Carolina Montealegre Talero

Spatial and temporal aspects of avian spillover in anthropogenic landscapes

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Spatial and temporal aspects of avian spillover in anthropogenic landscapes

Aspectos espaciais e temporais do transbordamento de aves em paisagens antropogênicos

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

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Prof(a). Dr(a).

Prof. Dr. Jean Paul Metzger

Orientador

Dedication

Para Aura Ismaelina Moure

Quien me enseñó a amar y a respetar la naturaleza

Epigraph

“O isolamento nos une num único planeta”

— Domenico de Masi

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General Introduction

Human demand for food production has a great impact over earth´s ecosystems (Tilman et al., 2011). Across the globe, almost 40% of natural habitats have been cleared and altered to maintain human food production (Foley et al., 2011). From this, pastures for cattle cover more than 25% of the global land surface and are the largest type of land use (Asner et al., 2004). Therefore, it is undeniable that agriculture holds a global environmental impact, related to land use and land cover changes and native habitat fragmentation, which threatens biodiversity across the globe (Dirzo & Raven, 2003). The Atlantic Forest of Brazil, one of the most biodiverse biome on Earth (Rezende et al., 2018; Ribeiro et al., 2009), is threatened by the implementation of pastures for cattle, coffee, sugar cane, and *Eucalyptus* plantations (Baptista & Rudel, 2006; Rudorff & Sugawara, 2007), which has reduced patch connectivity and effected animal movement through landscapes.

As humanity continues to over use natural ecosystems, it is increasingly important to understand animal movements in agricultural landscapes. Agricultural landscapes are seen as mosaics of habitat patches interspersed with unsuitable habitats or a hostile matrix (Fahrig et al., 2011). From a functional point of view, these landscapes combine a gradient of areas that span the full spectrum from suitable to unsuitable habitats, and organisms can utilize resources from both crop and non-crop patches (Kupfer et al., 2006). In this condition, species movement across the landscape is important for their survival. The increase in landscape connectivity, through the conservation or implementation of corridors, stepping stones and non-hostile matrices have classically been proposed as a solution to favor animal movements in modified landscapes

(Doherty & Driscoll, 2018) and thus to mitigate the negative effects of agricultural intensification on native species (Awade & Metzger, 2008; Fahrig, 2007; Uezu et al., 2005).

The movement of species across habitat edges, an ecological process denominated as spillover, is an essential feature of the ecology of many species, due to their dependence on resources that are spatially separated (Tscharntke et al., 2012). Spillover movements have been mostly studied in insects (Frost et al., 2015; Rand et al., 2006; Tscharntke et al., 2005) and recently some authors have studied this process in birds (Barros et al., 2019; Boesing et al., 2017). Spillover movements can have strong effects on ecosystem processes, particularly on food web interactions of local communities (Schneider et al., 2013). Such trophic interactions may be important for the provision of important regulation ecosystem services, such as pollination and pest control (Bianchi et al., 2006; Kremen et al., 2007). Natural habitats can be important sources of natural enemies that move into cultivated lands and may perform, for example, important pest control activities (Bianchi et al., 2006).

Natural enemies are organisms that exert biological control over plague populations and reduce the potential damage they could cause to crops of economic importance (Holt & Lawton, 1994). Particularly, insectivorous birds have been proposed as important pest controllers, since they reduce arthropods and plant damage in agroforestry systems (Greenberg et al., 2000; Van Bael et al., 2008). Several characteristics of landscape structure, like forest cover, affect pest suppression carried out by birds (Boesing et al., 2017; Librán-Embid et al., 2017). Therefore, spillover of insectivorous birds should be taken into account when planning landscape management, in order to guarantee the provision of pest suppression in crops. To manage the landscape efficiently, it is thus important to understand how agricultural landscape structure promotes ecological services like avian spillover and this, in turn, influence the provisioning of ecosystem services.

The main objective of this thesis is to advance our current knowledge on how the ecological process of avian cross-habitat spillover is affected by landscape structure. We start this work by systematically reviewing the literature for empirical evidence of landscape structure effects on pollinators and natural enemies. Then, using bird data collected in fragmented landscapes in the Brazilian Atlantic forest, we test how landscape structure features affect bird spillover and community dissimilarity. Finally, we investigate the temporal aspects of avian spillover in anthropogenic landscapes. We hope a better understanding of this avian spillover process can help identify landscape conditions that may favor the provision of ecosystem services, in particular pest control. The main justification and objectives of each chapter are detailed below.

Chapter one is a systematic literature review investigating current empirical evidence of the influence of landscape structure on pollinator and natural enemy spillover. We start by describing the general patterns found in the literature review: year of publication, amount of studies conducted in tropical or temperate zones, type of crops and natural covers surveyed and type of organism studied (vertebrate or invertebrate). To identify if landscape features have an effect over the abundances and richness of both pollinators and natural enemies, we used two analytical methods: vote counting and effect size calculation. With the first method, we found that adjacent habitat type contrast affects spillover of both natural enemies and pollinators. However, with the effect size calculation, we did not find evidence that landscape features affect spillover. Our results suggest that landscapes with soft edges between natural areas and crop fields, are more favorable for spillover movements from natural to anthropic covers, and can thus enhance the provision of pollination and pest control services.

In chapter two we investigated how landscape structure, represented by matrix type, forest cover percentage and fragment size, affect avian spillover direction and community dissimilarity. In our study, bi-directional movements of generalist, forest dependent and insectivorous birds across interfaces were monitored in fragmented landscapes in the Brazilian Atlantic forest. We found strong evidence of an inverse spillover in highly deforested landscapes (i.e. birds moving from crop fields into forest patches). Our results indicate that interface type is a key driver of spillover, given that most of individuals where performing spillover from coffee matrices and not from pastures. Also, interface type interacted with other landscape features, as forest cover and fragments size. In the first case, we evidenced a trend of spillover ratio increasing with forest cover at coffee interfaces. In the second case, larger fragments acted as fonts of individuals in less contrasting matrices. Finally, dissimilarity between individuals coming in and out of the fragments was higher in pasture matrices, evidencing that cross-habitat spillover is more rare in this matrix.

In chapter three we explore how time of day and landscape structure, represented by matrix type, forest cover percentage and fragment size, affect bird spillover direction. Like in chapter two, bi-directional movements of generalist, forest dependent and insectivorous birds across interfaces were monitored in fragmented landscapes in the Brazilian Atlantic forest. This study highlights that interface type is a key factor influencing birds' daily movement across forest edges. The general pattern is a bi-modal peak of activity, with birds more active in the early mornings and in the afternoons, and less active around noon. Interface type was the main factor influencing birds' daily movement across forest edges. In the coffee matrix birds clearly leave forest patches for foraging outside patches in the morning and in the afternoon move back into patches for roosting, while at pasture interfaces, the general pattern is a constant movement into forest patches. We also found additional effects of both forest cover and fragment size where the first influenced spillover of insectivorous species and the second mediated spillover of forest dependent species. These findings highlight the role that landscape structure, particularly matrix type, has over bird temporal spillover.

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CHAPTER 1

IS THERE AN EFFECT OF LANDSCAPE STRUCTURE ON POLLINATOR AND NATURAL ENEMY SPILLOVER? A SYSTEMATIC REVIEW

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Eduardo S. A. Santos, Jean Paul Metzger

Abstract: Cross-habitat spillover, defined as the movement of individuals between distinct habitat types, is an important connectivity process that can at the same time allow species to survive in fragmented landscapes and contribute in ecosystem services provision. However, the links between landscape structure characteristics and spillover movements are still poorly understood. Here we performed a systematic review of the existing literature focused on this topic, considering natural enemy and pollinator spillover movements. We found 50 studies, mostly published in the last four years, and most of them focused on a small group of crops from temperate regions. We used two analytical methods: vote counting and effect size calculation. With the first method, we found that adjacent habitat type contrast affects spillover of both natural enemies and pollinators. However, with the effect size calculation, we did not find evidence that landscape features affect spillover. Our results suggest that landscapes with soft edges between natural areas and crop fields, are more favourable for spillover movements from natural to anthropic covers, and can thus enhance the provision of pollination and pest control services. Yet there is urgent need to develop this research topic in tropical and subtropical regions, where spillover movements can be particularly important to integrate biodiversity conservation with the provision of ecosystem services.

Keywords: agricultural landscape, landscape composition and configuration, ecosystem services, pest control, pollination, effect size.

INTRODUCTION

Agricultural landscapes are seen as mosaics of natural or semi-natural habitat patches interspersed with a matrix of cultivated areas that generally represent inhospitable environments for most native species (Fahrig et al., 2011). This mosaic emerges from the organization of cropping systems by farmers and is not just heterogeneous in space, but also in time, due to crop phenology and management (Vasseur et al., 2013). Nevertheless, for several species the landscape presents itself as a gradient of suitable to unsuitable habitats that can provide multiple and complementary resources (Duelli et al., 1990). In this condition, individual movement across the landscape is important to obtain resources, and thus to ensure survival. The level of habitat edge contrast and the spatial arrangement of habitat and cultivation areas are thus important features influence landscape connectivity, and therefore can modulate the negative effects of agricultural intensification on native species (Haenke et al., 2014). Spillover, defined as the movement of individuals between distinct habitat types, including dispersal and foraging, influences landscape-wide community structure (Tscharntke et al., 2012), which in turn influences ecosystem functioning and food web interactions of local communities (Schneider et al., 2013). The spillover process from natural to human-modified habitats, or in the opposite direction, is an important connectivity process that affects wildlife populations in fragmented landscapes (Blitzer et al., 2012; Tscharntke et al., 2012) and can ensure the provision of important ecosystem services, such as pest control and pollination.

Understanding the ability of species to move in fragmented landscapes is a key issue for species conservation (Fahrig, 2007; Kupfer et al., 2006), and also for the maintenance of the functions and ecosystem services provided by biodiversity (Bianchi et al., 2006; Veres et al., 2013). Some studies have empirically assessed the association between gap-crossing movements and different landscape structure features, particularly, the amount of remaining native habitat, their degree of structural connectivity and the quality of the matrix (Awade & Metzger, 2008; Uezu et al., 2005). Other studies have reviewed the association between cross-habitat spillover and landscape structure, finding that natural pest control increases in complex and patchy landscapes with a high proportion of semi-natural habitats (Bianchi et al., 2006; Tscharntke et al., 2012; Veres et al., 2013). Moreover, the study of spillover movements of wildlife populations from natural to anthropogenic habitats, or *vice versa,* is important for understanding how organisms will use resources in fragmented landscapes.

There is ample evidence that landscape structure influences spillover of pollinators (Garibaldi et al., 2011; Saturni et al., 2016) and natural enemies (Bianchi et al., 2006; Veres et al., 2013), potentially modulating the provision of pollination and pest control services in agricultural landscapes. Some authors have performed empirical studies relating landscape structure variables, like distance to habitat margin, adjacent habitat type or percentage of crop or non-crop habitat, to the spillover of organisms that provide pest control and pollination services. Gaigher et al., (2015) found limited evidence of spillover of parasitoids from natural habitat to the vineyard matrix, evidencing an isolating effect and the need to increase the permeability of the matrix. Also, Garratt et al., 2017 showed that in order to support abundant and a broad range of natural enemies and pollinators in agricultural landscapes, both hedgerows and semi-natural habitats need to be protected and managed. Other authors have performed meta-analyses to assess the relationship between landscape structure and natural enemies, pests or pollinator spillover. In one of these reviews, Garibaldi et al., (2011) found that stability of flower-visitor richness, pollinator visitation rate and fruit set decrease with distance from natural areas. Likewise, Chaplin-Kramer et al., (2011) performed a meta-analysis in which they found that natural enemies have a strong positive response to landscape complexity.

A broad range of studies has assessed spillover patterns by measuring organism richness and abundance inside anthropic and natural covers. For example, Gaigher et al., (2015) measured parasitoid abundance inside natural vegetation and inside vineyards patches in order to detect positive effects of adjacent natural habitat on parasitoids abundance, as an indirect way to evidence parasitoids spillover between both cover types. In contrast, other authors have assessed spillover processes by directly measuring the movement across interfaces. For example, Frost et al., (2015) used flight intercept traps to measure spillover of parasitoids across habitat edges between native forest and exotic plantations. In this way, there are at least two ways of measuring spillover of organisms across interfaces, that can be useful to evaluate the effect of landscape structure on spillover's patterns or processes.

Despite the existence of these studies, research on spillover is still occasional, and there is scarce general understanding on how the landscape affects spillover. To move in this direction, we performed a wide literature review on the theme and analyzed the broad research pattern by classifying studies by the type of ecosystem service assessed, year of publication, geographic zone, type of crop, type of natural habitat, and taxonomic group. Additionally, we evaluated the methods of each study according to how spillover was measured: indirectly or directly. Then we performed a quantitative analysis in order to measure the effect size of landscape features over spillover. We hypothesized that distance from habitat edges, contrast between habitat types and forest cover percentage would influence the abundance and/or richness of pollinators and natural enemies. Specifically, we predict that spillover (measured as abundance or richness of natural enemies and pollinators that occurred at crop patches) would be (i) negatively influenced by distance to the crop/non-crop interface, (ii) negatively influenced by the contrast between habitats, and (iii) positively influenced by forest cover.

