects were composed of a high proportion of matrix-associated and habitat generalist species, often favored by an increment of native habitat loss and fragmentation, since they are adapted to use various environment types in the landscape (Batáry *et al*. 2007, Spiesman & Cumming 2008, Brückman *et al*. 2010, Stefanescu *et al.* 2011, Audino *et al.* 2014, Ferrante *et al.* 2017). On the other hand, the higher number of forest-associated species in the less fragmented and more forested landscapes indicates a high level of sensibility to habitat disturbance and fragmentation, given that forest specialists have a more limited habitat use and their development is favored by more stable environments (DeVictor *et al*. 2008, Ekroos *et al.* 2010, Estavillo *et al*. 2013). With habitat loss and fragmentation, this environmental stability is lost through habitat degradation and shifts in community composition caused by invasion of matrix species, making the population of forest-associated species prone to demographic and environmental stochasticity, resulting in further diversity loss (see Pardini *et al*. 2017). Usually there is a native habitat cover threshold around 30-50% at which communities experience a turnover in composition, shifting from a prevalence of native habitat specialists to habitat generalists and matrix specialists when under this threshold (Gibbs 1998, Desrochers *et al*. 2011, Martensen *et al.* 2012, Banks-Leite *et al*. 2014, Morante-Filho *et al*. 2015). Thus, maintaining forest cover in agricultural landscapes around this value could help to avoid taxonomic and functional homogenization, where the native species are lost through colonization of more opportunistic ones and the ecosystem functioning is greatly reduced (Olden *et al*. 2004, Olden 2006).

Contrary to what we expected, overall carrion removal did not depend on high species richness, but on the occurrence of efficient scavenger insect groups more frequently found in forest patches, such as ants, beetles and some fly families. Even though our findings contrast with other studies relating higher provision of ecosystem services with higher species richness (such as water treatment, Engelhardt & Ritchie 2001; seafood production, Worm *et al.* 2006; net primary productivity, Costanza *et al.* 2007; seed dispersal, García & Martínez 2012; and production of tree biomass and soil carbon storage, Gamfeldt *et al.* 2013) the opposite pattern is also reported. Straub & Snyder (2006) and Rizali *et al*. (2018) found that the identity of predator species is more important for pest control than species richness per se. Likewise, Farwig *et al.* (2014) found that carrion removal depends more on the community composition than on species richness.

In our study system the most efficient forest groups occurred also in coffee plantations due to spillover movement. Although the spilling over species occurred in lower frequency in coffee plantations, their presence was related to higher carrion removal, while in cattle pastures they were completely absent. It has been proven that coffee plantations can facilitate the cross-habitat spillover process of forest-associated species, compared to more-contrasting matrices like cattle pastures (Boesing *et al*. 2017). Nonetheless, even when the forest associated species were absent, the ensembles found in coffee plantations were able to remove carrion as much as the ensembles of forest patches. Slade *et al*. (2017) demonstrated that, while some species are more efficient providing an ecosystem service than others, in their absence the remaining species are capable of maintaining a similar service provision. Since the ensembles of scavenger insects in coffee plantations were richer compared to cattle pastures, functional diversity could be higher in this less contrasting matrix, increasing the possibility of compensation of forest species absence (Van Mechelen *et al*. 2015).

With community composition emerging as an important mediator of carrion removal ecosystem service, functional traits could unravel the mechanisms behind the service provision (Philpott *et al*. 2009). Some of these functional traits in scavenger insects could include the social organization, the strategies some flies use to first colonize the carcass and reduce interspecific competition in the larval component (Braack 1987), or body size, which translates in a higher amount of resource manipulated per individual. Farwig *et al.* (2014) found that larger groups of scavenger insects are more efficient removing carcasses than the smaller ones. In general, there is a trend of larger insect species to be more frequent in native habitats, while in the matrix the biomass of these groups tends to be lower as the intensity of land-use increases (Gibss & Stanton 2001, Larsen *et al*. 2008, Hidayat *et al*. 2010). Almost half of the species recorded in our study system were of small size (<5 mm of body length), while the larger ones (15-25 mm) comprised only 6% of the total community. These larger groups (mainly beetles, some ant species and the mesembrinellid flies) were associated with higher carrion removal and were more frequently found in forest patches. Deforestation and fragmentation thus affect negatively these larger and more efficient groups, in turn hindering the provision of ecosystem services (Hall *et al.* 2019).