METHODS

Search protocol

We conducted a systematic literature review using the search term: *land* AND (composition OR physiog* OR structure OR arrangement OR pattern) AND (spillover OR "spill over" OR "cross-habitat movement" OR "crop-non crop interface" OR complementation) AND (pollination OR "pest control" OR "natural enemies").* We performed searches in Scopus, Web of Science and Science Direct databases. We included all available timespan, with the last update on October 2017. Our combined search returned a total of 84 studies and after eliminating duplicates, 46 articles remained. Also, we removed 10 additional studies that were not primary studies (i.e., they were meta-analyses, systematic reviews or perspective papers). The remaining 36 articles were fully evaluated and among them, another 11 articles were removed because, even though the term spillover was mentioned in some part of the articles, it was not empirically investigated. This means that those studies did not relate diversity patterns of pollinators and/or natural enemies to landscape features. With the remaining 25 empirical studies, we performed a forward search in Google Scholar in order to find primary studies that cited those 25 empirical articles we found using our initial search term. As a result, we compiled a dataset of 50 research articles that suited our criteria (Fig. 1).

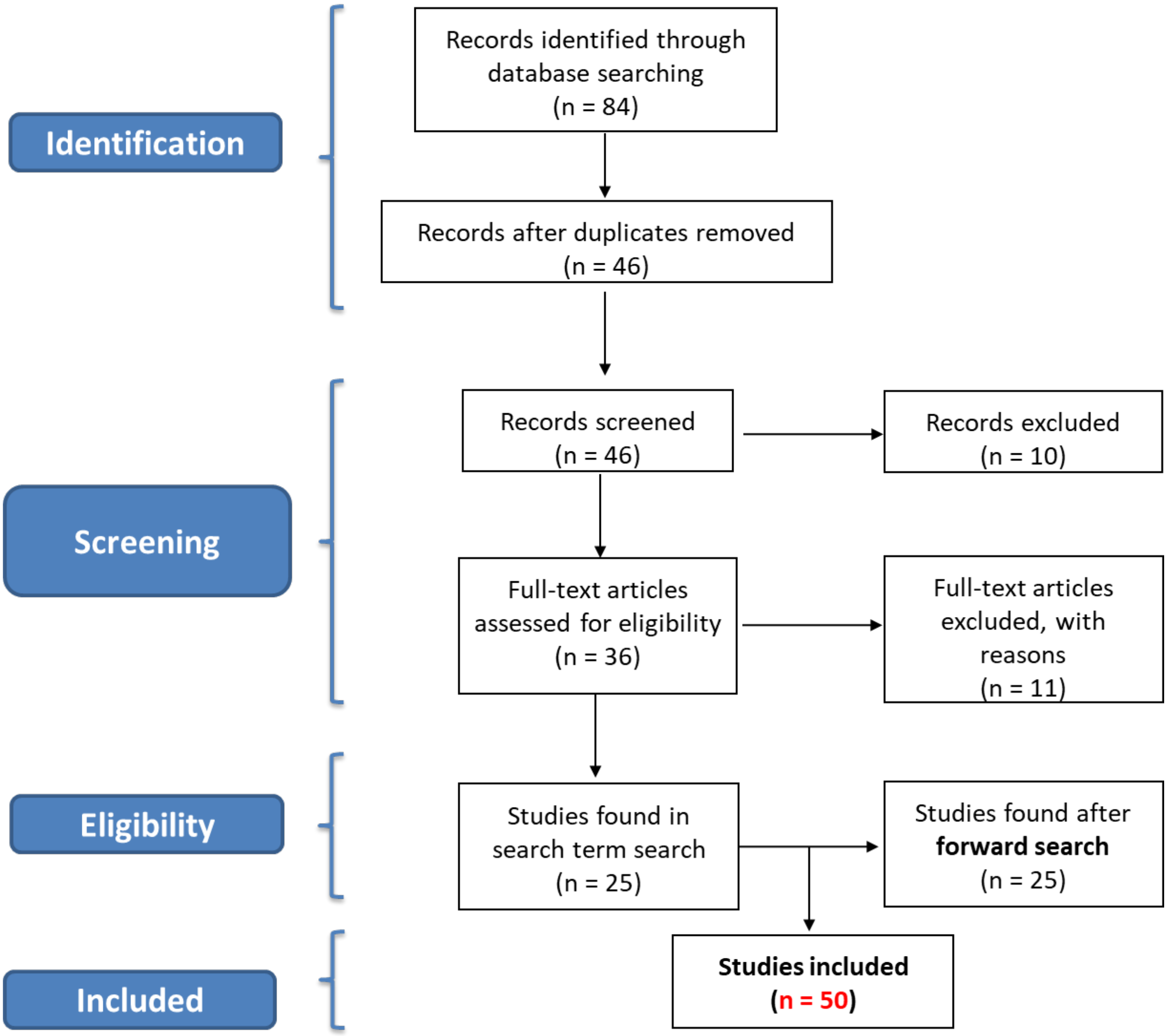

Figure 1. PRISMA diagram showing the different steps used to select 50 studies for the systematic review. The ten articles excluded after screened correspond to reviews, meta-analysis or perspective papers. The eleven articles excluded in the next step did not assess spillover.

Qualitative assessment

From each paper we determined: (1) type of ecosystem service assessed; (2) year of publication; (3) geographic zone; (4) type of crop; (5) type of natural habitat; and (6) taxonomic group. Also, we evaluated the methods of each study according to how spillover was measured:

(1) *Indirectly*, by using pitfall traps or sticky traps for natural enemies and transects for pollinators. In those cases authors were not measuring the process itself (i.e., the movement) - they were inferring the spillover process through diversity patterns, i.e. by the abundance or richness of native species that occur in plantations, and that supposedly made a spillover movement from habitat to crops.

(2) *Directly*, by capturing individuals moving across the interfaces using Malaise traps in the case of insects and mist nets for birds. In these cases, authors were studying the spillover movement.

Vote counting analysis

We used two analytical methods to account for the effect of landscape structure on spillover pattern or movement. In the first approach, we examined all events where landscape variables (e.g., distance to habitat, habitat type, natural habitat cover; Table 1) had positive, negative or non-significant effects on spillover dependent variables (e.g., abundance, richness, composition, etc.). As reported in our hypotheses, we expect a negative effect of habitat distance and edge contrast, and a positive effect of coverage on the spillover. A negative effect of distance was defined as a decrease in spillover variables as distance from habitat interfaces increased. For habitat type, a negative effect was considered when spillover dependent variables were lower as the contrast between habitat and non-habitat increased. A negative effect of natural cover was considered when spillover variables decreased when natural cover increased. The inverse was considered for positive effects. Non-significant effects were recognized when authors reported no effects of the landscape variable over the response variable (See Table S1 for complete explanation). For each landscape variable we built contingency tables (separately for pollination and pest control spillover movements) using the direction of the effect (positive, negative, non-significant) in order to evaluate if there were significant differences between observed and expected frequencies using a chi-square test (Garson & Moser, 1995).

Table 1. Adopted definitions of the landscape variables used in the vote counting analyses.

Landscape variable	Definition
Distance	Euclidean distance (in meters) from the nearest native habitat edge to the crop field where spillover was detected
Adjacent habitat type contrast	Structural dissimilarity between adjacent habitats
% Forest cover	The percentage of forest cover vegetation in the surrounding landscape (radii values of 500 m to 2000 m)

Data extraction for effect size calculation

The second approach used to account for the effect of landscape structure on spillover was a meta-analysis (Koricheva et al., 2013). Of the 50 articles we found in our systematic literature review, we were able to collect quantitative data and estimate the effect size of the three landscape metrics for 14 original papers. In this analysis, we use only indirect measurements of spillover (abundance and richness of pollinators and natural enemies) because they were the diversity measures most commonly used in the original studies and, therefore, could be standardized. We did not include direct spillover metrics (i.e. movement across interfaces), due to the few articles that assessed them (7) and the impossibility to standardize movement parameters or indicators. To estimate effect sizes we needed: a) the mean values of abundance or richness on each distance or habitat type; b) the associated standard deviations; and c) the number of traps used on each original study. The number of traps or transects used in the original studies was used in our study as an estimate of the sample size associated with each original effect size. When data was available in plots from the original studies, we extracted the information using the MetaDigitise package (Pick et al., 2019) on RStudio (RStudio Team 2015). For each effect size we also recorded: a) author name and year; b) diversity measure (abundance or richness); c) taxonomic group; d) functional group (pollinator or natural enemy); and e) cover type (natural or crop). Also, we classified the level of contrast between habitat types into two categories: *low* for habitats that are structurally similar, and *high* for habitats that are structurally more different. We chose to calculate a standardized difference in means using a Hedge's d value, because unlike other standardized difference metrics, this one is not affected by unequal sampling variances in the paired groups, and includes a correction factor for small sample sizes, therefore it works well with as few as five to ten studies. This measure requires means, sample sizes and variances values from the original papers (Koricheva et al., 2013). Hedge's d is calculated with the following equation:

$$d = \frac{\overline{(X}_T - \bar{X}_C)}{s} J$$

$$J = 1 - \frac{3}{4\,(n_T + n_C) - 9}$$

$$s = \sqrt{\frac{(n_T - 1) {SD_T}^2 + (n_C - 1) {SD_C}^2}{n_T + n_C - 2}}$$

Where d=effect size, $\bar{X}$=sample mean, T and C=treatment and control groups, SD=standard deviation, n=sample size, *J*=bias correction factor and S=pooled SD.

Statistical analyses

All statistical analyses were performed in RStudio (RStudio Team 2015). All meta-analyses/meta-regressions were run on effect size estimates weighted by their variances using multi-level models, fitted with restricted-maximum likelihood in the R package “metafor” (Viechtbauer, 2010). We modelled multiple effect sizes from the same study and species by including the study ID and the 'taxonomic group' as random factors in the multilevel models with the function rma.mv in “metafor”.

RESULTS

Qualitative assessment

We found 50 papers that studied the relationship between landscape structure and pollinator or natural enemy spillover, of which 30 analyzed pest control services, 14 assessed pollination, four did not assess any ecosystem service and two studies assessed both (Table S2). The research on this topic is relatively recent, beginning in 2006, with more than half of the articles published in the past four years (Fig. 2). In general, the majority of the studies were performed in temperate regions (n = 40); fewer were located in subtropical (n = 9) and tropical zones (n = 1) (Fig. 3). Empirical studies that assessed both pollination and pest control services were concentrated in mass-flowering crops, like oilseed rape (canola), and crops important for human feeding, like wheat and cornfields (Fig. 4). The most studied native habitats were forests, followed by grasslands, and by mixed habitats, which refer to a mixture of the first two and sometimes semi-natural habitats like fallows, hedgerows, orchards or wood margins (Fig. 5). Finally, the vast majority (49 out of 50) of original papers studied spillover of invertebrate organisms and only one article studied a vertebrate group (birds). Throughout the evaluated articles, we identified that cross-habitat spillover was measured in two ways: 86% of the studies (43 articles) measured spillover indirectly, performing captures or observations inside crops and/or natural habitats. In contrast, only 14% of the studies (seven articles) assessed spillover in a direct way, evaluating movement through the interfaces. This was done exclusively for natural enemies (Table S2).