In addition to the landscape structure influence over the scavenger insect community and the carrion removal service, the properties of the carrion themselves could have a bottom-up effect over the community and, in turn, over the ecosystem service as well. Communities get structured around resources depending on the traits they present, with loss of these traits resulting in simpler communities (Bukoviszky *et al.* 2008, Le Lann *et al.* 2014, Korboulewsky *et al.* 2016, Pintar &Resetarits 2017, Ziesche 2017). Carrion, for example is very diverse in sub-resources, particularly in fluids containing blood, fat and bacteria, which get enriched by larval activity (Braack 1987). As we demonstrated with our control treatment, carrion in cattle pastures experienced higher dehydration compared to both forest patches and coffee plantations due to higher solar radiation, meaning a loss of these rich fluids. Coupled with a reduced larval activity (S.A-M, personal observation), carrion in cattle pastures may result less attractive and its characteristics may restrict how much of the resource can be used by the scavenger community, structuring a simpler community that is unable to provide a good ecosystem service.

Finally, it is important to acknowledge some limitations of our study design and implications when drawing our conclusions. First, there is a huge challenge of identifying insects to the highest taxonomic level, limiting the identification of some groups to morpho-species due to the unavailability of taxonomic specialists. Nonetheless, the morpho-species level of identification has been found to be an accurate approximation to community composition when the full identification is unavailable (Oliver & Beattie 1996, Derraik *et al.* 2002). Second, although incorporating the abundance of specimens provides key information regarding the provision of ecosystem services (Winfree *et al.* 2015), we performed our community composition analysis based on presence-absence data. The reason for this is that our communities included an important component of eusocial insects (mainly ants and wasps), which abundance could not be taken into account in the same way as with the other groups using the applied methodology of data collection. Nonetheless, using presence-absence data was enough to understand under which conditions the scavenger insect groups are present and how it relates to the ecosystem service provision. Third, working in one of the most diverse biomes of the world may need for extensive sampling effort. However, we found nearly 70% of the total estimated richness of scavenger insects in our study, indicating that our sample is representative of the scavenger insect community.

Concluding remarks: Our findings advance the understanding on landscape effects on scavenger communities and the carrion removal service they provide. Since the groups providing more efficient carrion removal were forest-associated species, the conservation of forested areas or restoration of less productive environments could ensure or increase carrion removal services in agricultural landscapes. Since matrix type was found to be the main driver of species spillover from forest patches into less contrasting matrices, consequently influencing the provision of carrion removal in anthropogenic environments, our results suggest more permeable matrices (more structurally similar to forest patches) could increase service provisioning. One way of reducing matrix contrast without affecting production area could be through the implementation of hedgerows (which were practically nonexistent in our region of study), preferably using native species. For instance, Pollard & Holland (2006) demonstrated how hedgerows improve the diversity of several insect groups inside of agroecosystems, including the scavenger component. This has been corroborated in other insect groups and various crop types (Baudry *et al*. 2000, Morandin *et al.* 2011, Paoletti *et al.* 2012, Morandin *et al*. 2014, to name a few).

Given that the scale at which landscape structure best explained the community of scavenger insects was a smaller scale (200 m), these conservation measures could be implemented at the farm level, allowing the owner to better control the management process and the benefits received in return. Thus, the conservation and restoration of native habitats, as well as the reduction of matrix contrast, could help create biodiversity-friendly agricultural landscapes that ensure sufficient carrion removal services, avoiding the cost of manually removing carcasses, preventing outbreaks of diseases, helping to reincorporate nutrients more easily into crops and improving overall human well-being.

Acknowledgments

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Supplementary Material

Table S1. Classification of the scavenger insects registered in the three types of habitat and the number of sample units they appeared during the sampling period.

Order	Family	Morpho-species	Forest	Coffee	Pasture	Total
Blatodea	-	Blatodea		1		1
	-	Isoptera	1			1
Coleoptera	Histeridae	Histeridae 1		3	1	4
		Histeridae 2	2	4		6
		Histeridae 3		3		3
		Histeridae 4	3			3
	Hydrophilidae	Hydrophilidae		1		1
	Nitidulidae	Nitidulidae	2	1		3
	Scarabaeidae	*Ateuchus* sp		1		1
		Canthon angularis	2	5	1	8
		Coprophanaeus cerberus	1			1
		Coprophanaeus saphirinus		1		1
		Deltochilum furcatum	3			3
		Deltochilum morbilosum	10	1		11
		Deltochilum rubripenne	4			4
		Deltochilum sp	6			6
		Dichotomius bicuspis	1			1
		Eurysternus paralelus	4	1		5
		Scybalocanthon nigriceps	1			1
	Silphidae	Silphidae	16	5	1	22
	Staphylinidae	Staphylinidae 1	1	4		5
		Staphylinidae 2	1	2		3
		Staphylinidae 3		2		2
		Staphylinidae 4	5	1		6
		Staphylinidae 6	3			3
		Staphylinidae 7	1			1
		Staphylinidae 8		1		1
		Staphylinidae 9		1		1
		Staphylinidae 11	1			1
		Staphylinidae 12	2			2
		Staphylinidae 13	1			1
	Tenebrionidae	Tenebrionidae		1		1
	Trogidae	*Polynoncus* sp	1			1
Dermaptera	Forficulidae	Forficulidae		1		1
Diptera	Anthomyzidae	Anthomyzidae		2	2	4
	Calliphoridae	*Chrysomya albiceps*		12	5	17
		Chrysomya putoria		1	1	2
		Cochliomyia macellaria		6		6

	Hemilucilia segmentaria	1	1		2
	Hemilucilia semidiaphana	4	1		5
	Hemilucilia townsendi	2	1		3
	Lucilia eximia	3	13	5	21
	Lucilia japuhybensis	10	5		15
Chloropidae	Chloropidae 1	2	13	2	17
	Chloropidae 2		3	8	11
	Chloropidae 3	1	8	6	15
	Chloropidae 4	14	12	7	33
	Chloropidae 5	1	1	1	3
	Chloropidae 6		2	1	3
	Chloropidae 7		1		1
	Chloropidae 8	1	3		4
	Chloropidae 10			1	1
Drosophilidae	Drosophilidae 1	5	9	4	18
	Drosophilidae 2	15	1		16
	Drosophilidae 3	5	2		7
	Drosophilidae 4	2	1		3
	Drosophilidae 5	11	1	1	13
	Drosophilidae 6	1			1
	Drosophilidae 7	3	1		4
	Drosophilidae 9	2	1		3
	Drosophilidae 10	2			2
	Drosophilidae 11	8			8
	Drosophilidae 12	1			1
Fanniidae	*Fannia* sp. 2	9	10	8	27
	Fannia sp. 5	13	4	3	20
	Fannia sp. 6	3	10	5	18
	Fannia sp. 7	2	2	1	5
Lauxaniidae	Lauxaniidae 1			1	1
Mesembrinellidae	*Mesembrinella bellardiana*	29	1		30
Micropezidae	Micropezidae 1	1	1	1	3
	Micropezidae 2	2		1	3
	Micropezidae 3	1			1
Milichiidae	Milichiidae	1	2	2	5
Muscidae	*Atherigona* sp.	1	8	5	14
	Cariocamyia sp.	1			1
	Cyrtoneurina sp.	4	4	2	10
	Helina sp. 1	1			1
	Musca domestica		1	3	4
	Mydaea sp.		2		2

	Neodexiopsis sp.	1		2	3
	Neomuscina sp. 1	4		1	5
	Neomuscina sp. 3	34	3		37
	Neomuscina sp. 4	4	3	2	9
	Parapyrellia maculipennis	1			1
	Polietina sp.		1		1
	Psilochaeta pampiana		2		2
Neriidae	Neriidae 1	4			4
	Neriidae 2	1			1
Phoridae	Phoridae 1	3	1	2	6
	Phoridae 2	1	5		6
	Phoridae 3	5	1		6
	Phoridae 4	5	4	3	12
	Phoridae 5	1			1
	Phoridae 6	1			1
	Phoridae 7		1		1
	Phoridae 9	1			1
	Phoridae 11	1			1
	Phoridae 12	1			1
	Phoridae 13			1	1
Richardiidae	Richardiidae 2		1		1
	Richardiidae 3	1			1
Sarcophagidae	*Helicobia aurescens*		5	7	12
	Helicobia morionela			3	3
	Lipoptilocnema crispina		1		1
	Lipoptilocnema crispula	3	2	1	6
	Microcerella halli		2		2
	Oxysarcodexia admixta	2			2
	Oxysarcodexia amarali		3	2	5
	Oxysarcodexia fluminensis			1	1
	Oxysarcodexia parva		2		2
	Oxysarcodexia thornax		17	8	25
	Peckia anguilla		9	3	12
	Peckia chrysostoma			1	1
	Peckia collusor		6		6
	Peckia ingens		1	1	2
	Peckia intermutans	1			1
	Peckia lambens	1	2	1	4
	Peckia resona	2		1	3
	Peckia tridentata		3		3
	Ravinia sp.		2		2