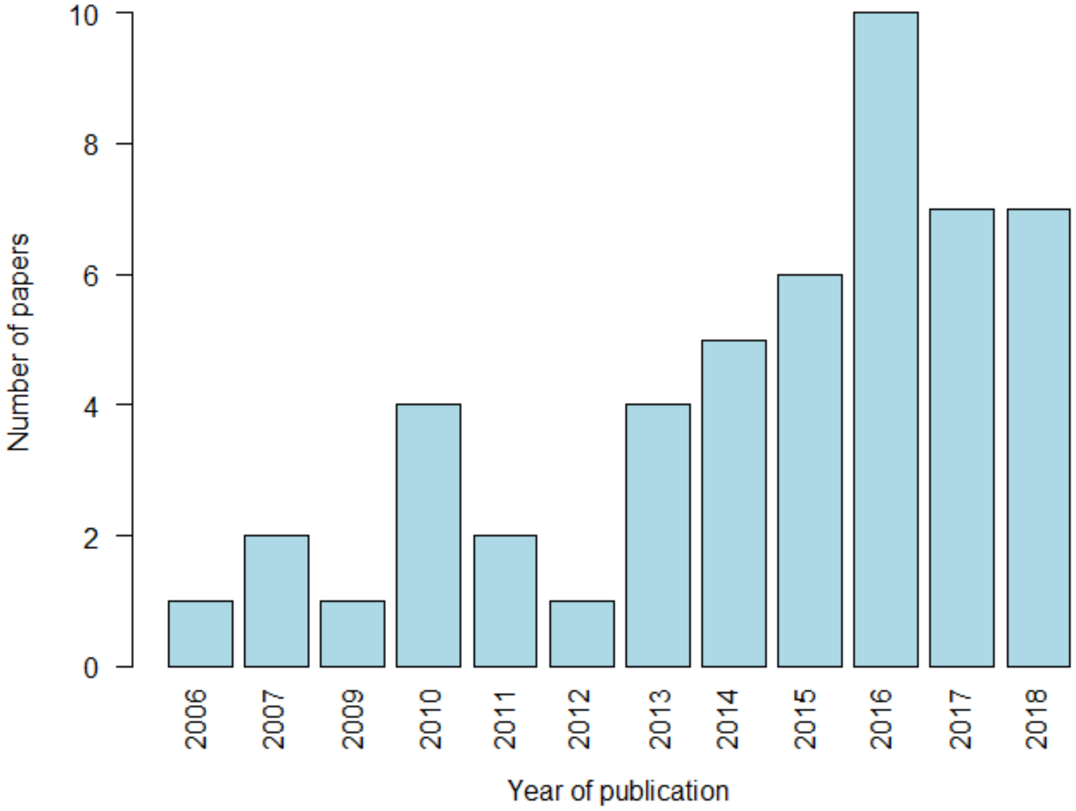

Figure 2. Publication dates of articles that studied the relationship between landscape structure and pollinator or natural enemy spillover.

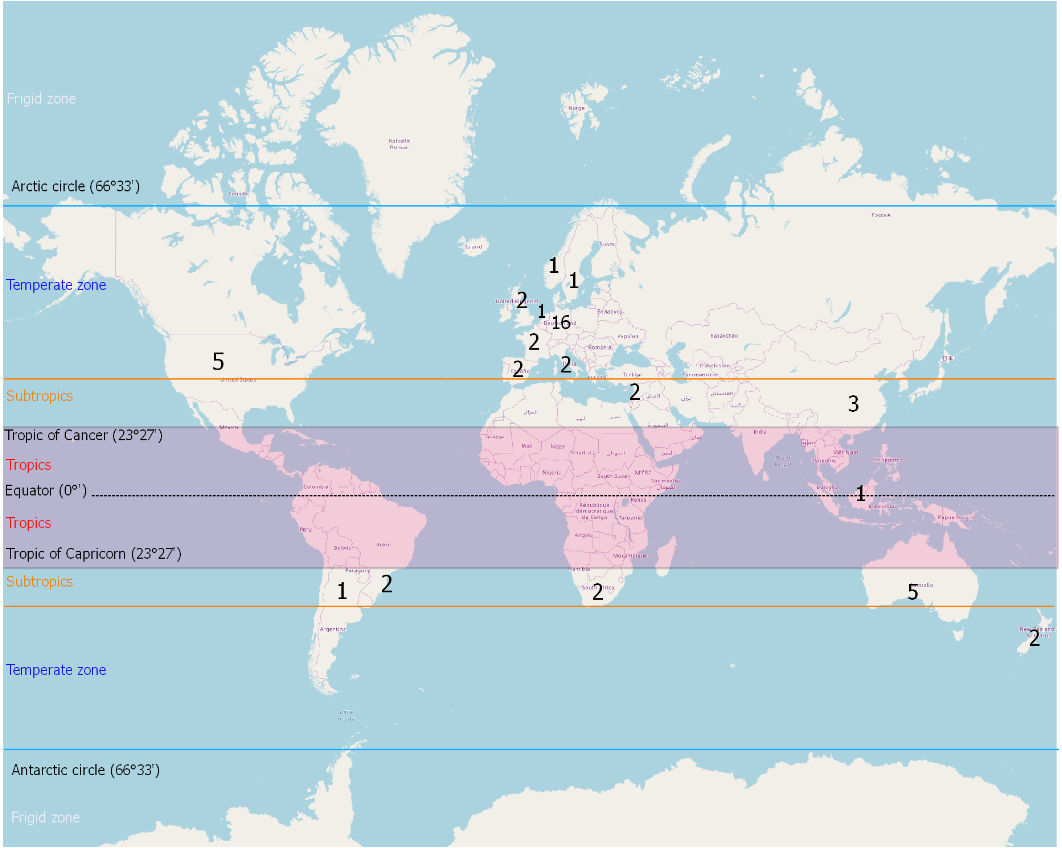

Figure 3. Geographical location of the 50 analyzed studies that conducted primary studies on spillover process. In general, the majority of the studies were performed in temperate regions (n =34) and fewer were located in subtropical (n = 15) and tropical zones (N = 1)

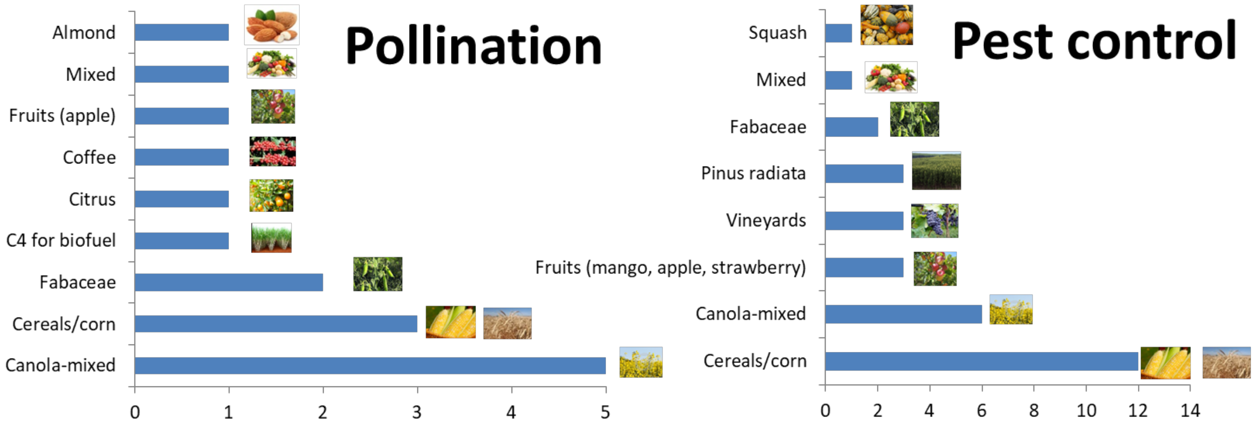

Figure 4. Crop types considered in the 50 studies that explored the influence for landscape structure on pollinators and natural enemies spillover.

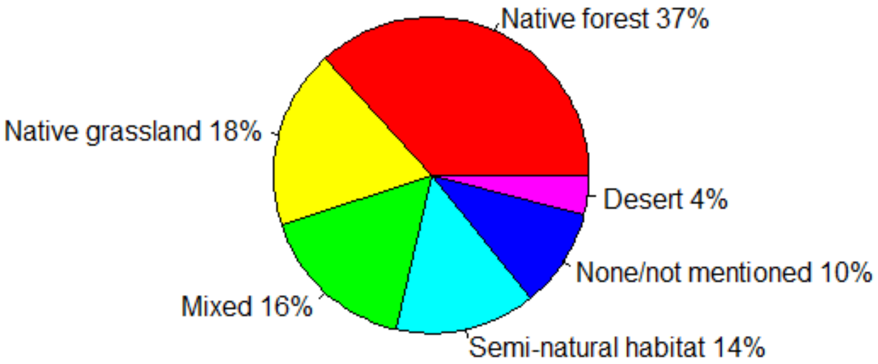

Figure 5. Natural or semi-natural habitats considered in the 50 analyzed studies that conducted primary studies on spillover process.

Vote counting

From the 50 articles we were able to compile 258 effects of landscape structure variable over spillover responses (Table S2). We analysed the responses corresponding to adjacent habitat type contrast, distance and forest cover % (a total of 97; Table 2). For pollination, one landscape variable seemed to significantly influence spillover movements: adjacent habitat type contrast ($\chi^2 = 7.6$, $p = 0.02$) (Table 2). Saunders and Luck (2014) found that the mallee woodland/almond plantation structural contrast was not a barrier to potential wild pollinators of almond trees and there was evidence of a spillover of bees and wasps from the natural habitat into almond plantations during crop flowering. Schirmel et al. (2018) found that species richness of hoverflies was higher in woody than in herbaceous semi-natural habitat; these two habitats differ structurally. Hanley et al. (2011) evidenced spillover of pollinators from bean crops to nearby semi-natural habitat, due to a low structural contrast between both land covers.

For pest control, the landscape that seemed to significantly influence spillover movements was also adjacent habitat type contrast ($\chi^2 = 10.1$, $p = 0.006$) (Table 2). Gaigher et al. (2015) found that natural habitat remnants had significantly higher parasitoid abundance and richness than neighboring vineyards, suggesting that spillover is limited between these two structurally contrasting cover types. Schneider et al. (2013) found stronger spillover evidence for carabid beetles from calcareous grasslands to adjacent cereal crops (low contrast) than from grasslands adjacent to coniferous forests (high contrast). Finally, Li et al. (2018) found no significant difference in carabid abundance between semi-natural habitats and cropland, because the two covers were not structurally contrasting.

Table 2. Landscape effects on pollination and pest control provision due the spillover of mobile organisms. df=2; $^*p < 0.05$, $^{**}p < 0.01$.

Pollination					
	Positive	Negative	Non-significant	χ^2	P value
Distance	5	3	7	1.6	0.449
% Forest cover	1	3	4	1.75	0.416
Adjacent habitat type contrast	8	0	7	7.6	0.020*
Pest control					
Distance	4	7	8	1.36	0.504
% Forest cover	2	0	4	4	0.135
Adjacent habitat type contrast	20	8	6	10.1	0.006**

Effect size analysis

Fifty-seven effect sizes from 14 studies for three landscape metrics were extracted: 14 for distance (Fig. 6), 25 for habitat type contrast (Fig. 7); and 18 for habitat cover percentage (Fig. 8).

For distance effects over richness and abundance, we were able to calculate 14 effect sizes, exclusively for natural enemies. The majority of effects (8) were positive, the rest were non-significant (confidence interval superimposed the 0) (6) and no negative effects were estimated (Fig. 6). The mean effect size was negative, but not different from zero (Table 3), which also means we were unable to detect an effect of distance on the abundance and richness of pollinators and natural enemies.

For the effect of habitat type contrast over richness and abundance, 22 effect sizes were obtained for natural enemies (beetles, hoverflies, parasitoids and spiders) and 3 for pollinators (bees, bumblebees and hoverflies). The majority of effects (13) were non-significant, 10 were positive and only two were negative, as initially expected (Fig. 7). The majority of the original papers studied highly structurally contrasting habitat types (18 out of 25), making measurements inside forest and inside crops. In comparison, seven studies assessed the influence of habitat type and chose low contrasting covers, for example, semi-natural habitats versus crops. Contrary to expectations, there were no differences in abundance and richness between contrasting habitat types (Table 4).

For forest cover percentage we were able to calculate 18 effect sizes: 13 for pollinators (bees and bumblebees) and five for natural enemies (syrphids, spiders and hoverflies). The majority (11) were non-significant effects; five effects were positive (as expected); and two were negative (fig. 8). The mean effect size was positive but not different from zero, which means we were unable to detect an effect of forest cover percentage over pollinator and natural enemies abundances and richness.