		Titanogrypa larvicida			1	1
	Sepsidae	Sepsidae 1	9	8	2	19
		Sepsidae 2	8	2		10
		Sepsidae 3	2		1	3
		Sepsidae 4	1	1	1	3
		Sepsidae 5	2	1		3
	Sphaeroceridae	Sphaeroceridae 1	9			9
		Sphaeroceridae 2		5	3	8
		Sphaeroceridae 3	2	2	1	5
	Stratiomyidae	Stratiomyidae			1	1
	Syrphidae	Syrphidae 1	1			1
		Syrphidae 2		1		1
		Syrphidae 5	2			2
	Tachinidae	Tachinidae 1		2		2
		Tachinidae 2	2	1	2	5
		Tachinidae 3			2	2
		Tachinidae 6			1	1
		Tachinidae 7			1	1
		Tachinidae 8	2			2
		Tachinidae 9	1	1		2
	Ulidiidae	Ulidiidae 1	3	24	15	42
		Ulidiidae 2	1	7	9	17
		Ulidiidae 3	1	1	4	6
		Ulidiidae 4		2	2	4
		Ulidiidae 5			1	1
		Ulidiidae 6			1	1
		Ulidiidae 7			1	1
		Ulidiidae 8		1		1
Hymenoptera	Apidae	*Apis melifera*			1	1
		Meliponini			2	2
	Formicidae	*Acromyrmex* sp	1	1	2	4
		Camponotus rufipes	21	6	6	33
		Camponotus serecieventris	3			3
		Ectatomma edentatum		1		1
		Gnamptogenys moelleri		1		1
		Linepithema neotropicum	1		1	2
		Neoponera verenae			1	1
		Pheidole alpinensis	1	5	2	8
		Pheidole gertrudae	1			1
		Pheidole megacephala	1			1
		Pheidole oxyops		4	2	6

		Solenopsis sp		10	11	21
	Halictidae	Halictidae		1		1
	Vespidae	*Agelaia angulata*	1	1		2
		Agelaia multipicta	1			1
		Agelaia vicina	1	5	2	8
		Polybia scutellaris			1	1

Table S2. Summary statistics of the model selection analysis describing the best landscape scale at which species richness and community composition respond to landscape structure.

Response Variable	Landscape Metric	Scale	AIC	ΔAIC	ωAIC
Species Richness	Forest Cover	200 m*	476.0	0.00	0.59
		800 m	479.8	3.82	0.09
		600 m	479.8	3.85	0.09
		1000 m	479.9	3.92	0.08
		400 m	479.9	3.94	0.08
		1200 m	480.0	4.04	0.08
		Null Model	534.6	58.36	0.00
	Number of Patches	200 m**	471.1	0.00	0.93
		800 m	478.5	7.34	0.02
		600 m	479.4	8.28	0.02
		1200 m	479.8	8.67	0.01
		1000 m	479.9	8.81	0.01
		400 m	480.1	8.95	0.01
		Null Model	534.6	63.49	0.00
	Edge Density	800 m	477.3	0.00	0.29
		400 m	477.8	0.44	0.23
		200 m	478.5	1.20	0.16
		600 m	479.0	1.68	0.13
		1000 m	479.4	2.08	0.10
		1200 m	479.5	2.22	0.10
		Null Model	534.6	57.30	0.00
	Aggregation Index	200 m*	474.6	0.00	0.70
		800 m	479.0	4.41	0.08
		600 m	479.4	4.80	0.06
		400 m	479.5	4.89	0.06
		1000 m	479.9	5.28	0.05
		1200 m	479.9	5.34	0.05
		Null Model	534.6	60.03	0.00
Community Composition (MDS1)	Forest Cover	Null Model	155.9	0.00	0.29
		400 m	157.1	1.26	0.16
		1000 m	157.8	1.93	0.11
		1200 m	157.8	1.96	0.11
		800 m	157.8	1.96	0.11
		200 m	157.8	1.99	0.11
		600 m	157.9	1.99	0.11
	Number of Patches	200 m	471.1	0.00	0.93
		800 m	478.5	7.34	0.02
		Null Model	479.4	8.28	0.02
		400 m	479.8	8.67	0.01

		1200 m	479.9	8.81	0.01
		1000 m	480.1	8.95	0.01
		600 m	534.6	63.49	0.00
	Edge Density	800 m	155.3	0.00	0.25
		Null Model	155.9	0.53	0.19
		400 m	156.0	0.63	0.18
		200 m	156.7	1.34	0.13
		1000 m	157.4	2.09	0.09
		1200 m	157.5	2.16	0.08
		600 m	157.5	2.18	0.08
	Aggregation Index	Null Model	155.9	0.00	0.29
		200 m	157.4	1.53	0.14
		800 m	157.5	1.64	0.13
		1200 m	157.8	1.92	0.11
		400 m	157.8	1.92	0.11
		1000 m	157.8	1.93	0.11
		600 m	157.9	1.99	0.11
Community Composition (MDS2)	Forest Cover	200 m***	137.7	0.00	1.00
		Null Model	164.7	27.01	0.00
		800 m	165.7	27.94	0.00
		1000 m	166.0	28.25	0.00
		600 m	166.2	28.50	0.00
		1200 m	166.3	28.52	0.00
		400 m	166.7	29.01	0.00
	Number of Patches	200 m***	150.1	0.00	1.00
		400 m	162.9	12.83	0.00
		600 m	163.5	13.42	0.00
		Null Model	164.7	14.68	0.00
		800 m	165.9	15.79	0.00
		1200 m	165.9	15.82	0.00
		1000 m	166.7	16.61	0.00
	Edge Density	600 m	164.7	0.00	0.21
		Null Model	164.7	0.08	0.20
		400 m	165.5	0.84	0.14
		800 m	165.5	0.89	0.13
		1000 m	165.8	1.12	0.12
		200 m	166.0	1.30	0.11
		1200 m	166.1	1.46	0.10
	Aggregation Index	200 m***	144.5	0.00	1.00
		Null Model	164.7	20.25	0.00
		400 m	165.2	20.69	0.00

1000 m	166.3	21.81	0.00
600 m	166.5	21.97	0.00
1200 m	166.5	21.98	0.00
800 m	166.5	22.00	0.00

Likelihood Ratio Tests significance levels: * $p = 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table S3. Number of observed species of scavenger insects, richness estimate according to Chao (1987) and percentage of missing species according to this estimation.

Species Richness	Forest	Coffee	Pasture
Observed	107.00	105.00	74.00
Chao Estimate	163.40	157.11	105.17
Chao Standard Error	21.87	20.84	14.14
Species missing (%)	34.52	33.17	29.64

Figure S1. The three environments where the sampling of the community of scavenger insects and the carrion removal ecosystem service was conducted. From left to right: Brazilian Atlantic Forest, Coffee Plantation and Cattle Pastures.

Figure S2. a) Vertebrate-exclusion experiment used to sample the scavenger insect community and measure the carrion removal ecosystem service. b) Control experiment to determine the amount of bait mass loss due to dehydration.