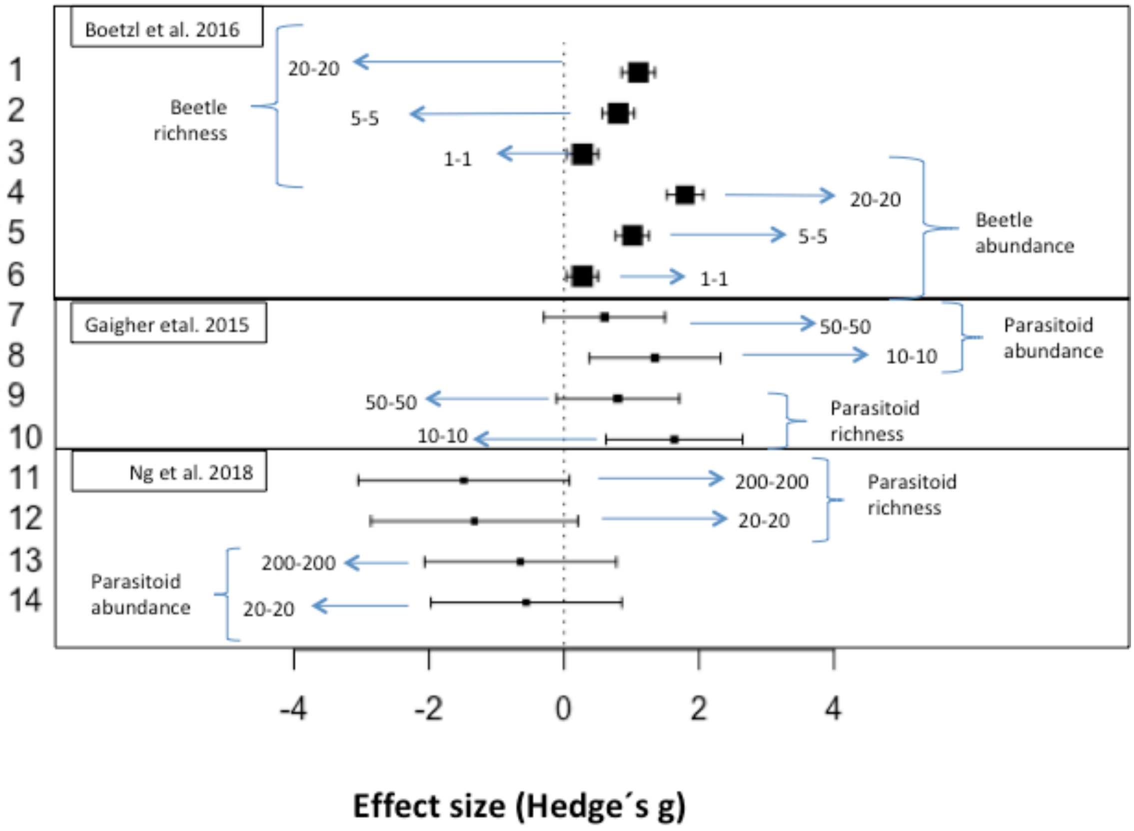

Figure 6. Arthropod response to distance to forest edge, based on three studies and 14 total responses. Whiskers represent 95% confidence interval around mean effect size. Distance values are given in meters from, the natural habitat-crop interface. Effect sizes for distance values were extracted from three different published papers (Boetzl, 2016; Gaigher et al., 2015; Ng et al., 2018). Positive effects mean that the greater the distance to forest edge, the greater the abundance of species in the crop.

Table 3. Results of meta-analytic model considering the effect of the distance from habitat on spillover variables.

	Estimate	**SE**	**zval**	**pval**	**ci.lb**	**ci.ub**
Intercept	0.666	0.617	1.078	0.280	-0.544	1.876
Distance	**-0.191**	0.275	-0.692	0.488	**-0.731**	**0.349**

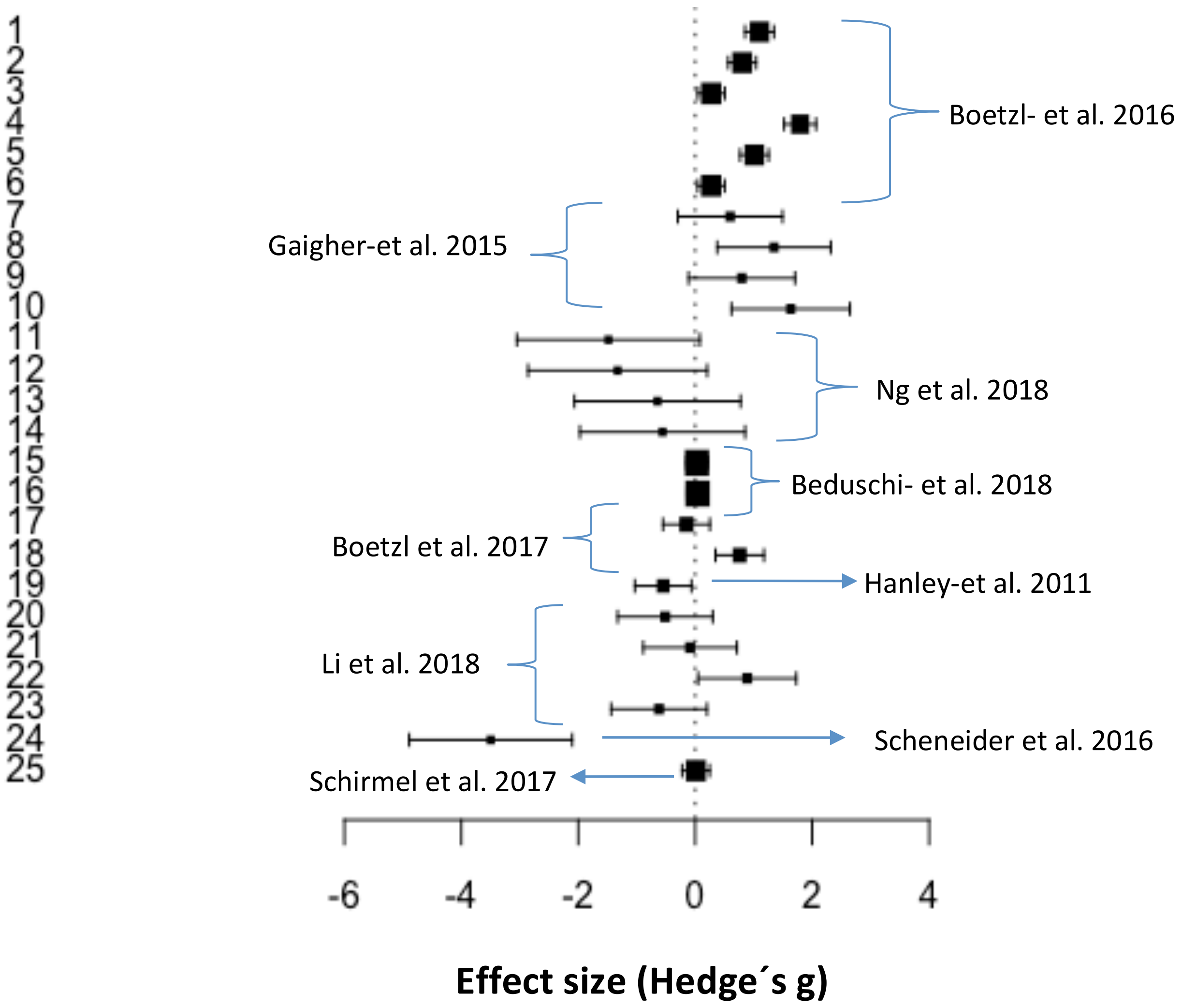

Figure 7. Arthropod response to habitat type contrast, based on nine studies and 25 total responses. Whiskers represent 95% confidence interval around mean effect size. Effect sizes for habitat type contrasting values were extracted from nine different published papers (Beduschi et al., 2018; Boetzl, 2016; Boetzl et al., 2017; Gaigher et al., 2015; Hanley et al., 2011; Li et al., 2018; Ng et al., 2018; Schirmel et al., 2017; Schneider et al., 2016). Positive effects mean that the greater the contrast between habitats, the greater the abundance of species in the crop.

Table 4. Results of meta-analytic model considering the effect of habitat contrast (high vs low) on spillover variables.

Contrast level	Estimate	SE	zval	pval	ci.lb	ci.ub
High	-0.180	0.496	-0.362	0.716	**-1.153**	**0.793**
Low	-0.184	0.688	-0.267	0.789	**-1.533**	**1.165**

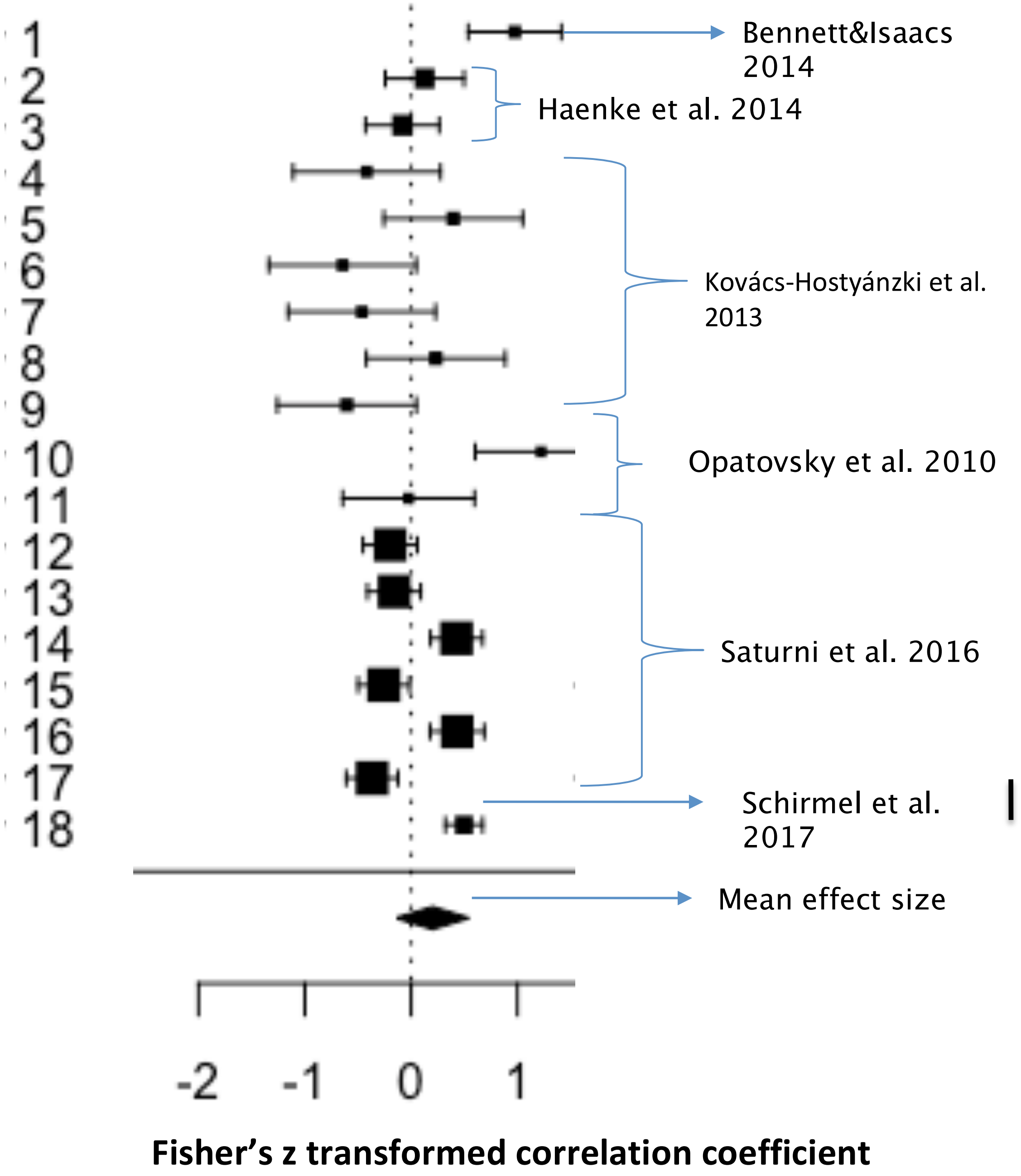

Figure 8. Arthropod response forest cover percentage, based on six studies and 18 total responses. Whiskers represent 95% confidence interval around mean effect size. Effect

sizes for forest cover percentage values were extracted from six different published papers (Bennett & Isaacs, 2014; Haenke et al., 2014; Kovács-Hostyánszki et al., 2013; Opatovsky et al., 2010; Saturni et al., 2016; Schirmel et al., 2018). Positive effects mean that the greater the forest cover in the surrounding landscape, the greater the abundance of species in the crop.

DISCUSSION

The current state of knowledge of the effect of landscape structure parameters on spillover is still incipient and inconclusive. None of our initial hypotheses, except for adjacent habitat type contrast, are supported by scientific evidence, which suggests three possible implications: (i) studies are still scarce to obtain a clearer pattern on the effect of landscape on spillover; (ii) the methods used to infer indirectly the spillover are not sufficiently consistent, and thus we need to measure more directly the movement; and (iii) there is no consistent effect of the landscape on the different pollinators and natural enemies that make spillover movements.

Spillover movements have been studied for a short time (essentially since 2006), and are largely limited to studies in temperate regions and a few crops. The scarcity of data makes it extremely difficult to identify consistent patterns, especially given that a large proportion of these studies do not present statistical data that allow meta-analysis. From the 50 papers found in our search term, we were able to extract numeric values from only 14 studies, considerably limiting the power to test our hypotheses, which is a common problem in reviews with small sample sizes (Koricheva et al., 2013). Effect sizes like Hedge's d are disfavoured because they require too many within-study statistics, therefore, excluding studies with missing information could exacerbate publication bias and produce unauthentic results (Koricheva et al., 2013). To overcome this problem, besides stimulating more studies on spillover, particularly in tropical regions, diversifying the types of crops, habitats, species, and types of landscapes studied, it would be necessary that the authors systematically present statistical information, either in the main text, figures, or even in the supplementary material.