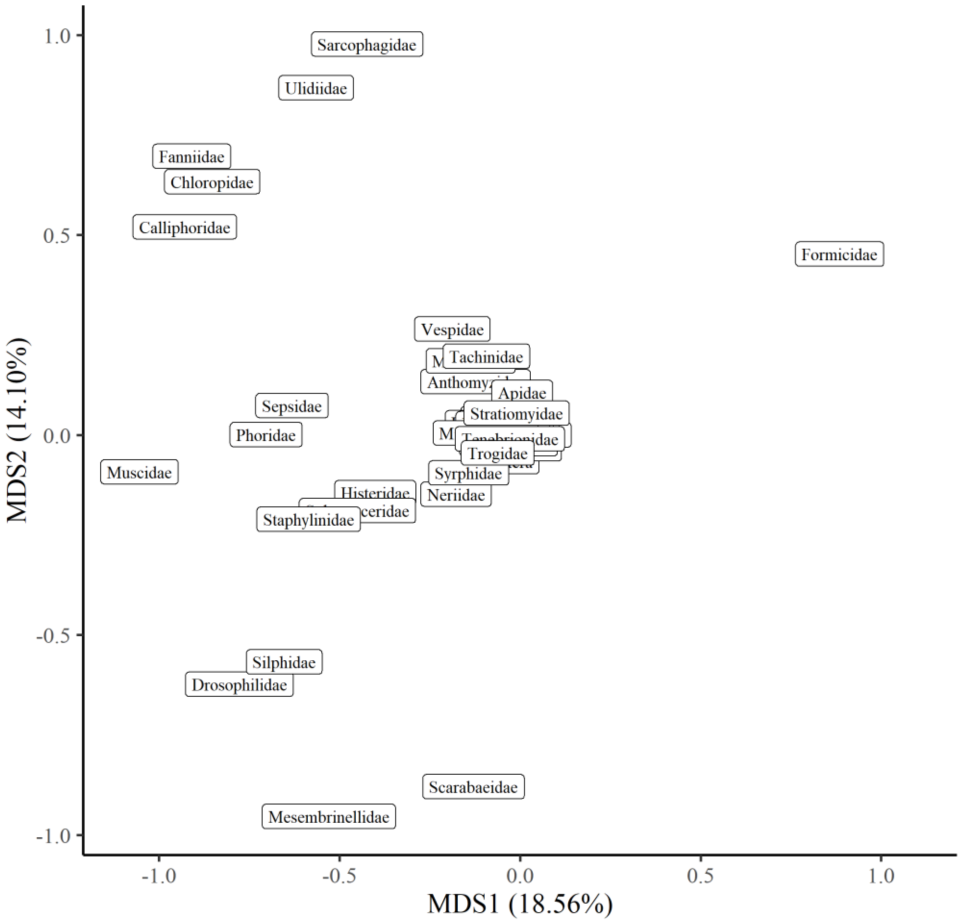

Figure S3. First two components derived from the Analysis of Principal Coordinates for the community of scavenger insects grouped at the family level. The percentage at each axis represents the amount of variance explained by each component.

Discussão Geral e Conclusões

Os nossos resultados demonstraram o claro efeito que a estrutura da paisagem exerce sobre a comunidade de insetos necrófagos, e os efeitos na provisão do serviço ecossistêmico de remoção de carniça. Paisagens agrícolas mais florestadas favorecem a presença das espécies associadas com estes ambientes nativos, enquanto que as paisagens mais alteradas apresentam uma maior riqueza de espécies relacionadas com a matriz ou generalistas de hábitat. Com a perda e fragmentação de hábitat se degradam e perdem as condições ambientais com as quais as espécies associadas a floresta estão adaptadas, mudando a composição da comunidade ao facilitar a invasão das espécies da matriz, o que agudiza a perda de espécies dentro da floresta (Pardini *et al*. 2017). Usualmente esta mudança na composição de espécies por degradação de hábitat tem como limiar 30-50% de cobertura florestal, sendo que paisagens sob esse limiar apresentam comunidades compostas principalmente por espécies de matriz ou generalistas (Gibbs 1998, Desrochers *et al*. 2011, Martensen *et al.* 2012, Banks-Leite *et al*. 2014, Morante-Filho *et al*. 2015). Por tanto, manter as paisagens sobre esse limite de cobertura florestal ajuda a prevenir a perda de espécies e da funcionalidade do ecossistema (Olden *et al*. 2004, Olden 2006).