In addition, it is possible that the most commonly used methods to infer spillover indirectly (through species abundance, richness or community composition pattern) are not the most suitable. Unfortunately, we could not estimate an effect size for studies that assessed movements through interfaces, because they were too few (7 of 50) and difficult to homogenize. The difficulties in homogenization were due to the broad range of measures that each study used to characterize spillover: density of insects moving across different edge-types (Macfadyen & Muller, 2013); ratio of individuals moving in the managed-to-natural vs. natural-to managed direction (Frost et al., 2015); ratio of the overall richness (S_{ratio}) and abundance (A_{ratio}) of forest-dependent bird species within coffee plantations or cattle pastures in relation to its adjacent forest (Boesing et al., 2017); density of insects recaptured in different treatments (Haynes et al., 2007); recapture data to examine movements of butterflies across the ecotone (Lucey & Hill, 2012); movement direction, as a factor with two levels: forest to crop, crop to forest (González et al., 2016); or the number of individuals captured on each side of the traps (Ng et al., 2018). Therefore, in order to infer spillover process, instead of the patterns, a unified way to measure the movement of individuals through the crop/non-crop interface should be developed and used to allow comparisons among studies and integrate analyses. In this study, our conclusions have to do with spillover patterns and not the process.

The pattern observed (or the absence of a pattern) may be linked to the sensitivity of the statistical approach. For this purpose, it is relevant to compare the results of the vote counting with the effect size calculation. Although we have no significant results with effect size tests, the vote counting method (which is a less rigorous and accurate method) suggests a consistent positive effect of habitat type contrast. The other two variables calculated both by vote counting and effect size (distance to habitat edge and forest cover percentage) had no effect over arthropod abundance and richness. In other words, there may be a more consistent spillover response to landscape structure, but the sample size is still limited to show this clearly with more rigorous statistical methods.

The effect of the landscape may be more limited than expected, or vary greatly among species. We know that species have different requirements, movement capabilities, and sensitivity to habitat degradation, and thus can respond to landscape structure at different scales or be sensitive to different landscape features. This variability in response pattern can be observed in the studies reviewed, where for the same landscape, we have distinct responses to landscape structure, for example with trends of positive or negative responses to edge contrast (Li et al. 2018, Kovácz-Hostyánszki et al. 2013; Figure 7) or to forest cover (Saturni et al. 2016; Figure 8) depending on the group of species considered.

The strongest and clearest relationship we observed was with habitat type contrast. This contrast is likely to have a strong influence on pollinator spillover for two main reasons. First, because habitat heterogeneity and complexity are usually higher in natural habitats (such as mallee woodlands), when compared with human land use area (e.g.

almond plantations) (Saunders & Luck, 2014). Heterogeneity and complexity increase niche availability and can potentially increase the attractiveness of the environment to receive spillover movements (Tscharntke et al., 2016). Second, native habitats and agricultural habitats can offer different kinds of resources; for example, species richness of hoverflies was found to be higher in woody than in herbaceous semi-natural habitat; these two habitats differ structurally, and provide different resources: woody habitat provides shelter from harsh weather conditions, meanwhile herbaceous habitat provides floral resources (Schirmel et al., 2018).

Habitat type contrast may also affect the spillover of natural enemy species in agricultural landscapes because it represents a key element for natural enemy survival, as crop fields can be hostile environments for their persistence (Inclán et al., 2015). Results are consistent with the "edge-permeability hypothesis" where a greater spillover of natural enemies is expected to occur when the field margin is structurally more similar to the adjacent crop (Stamps et al., 1987). Gaigher et al. (2015) expected that remnants of natural habitats (Fynbos) to have a positive effect on parasitoid diversity in adjacent vineyards, but they did not find evidence for this; instead, there was a sharp decline in parasitoid abundance and richness across the natural/crop edge. This resembles what Boesing et al. (2017) found for bird spillover in pasture matrices, suggesting that even in the presence of natural or semi-natural habitats, when the matrix is too inhospitable to species, they will not spillover to non-native areas. Schneider et al. (2013) found stronger spillover evidence for carabid beetles between calcareous grasslands and adjacent cereal crops than for grasslands adjacent to coniferous forests, supporting that natural enemies are performing spillover to habitats with the less structural contrast. Similarly, Inclán et al. (2016) reported spillover between similar adjacent habitat types, but specifically for tachinid parasitoids inhabiting grass margins. They were more likely to move into adjacent maize field compared with tachinids inhabiting hedgerows, which suggests that species are more likely to move across habitat edges of low contrast (i.e., with similar vegetation structure). Therefore, tachinids inhabiting grass margins are more likely to visit maize fields than tachinids inhabiting hedgerows, since the former could perceive the maize field as a similar habitat.

In the same way, habitat contrast, specially the presence if semi-natural habitats plays an important role on natural enemies spillover. Inclán et al. (2015) found that spillover of parasitoids is likely to depend on the semi-natural areas present in the landscape; therefore, as crop fields can be hostile environments for the persistence of natural enemies, the surrounding natural or semi-natural habitats represent a key element for their survival. Rand & Louda, (2006) report that spillover of generalist predators (Coccinellids) from the surrounding cropland landscape matrix to grassland increases the consumer pressure on aphids within nearby natural habitat remnants. Haynes et al., (2007) found that a grass matrix had a positive effect on the spillover of adult grasshopper individuals from habitat patches to the matrix when it contained complementary resources (foraging and nesting sites), in comparison to matrix that does not offer such resources. For parasitoids these habitats provide alternative host species, nectar and pollen sources for adults, over-wintering sites and pesticide-free zones (Tscharntke et al., 2007). This highlights that landscape heterogeneity in terms of configuration, where contact between native and crop habitat is more frequent (Perović et al., 2010) increases the opportunity for spillover movement, and may also increase the propensity of individuals to leave their source habitat.

Also, native habitats can be considered as stable refuges for species over time; for example, oil seed rape had a negative effect on bumble bees in hedges during flowering due to dilution of pollinators, but there was a positive effect after crop flowering because bumble bees moved to the hedges, which provided resources (Kovács-Hostyánzki et al., 2013). Garratt et al. (2017) found a positive relationship between hedge type and abundance of natural enemies: the presence of trees within the hedgerow supports lycosid spiders. They propose that hedgerows can provide key resources for functionally important taxa in intensive agricultural landscapes, but the extent of this benefit depends on the characteristics of the hedgerow and the landscape context in which the hedgerow is found. Therefore, we can see that these natural landscape elements often remain the only refuges for pollinators and natural enemies in intensively managed agricultural landscapes, providing valuable pollen and nectar resources, as well as suitable nesting habitats (Hannon & Sisk, 2009; Hopwood, 2008).

Concluding remarks:

Identifying for what species and under what conditions landscape structure affect spillover, and how different landscape features affect pollination and pest control spillover movements can help to plan and manage landscapes in order to maintain biodiversity, ecosystem services provision and agricultural production. This is a new and emergent area of research, but still largely limited to temperate regions, to few crop types, and usually assessed only indirectly, which currently limits the use of these data for the planning of more sustainable agricultural landscapes. The current state of knowledge suggests that landscapes with soft edges between (semi) natural areas and crop fields, are more favourable for spillover movements from (semi) natural to anthropic covers, and can then enhance the provision of pollination and pest control services. Understanding better these landscape factors driving the fluxes of arthropods in agricultural landscapes is a prerequisite to the development of management guidelines for enhancing pollination and pest control services (Holland et al., 2005; Thomas et al., 2001) and thus potentially for improving crop productivity in a sustainable way. There is urgent need to develop this research topic, particularly considering emergent and expanding agricultural crops in highly biodiverse tropical and subtropical regions.

Supplementary material:

Table S1. Explanation of landscape characteristics over response variables

Landscape variable	Dependent variable	Type of effect	Explanation
Distance	Abundance	Positive	Abundance increased from the field edge towards the field center
		Negative	Abundance decreased from the field edge towards the field center
		Non-significant	Abundance did not differ significantly with distance
	Species richness	Positive	Species richness increased from the field edge towards the field center
		Negative	Species richness decreased from the field edge towards the field center
		Non-significant	Species richness did not differ significantly with distance
	Community composition	Positive	Community composition more similar in field edge
		Negative	Community composition more dissimilar in field edge
		Non-significant	Does not apply
	Activity-density	Positive	Activity densities increased from the field edge towards the field center
		Negative	Activity densities decreased from the field edge towards the field center
		Non-significant	Activity-density did not differ significantly with distance
Habitat type	Abundance	Positive	Abundance is higher in crops than in natural habitats
		Negative	Abundance is lower in crops than in natural habitats
		Non-significant	Abundance did not differ significantly between the natural habitat and the crop
	Species richness	Positive	Species richness is higher in crops than in natural habitats
		Negative	Species richness is lower in crops than in natural habitats
		Non-significant	Species richness did not differ significantly between the natural habitat and the crop
	Activity-density	Positive	Activity-density is higher in crops than in natural habitats
		Negative	Activity-density is lower in crops than in natural habitats
		Non-significant	Activity-density is not affected by habitat type
Forest cover	Abundance	Positive	Abundance increased with increasing the amount of forest
		Negative	Abundance decreased with increasing the amount of forest
		Non-significant	Abundance was no affected by the amount of forest cover
	Species richness	Positive	Species richness increased with increasing the amount of forest
		Negative	Species richness decreased with increasing the amount of forest
		Non-significant	Species richness was no affected by the amount of forest cover

Table S2. Summary of the studies evaluating landscape structure effects on pollinators and natural enemies spillover

Study	Type of natural enemy / pollinator / pest	Ecosystem service	Interface movement evaluated?/ Methods of movement evaluation	Landscape variable	Spillover metric (dependent variable)	Effects of landscape variables on response variables-service provision perspective
1.Gaigher et al., 2015	Hymenopteran parasitoids	Pest control	None used	Habitat type	Parasitoid abundance	Positive
					Parasitoid species richness	Positive
					Parasitoid community composition	Positive
				Distance from habitat edge	Parasitoid abundance	Non-significant
					Parasitoid species richness	Non-significant
					Parasitoid community composition	Non-significant
2. Moxley et al., 2017	Diptera	Pest control	None used	Distance from habitat edge	Pest presence/ absence	Non-significant
					Pest abundance	Positive
3. Inclán et al., 2015	Tachinid parasitoid flies	Pest control	None used	Matrix type	Parasitoid species richness	Positive
					Parasitoid community composition	Negative
				Habitat type	Parasitoid species richness	Positive
					Parasitoid community composition	Negative
4. Inclán et al., 2016	Tachinid parasitoid flies, aphidophagous hoverflies	Pest control	None used	Crop cover %	Tachinid species richness	Non-significant
					Tachinid abundance	Non-significant
					Aphidophagous hoverfly species richness	Non-significant
					Aphidophagous hoverfly abundance	Non-significant
				Distance	Tachinid species	Negative

					richness	
					Tachinid abundance	Negative
					Aphidophagous hoverfly species richness	Non-significant
					Aphidophagous hoverfly abundance	Positive
				Adjacent habitat type	Tachinid species richnes	Positive
					Tachinid species abundance	Positive
					Aphidophagous hoverfly species richness	Non-significant
					Aphidophagous hoverfly abundance	Non-significant
5. Garratt et al., 2017	Carabids, Staphylinids, Linyphiid spiders, Lycosid spiders, Aphids, bumblebees, hoverflies, honeybees and solitary bees	Pest control and pollination	None used	Hedge quality	Aphid abundance	Non-significant
					Carabid abundance	Non-significant
					Staphylinid abundance	Non-significant
					Lycosid abundance	Non-significant
					Linyphiid abundance	Positive
					Bee abundance	Non-significant
					Honeybee abundance	Non-significant
					Solitary bee abundance	Non-significant
					Hoverfly abundance	Non-significant
					Bumblebee abundance	Positive
				% semi-natural area	Aphid abundance	Non-significant
					Carabid abundance	Non-significant
					Staphylinid abundance	Non-significant
					Lycosid abundance	Positive
					Linyphiid abundance	Non-significant
					Bee abundance	Negative
					Honeybee abundance	Non-significant
					Solitary bee abundance	Non-significant

					Hoverfly abundance	Non-significant
					Bumblebee abundance	Non-significant
				Distance	Aphid abundance	Positive
					Carabid abundance	Non-significant
					Staphylinid abundance	Negative
					Lycosid abun	Negative
					Linyphiid abundance	Negative
					Bee abundance	Negative
					Honeybee abundance	Non-significant
					Solitary bee abundance	Non-significant
					Hoverfly abundance	Negative
					Bumblebee abundance	Non-significant
				% semi natural habitat*distance	Staphylinid abundance	Positive
6. Montero-Castaño et al., 2016	Honeybees	Pollination	None used	Distance	Bee species richness	Non-significant
					Bee abundance	Positive
					Bee community composition	Positive
7. Frost et al., 2015	Hymenopteran parasitoids	Pest control	Malaise traps	Direction of movement	Number of individuals moving across the edge	Positive
8. Gladbach et al., 2011	Hymenopteran parasitoids	Pest control	None used	Landscape complexity	Larvae per flower	Positive
				Habitat type	Larvae per flower	Negative
				% crop cover	Larvae per flower	Non-significant
9. Kovács-Hostyánzki et al., 2013	Bees and bumblebees	Pollination	None used	Distance	Fruit set	Non-significant
					Fruit mass	Positive
					Seed number per fruit	Positive
				Habitat type	Fruit mass	Non-significant
					Seed number per fruit	Positive
10. Hanley et al., 2011	Bumblebees	Pollination	None used	Crop type	Bumblebee abundance	Positive
11.	Carabid	Pest control	None used	Habitat type	Carabid spp	Positive

Labruyere et al., 2016	beetles				1 abundance	
					Carabid spp 2 abundance	Positive
					Carabid spp 3 abundance	Positive
12. Macfadyen & Muller 2013	Arthropod parasitoids and predators	Pest control	Malaise traps	Adjacent habitat type	Insect community composition	Non-significant
					Herbivore density	Negative
					Predator density	Positive
					Parasitoid density	Positive
13. Opatovsky et al., 2012	Spiders	None	None used	% crop cover	Spider community composition	Non-significant
					Spider species richness	Non-significant
				Distance	Spider community composition	Non-significant
					Spider species richness	Non-significant
14. Rand & Louda 2006	Coccinellids	Pest control	None used	Matrix type	Coccinellid abundance	Positive
				Location in the field	Coccinellid abundance	Non-significant
15. Saunders & Luck 2014	Diptera and Hymenoptera	Pollination	None used	Habitat type	Fly abundance	Positive
					Wasp abundance	Positive
					Bee abundance	Positive
				Distance	Pollinator community composition	Negative
16. Riedinger et al., 2014	Bumblebees, honey bees and hoverflies	Pollination	None used	% OSR cover	Bumblebee density	Negative
				% semi-natural area		Non-significant
				% sunflower cover		Negative
				% OSR area*% semi-natural area		Non-significant
				% OSR area*% sunflower area		Positive
				% OSR cover	Hoverfly density	Non-significant
				% semi-natural area		Non-significant
				% OSR		Negative

				area*% semi-natural area		
				% crop cover	Honey bee density	Positive
				% semi-natural area		Non-significant
				% OSR area*% semi-natural area		Negative
17. Rand & Tscharntke 2007	Hymenopteran parasitoids, midges, coccinellids and spiders	Pest control	None used	Number of habitat patches	Aphid occupancy	Negative
	Hymenopteran parasitoids, midges, coccinellids and spiders	Pest control	None used	Area of habitat	Aphid occupancy	Negative
				Landscape complexity	Aphid population growth	Positive
					Aphid density	Negative
					Coccinellid density	Negative
					Spider density	Negative
18. Schneider, et al., 2013	Carabid beetles	Pest control	None used	Adjacent habitat type	Predation rate	Positive
				Location in the field		Non-significant
19. Ahrenfeldt et al., 2015	Bees, bumblebees and solitary bees	Pollination	None used	Location in the field	Bee density	Non-significant
					Solitary bee density	Non-significant
					Bumblebee density	Non-significant
					Bee species richness	Positive
20. Hanspetersen et al., 2010	Diptera, carabids, coccinellids, hymenopteran parasitoids, spiders, ants	Pest control	None used	Habitat type	Natural enemy abundance	Positive
					Predator abundance	Positive
					Spider abundance	Positive
					Pest abundance	Positive
					Ant abundance	Positive
					Melon worm and saltmarsh abundance	Non-significant
21. Boesing et al., 2017	Birds	None	Mist nets	Forest cover	Abundance of spillover	Positive
				Forest cover + edge density	Abundance of spillover	Positive
				Forest cover	Abundance	Non-significant

				* edge density	of spillover	
				Edge density	Abundance of spillover	Non-significant
				Forest cover	Richness of spillover	Positive
				Forest cover + edge density	Richness of spillover	Positive
				Forest cover * edge density	Richness of spillover	Non-significant
				Edge density	Richness of spillover	Non-significant
				Forest cover	Abundance ratio of spillover	Positive
				Forest cover + edge density	Abundance ratio of spillover	Positive
				Forest cover * edge density	Abundance ratio of spillover	Non-significant
				Edge density	Abundance ratio of spillover	Non-significant
				Forest cover	Richness ratios of spillover	Non-significant
				Forest cover + edge density	Richness ratios of spillover	Non-significant
				Forest cover * edge density	Richness ratios of spillover	Non-significant
				Edge density	Richness ratios of spillover	Non-significant
22. Haynes et al., 200	Grasshoppers	Pest control	Mark, capture-recapture	Area of habitat	Density of grasshoppers	Negative
				Habitat splitting		Non-significant
				Matrix type		Negative
				Area of habitat * Matrix type		Negative
				Area of habitat	Movement of grasshoppers	Non-significant
				Habitat splitting		Positive
				Matrix type		Non-significant
23. Liu et al., 2014	Beetle herbivores	Pest control	None used	Landscape context	Herbivore abundance	Non-significant
				Land use intensity		Non-significant
				Landscape context	Decomposer abundance	Non-significant
				Land use		Non-significant

				intensity		
				Landscape context* Land use intensity		Positive
24. Schneider et al., 2016	Beetles	None	None used	Habitat type	Beetle density	Positive
					Beetle species richness	Positive
					Beetle evenness	Non-significant
				Adjacent habitat type	Beetle density	Positive
					Beetle species richness	Positive
					Beetle evenness	Positive
25. Lucey & Hill 2012	Butterflies and ants	None	Mark, capture-recapture	Habitat type	Ant diversity	Negative
					Butterfly species richness	Negative
					Ant species richness	Negative
					Butterfly abundance	Negative
					Ant abundance	Non-significant
				Distance	Ant abundance	Positive
					Butterfly diversity	Negative
					Ant diversity	Non-significant
					Ant community composition	Non-significant
26. Schirmel et al., 2018	Aphidophagous hoverflies	Pest control	None used	Semi-natural habitat type	Aphidophagous hoverfly species richness	Positive
					Aphidophagous hoverfly abundance	Non-significant
					Aphidophagous hoverfly community composition	Positive
				Semi-natural habitat shape	Aphidophagous hoverfly species richness	Non-significant
					Aphidophagous hoverfly abundance	Positive
					Aphidophagous hoverfly community composition	Positive

				Landscape complexity	Aphidophagous hoverfly species richness	Positive
					Aphidophagous hoverfly abundance	Positive
					Aphidophagous hoverfly community composition	Non-significant
27. González-Varo & Vilà, 2017	Honeybees	Pollination	None used	Habitat type	Honeybee density	Positive
				Habitat cover	Honeybee density	Positive
28. Kallioniemi et al., 2017	Bumblebees	Pollination	None used	Shannon land use diversity index	Bumblebee density	Non-significant
					Bumblebee species richness	Non-significant
				Forest area	Bumblebee density	Negative
					Bumblebee species richness	Negative
				Pasture area	Bumblebee density	Negative
					Bumblebee species richness	Negative
29. González et al., 2016	Pollinators and natural enemies	Pest control and pollination	Bi-directional flight interception trap	Forest cover	Natural enemy species richness	Positive
					Natural enemy abundance	Positive
					Pollinator species richness	Positive
					Pollinator abundance	Non-significant
					Natural enemy movement	Positive
					Pollinator movement	Non-significant
30. Ng et al., 2018	Predator beetles	Pest control	Bi-directional traps	Habitat type	Predator beetle species richness	Positive
					Predator beetle abundance	Positive
				Distance	Predator beetle abundance	Positive
31. Peralta et al., 2018	Parasitoids	Pest control	Non used	Forest type	Parasitoid community	Positive

					composition	
				Edge effect	Parasitoid community composition	Positive
32. Grab et al., 2018	Parasitoids	Pest control	Non used	Semi-natural habitat area	Parasitism rate	Positive
33. Birkhofer et al., 2018	Spiders, ground beetles, rove beetles	Pest control	Non used	Adjacent habitat type	Natural enemy density	Positive
					Natural enemy community composition	Positive
34.Madeira et al., 2016	Carabids, rove beetles and spiders	Pest control	Non used	Adjacent habitat type	Carabid abundance	Positive
					Beetle abundance	Positive
					Spider abundance	Positive
35. Beduschi et al., 2018	Bees and hoverflies	Pollination	Non used	Habitat type	Bee species richness	Positive
					Hoverfly species richness	Positive
36. Holzschuh et al., 2016	Bumblebees, solitary bees, honeybees and hoverflies	Pollination	Non used	Crop cover	Bumblebee density	Negative
					Solitary bee density	Negative
					Honeybee density	Negative
					Hoverfly density	Negative
				Semi-natural habitat cover	Pollinator density	Non-significant
37. Haenke et al., 2014	Aphidophagous hoverflies	Pest control	None used	Semi-natural habitat type	Aphidophagous hoverfly abundance in SNH	Positive
				Adjacent SNH type*OSR cover	Aphidophagous hoverfly abundance in SNH	Positive
				Adjacent SNH type	Aphidophagous hoverfly abundance in crop	Positive
				Crop type	Aphidophagous hoverfly abundance in crop	Positive
38. Bennett & Isaacs 2014	Bees	Pollination	Non used	Grassland area	Bee abundance	Positive
				Forest area	Bee especies richness	Positive
39. Kleijn et al., 2018	Bumblebees and solitary bees	Pollination	Non used	Area of habitat	Bumblebee density	Non-significant
					Solitary bee density	Positive

				Distance	Bumblebee density	Positive
40. Duflot et al., 2016	Carabid beetles	Pest control	Non used	% of woody cover	Carabid species richness in wheat	Non-significant
					Carabid species richness in maize	Non-significant
41. Pluess et al., 2010	Spiders	Pest control	Non used	% of non-crop habitat	Spider species richness	Positive
42. Zhao et al., 2013	Ground-dwelling predators, leaf-dwelling predators and parasitoids	Pest control	Non used	Location in the field	Predator abundance	Positive
				Adjacent habitat type	Predator abundance	Non-significant
43. Thomson et al., 2010	Natural enemies	Pest control	Non used	Area of habitat	Natural enemy abundance	Positive
44. Boetzl et al., 2016	Carabid beetles	Pest control	Non used	Habitat type	Carabid species richness	Non-significant
45. Saturni et al., 2016	Bees (native and Apis)	Pollination	Non used	Forest cover	Native bee abundance	Positive
					Native bee richness	Positive
					Native bee diversity	Positive
					Honeybee abundance	Negative
46. Dong et al., 2015	Coccinellids	Pest control	Non used	% of woody cover	Coccinellid abundance	Positive
				Landscape diversity		Negative
				Crop area		Negative
47. Smith et al., 2015	Coccinellids	Pest control	Non used	Adjacent habitat type	Coccinellid abundance	Positive
				Habitat type		Positive
				Native vegetation cover		Non-significant
48. Li et al., 2018	Carabids and spiders	Pest control	Non used	Habitat type	Carabid abundance	Non-significant
					Carabid species richness	Non-significant
					Spider abundance	Positive
					Spider species richness	Non-significant
49. Jauker et al., 2009	Wild bees and hoverflies	Pollination	Non used	Matrix quality	Hoverfly species richness	Non-significant
					Bee	Non-significant

					abundance	
					Hoverfly abundance	Non-significant
				Distance	Bee species richness	Positive
					Hoverfly species richness	Non-significant
					Bee abundance	Negative
					Hoverfly abundance	Positive
50. Boetzl et al., 2017	Carabid beetles, staphylinid beetles and spiders	Pest control	Non used	Distance	Carabid, staphylinid beetles and spider density	Positive
					Carabid species richness	Positive
				Adjacent AES type	Carabid species richness	Positive
					Staphylinid abundance	Positive
					Spider abundance	Non-significant

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CHAPTER 2

INVERSE AVIAN CROSS-HABITAT SPILLOVER IS MODULATED BY MATRIX TYPE, FOREST COVER AND FRAGMENT SIZE

Carolina Montealegre Talero, Andrea Larissa Boesing and Jean Paul Metzger

ABSTRACT: Cross-habitat spillover is the movement of individuals between different habitat types, which is often coupled with the provision of ecosystem services. Despite the importance of this connectivity process, many aspects of its functioning still need to be better understood. Here we tested how avian spillover at edges is affected by landscape structure (represented as interface type, fragment size and forest cover), considering bird species with different biological characteristics. We performed mist netting across two interface types (forest/coffee plantations and forest/pastures), and estimated the ratio and the dissimilarity of birds moving in- and out- forest fragments, according to bird habitat association and feeding guilds. We found strong evidence of an inverse spillover in highly deforested landscapes (i.e. birds moving from crop fields into forest patches). Our results indicate that interface type is a key driver of spillover, given that most of individuals where performing spillover from coffee matrices and not from pastures. Also, interface type interacted with other landscape features, as forest cover and fragments size, with a trend of spillover ratio increasing with forest cover at coffee interfaces, and also with larger fragments acting as sources of individuals in less contrasting matrices. Finally, dissimilarity between individuals coming in and out of the fragments was higher in pasture matrices, evidencing that cross-habitat spillover is more rare in this matrix. We demonstrate here that landscape structure has an effect over avian spillover. Landscape management aimed at reducing the contrast between matrix and habitat, increasing habitat cover and maintaining large fragments can intensify spillover movements, and potentially promote pest control services that make agriculture production more sustainable.