Além da configuração dos fragmentos de floresta, a matriz agrícola resultou ser um fator crucial em manter as comunidades de insetos necrófagos e a provisão do serviço de remoção da carniça fora do ambiente nativo. Os cultivos de café, sendo uma matriz de menor contraste em relação à floresta, presentaram comunidades mais ricas do que a matriz de maior contraste, o pasto para gado. O café oferece uma maior proteção para os insetos contra as variáveis ambientais, principalmente temperatura, e contra predadores (Prevedello & Vieira 2010, Estay *et al.* 2014). Também pode virar uma importante fonte de recursos alimentícios suplementares caso não tiver carniça disponível (Tscharntke *et al.* 2008, Campbell *et al.* 2011). Estas características da matriz facilitam a ocorrência de insetos necrófagos associados à floresta dentro do café, mantendo uma provisão alta do serviço fora do seu hábitat. Já para outros grupos, como aves, foi demonstrado que cultivos de café permitem o fluxo de espécies fora dos fragmentos de floresta e o uso dos recursos presentes na matriz (Boesing *et al*. 2017). Por tanto, promover usos da terra menos contrastantes com os ambientes nativos ou reduzir o contraste das matrizes agrícolas se torna um requerimento para manter comunidades biológicas diversas e facilitar a presença de espécies nativas na paisagem.

O efeito da matriz sobre a comunidade de insetos necrófagos influenciou também a provisão do serviço de remoção de carniça, onde as comunidades do café conseguiram remover tanta carniça quanto as comunidades da floresta, enquanto no pasto a remoção se manteve sob o 50% do total de carniça disponível. Em contraste com outros serviços ecossistêmicos, que dependem de uma alta diversidade de espécies (Engelhardt & Ritchie 2001, Worm *et al.* 2006, Costanza *et al.* 2007, García & Martínez 2012, Gamfeldt *et al.* 2013), esta alta remoção de carniça esteve relacionada com conjuntos de poucas espécies, dado que a identidade dessas espécies resultou ser mais importante. Grupos específicos de insetos necrófagos, particularmente espécies de tamanho corporal grande e que estavam associados aos fragmentos de floresta, foram os que removeram mais carniça. Estes grupos ocorreram também no café, mas estiveram ausentes no pasto. Já outros estudos demonstraram que dentro de grupos de insetos, espécies de maior tamanho estão relacionadas com hábitats nativos, enquanto que as espécies ocorrentes na matriz tendem ser menores e sua biomassa diminui conforme a intensidade do uso da terra aumentar (Gibss & Stanton 2001, Larsen *et al*. 2008, Hidayat *et al*. 2010). Em insetos necrófagos, esta característica do tamanho corporal está relacionada com um maior fornecimento do serviço de remoção (Farwig *et al*. 2014), fazendo destas espécies associadas com floresta um componente desejável nas comunidades de necrófagos para manter uma alta provisão do serviço na paisagem.

Desta forma, o nosso trabalho ajuda a entender os efeitos da paisagem na comunidade de insetos necrófagos e no serviço de remoção de carniça. Dado que as espécies relacionadas com uma maior provisão do serviço de remoção de carniça são provenientes de florestas nativas, a conservação das áreas florestadas e a restauração dos ambientes menos produtivos vira um manejo necessário para assegurar a provisão deste serviço nas paisagens agrícolas. O tipo de matriz também é crucial para promover o serviço de remoção fora dos ambientes nativos. Portanto, usos da terra menos contrastantes com as florestas ou a implementação de estruturas como cercas vivas nas matrizes agrícolas menos permeáveis promove o fluxo de espécies dentro da floresta para a matriz (Baudry *et al*.

2000, Pollard & Holland 2006, Morandin *et al.* 2011, Paoletti *et al.* 2012, Morandin *et al*. 2014), levando com elas uma melhor provisão do serviço de remoção de carniça. Também é importante tomar em conta a escala na qual a paisagem atua sobre a comunidade de insetos necrófagos. Sendo uma escala pequena (200 m), as medidas de conservação aqui mencionadas podem ser implementadas no nível de fazenda ou propriedade. Isto permite que o proprietário tenha um melhor controle do processo de manejo e perceba de melhor forma os benefícios fornecidos por esta comunidade. Através da conservação e restauração dos ambientes nativos, assim como o aumento da permeabilidade da matriz, o produtor rural criaria paisagens agrícolas mais amigáveis e que assegurariam a provisão do serviço ecossistêmico de remoção de carniça, evitando a remoção manual das carcaças de gado, prevenindo o surto de doenças perigosas e facilitando a reincorporação de nutrientes nos cultivos, entre outros serviços, o que significa uma redução no custo econômico e um aumento no bem-estar humano.

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