Keywords: agricultural landscape, landscape structure, forest cover, fragment size, matrix type, community dissimilarity, birds, Brazilian Atlantic forest.

INTRODUCTION

In agricultural landscapes, where a great percentage of native habitat has been lost, cross-habitat spillover, defined as the movement of organisms among different habitats (Blitzer et al., 2012; Tscharntke et al., 2012), is an important ecological process, particularly related to food web interactions of local communities (Tscharntke et al., 2012, Schneider et al., 2013). When spillover movements occur from native habitats to agricultural fields, mobile agents can provide important services, such as crop pollination (Kremen et al., 2007) and pest control activities (Bianchi et al., 2006; Blitzer et al., 2012; Maas et al., 2015). Therefore, it is important to understand the role of landscape structure on spillover regulation (Boesing et al., 2017).

Spillover is a bi-directional process occurring from native habitats into agricultural land covers or from agricultural habitats into native patches (Blitzer et al., 2012; Rand & Louda, 2006). The main mechanism driving the directionality of spillover is resource availability (Rand & Louda, 2006). Resource attainment might be achieved if the landscape provides organisms with a full complement of spatially separated non-substitutable resources (complementation), or if the landscape provides organisms with supplemental habitats containing larger concentrations of substitutable resources (supplementation) (Dunning et al., 1992; Tscharntke et al., 2012). In this context, agricultural landscapes are highly dynamic environments, presenting opportunities for resource provision following temporal resource pulses encompassed with crop's development (Siriwardena, 2010). Thus, primary productivity in a given environment might be a factor that determines the flow of organisms between habitats (Polis et al., 1997) as they usually move from the higher productivity habitat to the lower (Oksanen et al., 1992; Polis et al., 1997)

The effects of spillover encompass exchanges of organisms and energy among different habitats, which can have impacts on a variety of ecosystem functions and trophic interactions in the recipient habitat (McCoy et al., 2009). For instance, in agricultural landscapes, when a rapid decline of one habitat type occurs (for example, during harvest) can result in the emigration of mobile predators into an alternative habitat, which results in a rise in predator abundance in the recipient habitat (Holt & Hochberg, 2001). Therefore, spillover across habitat types, especially in systems that differ in availability of resources, may be an important ecological process structuring communities. There is abundant evidence for spillover from natural to managed areas but little is known about the flow in the opposite direction (Blitzer et al., 2012).

Several characteristics of landscape structure can influence animal spillover. One of such is fragment size, which is intrinsically related with edge effects: as patches become smaller and more irregularly shaped, they become increasingly dominated by edge habitat (Ries et al., 2004). Edge density has an additive effect with habitat cover on spillover, because spillover increases in landscapes with more habitat and many edges; this is due to increased structural connectivity and complementation processes (Boesing et al., 2018). For species occurring in a network of habitat patches, movement between local habitat patches is a crucial component of metapopulation movements (Bergman et al., 2004; Öckinger & Smith, 2006), in which more productive (larger) fragments serve as source of emigrants that disperse to relatively less productive (smaller) fragments that act as sinks (Dunning et al., 1992). Habitat cover can also affect spillover movements both because of the higher richness and abundance of organisms in-patches (Martensen et al., 2012), and also due to the lower isolation between patches that facilitates organismal movement (Fahrig, 2003; Villard & Metzger, 2014)

Matrix surrounding habitat patches is another important factor influencing biodiversity spillover. Matrices might act both as barrier, or as facilitator of organismal movement (Kupfer et al., 2006). In this sense, according to the “edge-permeability hypothesis”, it is expected that matrices with a high degree of contrast will be relatively impermeable to movement, while those with low contrast will be more permeable (Stamps et al., 1987). For example, Haynes & Cronin (2003) found that planthoppers were less likely to leave patches surrounded by a hostile matrix, which resulted in their concentration at patch edges. The matrix surrounding habitat patches becomes extremely important because dispersal between patches occurs through the matrix and if it is inhospitable then isolation increases (Kennedy et al., 2011). In contrast, if the matrix has relatively low contrast with the habitat patches, then complete isolation is much less likely (Turner & Gardner, 2015).

Thus, in order to understand how landscape structure influences avian-spillover intensity, directionality and composition, we tested three hypotheses, relating landscape structure parameters (matrix type, forest cover and fragment size) with cross-habitat spillover. First, we expect forest birds to move from fragments to the matrix, mostly towards low-contrasting interfaces, because this type of matrix potentially offers more complementary resources (Cadenasso & Pickett, 2001; Didham & Lawton, 1999), with a lower risk of predation (Biz et al., 2017). Second we expect spillover to be intensified at intermediate values of forest cover because in such landscape condition there is a higher density of contacts between native habitats and the matrix (Perović et al., 2010). Third, we expect spillover movements to be more frequent from larger fragments due to source-sink dynamics, because larger, more productive fragments serve as sources of migrants, which disperse to less productive fragments or to the matrix, which act as sinks (Dunning et al., 1992). As a consequence of cross-habitat spillover, we expect to observe lower avian community dissimilarity between species that enter and leave forest fragments in low-contrasting interfaces, at higher amounts of forest cover and for larger fragments, because higher rates of movement across interfaces (which should be observed in all these three conditions) will homogenize the communities found in both sides of the edge.

METHODS

Study region

The study region is located in the limit between the states of São Paulo and Minas Gerais, in the region known as *Sul de Minas*. This region is highly important for coffee production, giving that nearly one third of the whole Brazilian production is harvested there (EMBRAPA, 2020). Moreover, Brazil produces almost 35% of the worldwide-commercialized coffee (USDA, 2020). This high-productive region is embedded within the Brazilian Atlantic Forest domain a highly biodiverse hotspot and extremely threatened biome (Myers et al., 2000), of which only 28% to 16% of its original forest cover remains (Rezende et al., 2018). Nowadays, the *Sul de Minas* region is characterized as an agricultural coffee landscape that displays a heterogeneous mosaic of patches of native forest and extensively sun-coffee farms (fig. 1). Other land use types are also present, such as pastures, *Eucalyptus* and urban settlements, but in a lesser proportion (Table S1).

Landscapes selection

We selected four 3 km radius “focal landscapes” ranging from 11% to 21% of forest cover remaining (Fig. 1; table S1), with similar abiotic conditions (i.e. soil type, altitude) and at least 6 km away from each other in order to avoid spatial overlap.

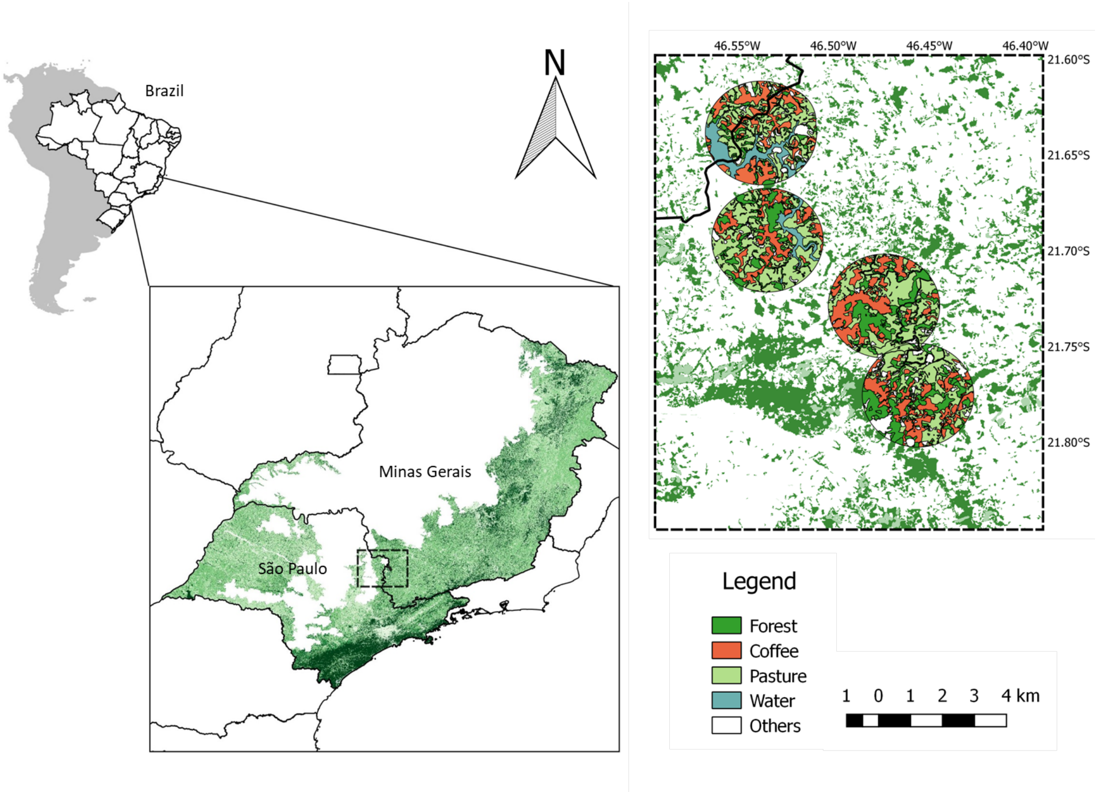

Figure 1. Study areas in the Brazilian Atlantic Forest biome between the states of São Paulo and Minas Gerais, and geographical location of the four (3 km radius) landscapes used in this study.

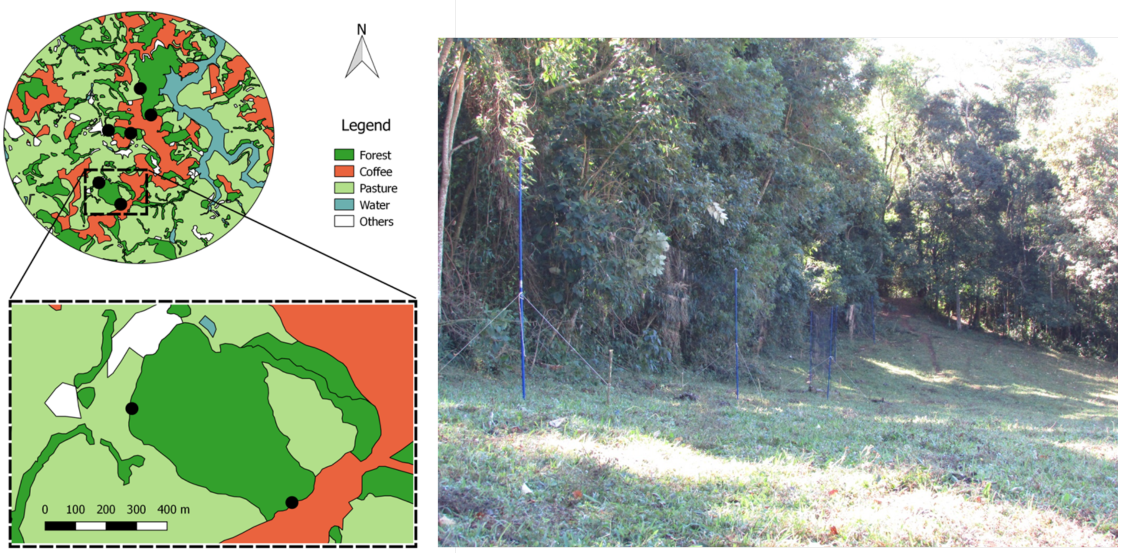

Figure 2. Experimental sampling design applied to collect field data. At each focal landscape, three forest patches of different sizes were sampled. For each fragment, we placed sampling sites in contact with pasture, on the one hand, and with coffee, on the other. For each interface (fragment-coffee and fragment-pasture) a line of five mist nets (~ 60 m) was placed.

Mist-net sampling

In each focal landscape, we selected three forest fragments (one small-sized < 10 ha, one medium-sized 10-50 ha, and one large-sized > 50 ha; Table S2) which had both pastures or coffee plantations in its adjacencies, composing a paired sampling design (hereafter sampling site). Therefore, for the same fragment we sampled both interfaces (N = 24 interfaces in total, 12 interfaces per matrix: pasture and coffee) simultaneously. Each sampling site was composed by two mist-net lines (5 mist-nets of 12 m. x 2.6 m; 60 m. aprox. in each line), one at a forest-coffee interface and another one at a forest-pasture interface, distant from each other 377.75 ± 166.74 (mean ± SD). Mist-nets were operated along 3 consecutive days, from 06:00 am to 12:00 m and from 14:00 pm to 18:00 pm (totaling 3600 net-hours, 300 per fragment). This number of days was estimated considering the time that resident birds learn to identify mist-net placements (Dunn & Ralph, 2004). The sampling was done during the dry season of 2018 (March, April, May), before coffee harvesting in the region. Whenever a bird was captured, the direction of entry or exit to/from the fragment was recorded, species identity recorded and each bird was marked with nail polish in a unique color combination in order to identify recaptures.

We classified species according to habitat specificity (forest-specialist and forest-generalists) and foraging habits. Forest specialists were defined as species that are mostly found in the interior of native forest and require forest areas for breeding and surviving (del Hoyo et al., 2020). Generalists were defined as species with a higher plasticity to use different forest types and agricultural areas (del Hoyo et al., 2020). Feeding guilds were obtained in Wilman et al., (2014) that identify numerically the contribution of different feeding items in birds' diet. Thus, we ended up with two insectivorous categories: *occasional insectivorous*, defined as species that occasionally feed on insects, but other feeding resources (fruit, nectar, seeds) are the most important; *restricted insectivorous* were defined as species that are predominantly insectivorous, but feed on other resources occasionally.

Spillover indicators

We used the information regarding birds entering or leaving the fragment as spillover indicator. A similar method was used by Frost et al., (2015) to evaluate spillover of generalist and specialist flying-insect predators of lepidopteran larvae across the edges of managed plantations and native forest. We used two approaches for measuring spillover. First an in/out spillover ratio ($R_{spillover}$) using birds' abundance was calculated using the following formula:

$$\boxed{\mathbf{Ratio} = \frac{\text{\# of individuals leaving fragment}}{\text{\# of individuals leaving fragment} + \text{\# of individuals entering fragment}}}$$

This equation results in a ratio that ranges between 0 and 1: Values higher than 0.5 indicate more individuals moving out of the fragment (leaving); values lower than 0.5 indicate more individuals moving into the fragment (entering). Values of 0.5 indicate that the number of individuals leaving or entering the fragment was the same.

Second, we used a spillover Bray-Curtis index ($\beta_{dissimilarity}$) to assess the dissimilarity between the number of individuals of different species that entered and left the interfaces. We estimated both Spillover ratios ($R_{spillover}$) and Bray-Curtis index ($\beta_{dissimilarity}$), according to birds' habitat specificity: forest-dependent ($R_{spillover}$FD, $\beta_{dissimilarity}$FD), habitat generalists ($R_{spillover}$G, $\beta_{dissimilarity}$G), total ($R_{spillover}$T, $\beta_{dissimilarity}$T) and according to insectivore degree: i.e. occasional insectivorous ($R_{spillover}$OI, $\beta_{dissimilarity}$OI), restricted insectivorous ($R_{spillover}$RI, $\beta_{dissimilarity}$RI) and total insectivorous

($R_{spillover}$TI, $\beta_{dissimilarity}$TI). Finally, spillover movement was also assessed for the four most abundant species.

Data analysis

First, in order to understand the general patterns of captures across interfaces we built generalized linear mixed models (GLMM) with a Binomial error distribution and logistic link function to test whether interface type predicted the number of total captures and to test whether direction type predicted the number of total captures. We included the focal landscape and the sampling site as random effect in the models.

To test our hypotheses that avian spillover intensity, directionality and dissimilarity are affected by landscape structure, we modeled spillover ratio and dissimilarity indices following both habitat specificity ($R_{spillover}$T, $R_{spillover}$G, $R_{spillover}$FD) and insectivore degree ($R_{spillover}$TI, $R_{spillover}$OI, $R_{spillover}$RI) and dissimilarity indexes ($\beta_{dissimilarity}$T, $\beta_{dissimilarity}$G, $\beta_{dissimilarity}$FD, $\beta_{dissimilarity}$TI, $\beta_{dissimilarity}$OI, $\beta_{dissimilarity}$RI) as a function of interface type (coffee or pasture), forest cover (at the best scale of response; see details below), and fragment size (ranging from 2 to 200) using GLMMs. For both $R_{spillover}$ and $\beta_{dissimilarity}$ we included in all models both the focal landscape ($N = 4$) and the sampling site ($N = 12$) as random factors. $R_{spillover}$ was modeled using a Binomial distribution, and $\beta_{dissimilarity}$ using a zero-inflated beta distribution. For $R_{spillover}$ we built 11 predictive models, (including a null model) which incorporated the individual, interactive, additive and quadratic effects of matrix type, forest cover and fragment size. For $\beta_{dissimilarity}$ we built six predictive models (including a null model) that incorporated the individual and interactive effects of matrix type, forest cover and fragment size. Finally, AIC model selection analysis was performed to identify the best predictive model (Burnham & Anderson, 2001) considering models with $\Delta AICc \leq 2$ as equally probable.

Using ArcGIS (version 10.7.1) we created multi-scale buffers (400, 600, 800 and 1000 meters), calculated forest cover at these different scales, and then used them to perform an AIC model selection (Burnham & Anderson, 2001) to estimate the best scale of response for each response index ($R_{spillover}$ and $\beta_{dissimilarity}$), considering ΔAICc ≤2 as equally probable. We obtained different scales for different groups: 1000 m for $R_{spillover}$T, 600 for $R_{spillover}$G, 600 for $R_{spillover}$FD, 1000 $R_{spillover}$TI, 800 for $R_{spillover}$OI, 400 for $R_{spillover}$RI, 600 for $\beta_{dissimilarity}$T, 400 for $\beta_{dissimilarity}$G, 600 for $\beta_{dissimilarity}$FD, 1000 for $\beta_{dissimilarity}$TI, 400 for $\beta_{dissimilarity}$OI and 800 for $\beta_{dissimilarity}$RI (Table S3). All analysis were performed in R environment (RStudio Team, 2015) using the "beta.part" (Baselga & Orme, 2012), "lme4" (Bates et al., 2015) and "bbmle" (Bolker & R Development Core, 2019) packages.

RESULTS

A total of 559 individuals of 89 bird species were captured, including 15 individuals recaptured (2.7 %). Generalists composed the majority of captures (48.3%; 42 species; 270 individuals), forest-associated constituted 29.7% (32 species; 167 individuals), and open-area associated species comprised 21.8% (12 species; 122 individuals) (full list in Table S4). More individuals were captured at coffee interfaces (329 individuals, mean = 9.13 ± 6.21) compared to pastures (230 individuals, mean = 6.39 ± 6.16; Z = -0.36, $p < 0.0001$; Table S5). In coffee interfaces the most abundant species where the Ruby-crowned Tanager (*Tachyphonus coronatus;* N = 53), the Stripe-crowned Warbler (*Basileuterus culicivorus*; N = 33) and the Rufus-collared Sparrow (*Zonotrichia capensis;* N = 23). In pasture, the most abundant species where the Double-collared Seedeater (*Sporophila caerulescens*; N = 41), the Ruby-crowned Tanager (*Tachyphonus coronatus;* N = 22) and the Rufus-collared Sparrow (*Zonotrichia capensis;* N = 20).

Contrary to our expectations, most spillover movements occurred entering from the matrix into the forest fragments (and not leaving fragments), both for generalists and forest dependent (Z = -0.58, P < 0.0001; Fig 3, Table S6).

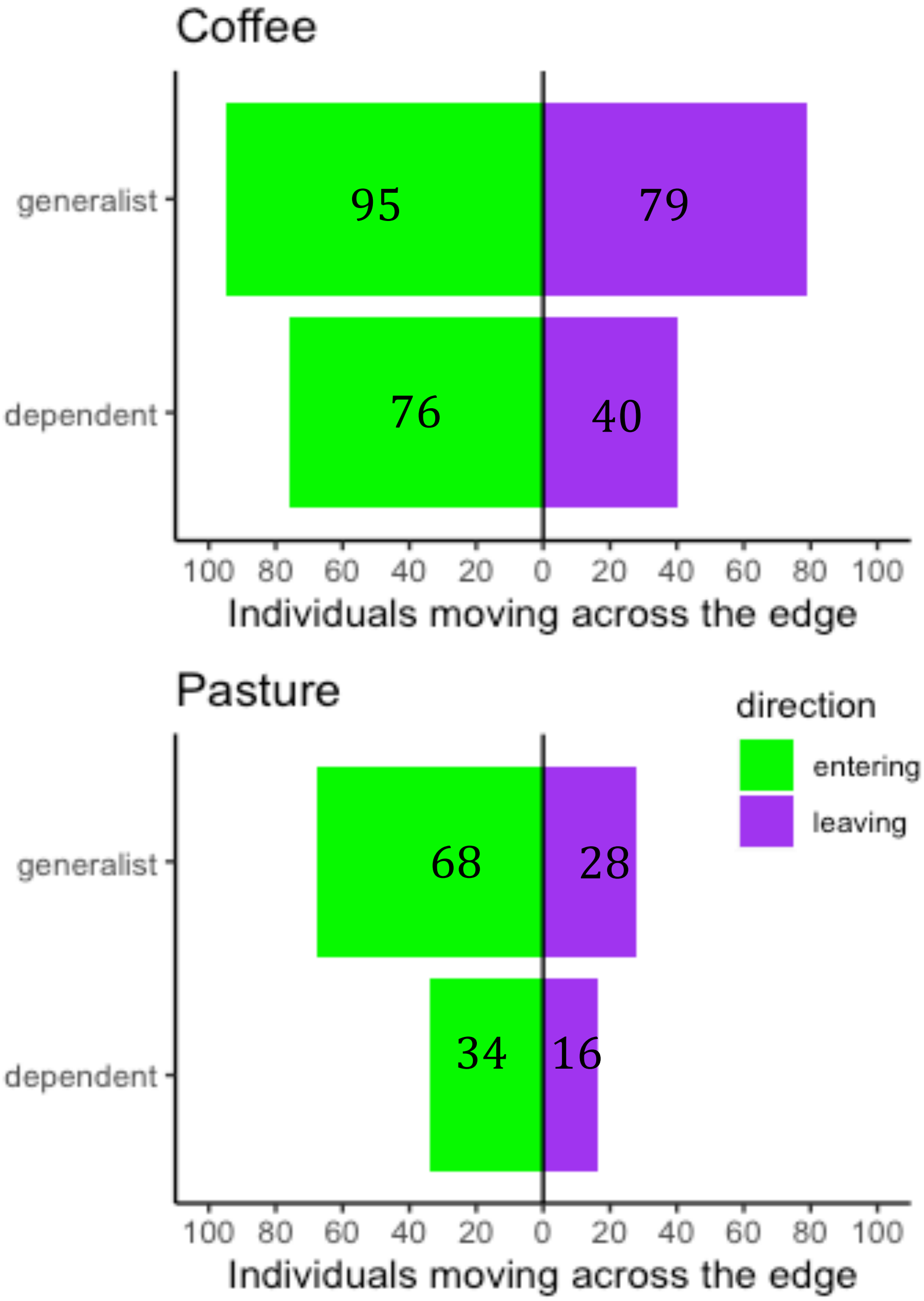

Fig 3. Number of captures of habitat generalist and forest dependent avian species moving into both coffee and pasture interfaces. The vertical line at zero represents the forest edge. Total number of individuals entering into the forest fragments from the coffee and pastures matrices

(green bars) and total number of individuals leaving the forest fragments (purple bars). Numbers in the bars indicate the number of individuals entering and leaving.

Total spillover (evaluating all species together; $R_{spillover}T$) was explained by the model that included interface type and also by the additive model containing interface type and forest cover (Table 1). In both matrices, spillover overwhelming occurs from the matrix into the forest. In coffee plantations, at lower amounts of forest cover, more species enter the forest fragment, and once forest cover increases, the balance of species leaving and entering increase. In pasture matrices, an opposite pattern occurs at higher amounts of forest cover: the number of individuals entering the forest increases (Fig 4A).

Regarding habitat-specificity, the spillover of habitat generalists ($R_{spillover}G$) was explained by the interactive model of interface and fragment size (Table 1). In coffee matrices, as forest fragment size increases, spillover ratio of generalists increased, i.e. more individuals are leaving the patch than entering. Around a 100 ha value, the spillover ratio is balanced. In pasture matrices, an opposite pattern was detected, as generalist spillover ratio decreased as fragment size increased (Fig. 4B). We did not find evidence for explaining forest-dependent species' spillover ratio ($R_{spillover}FD$), and the null model was the best model selected.

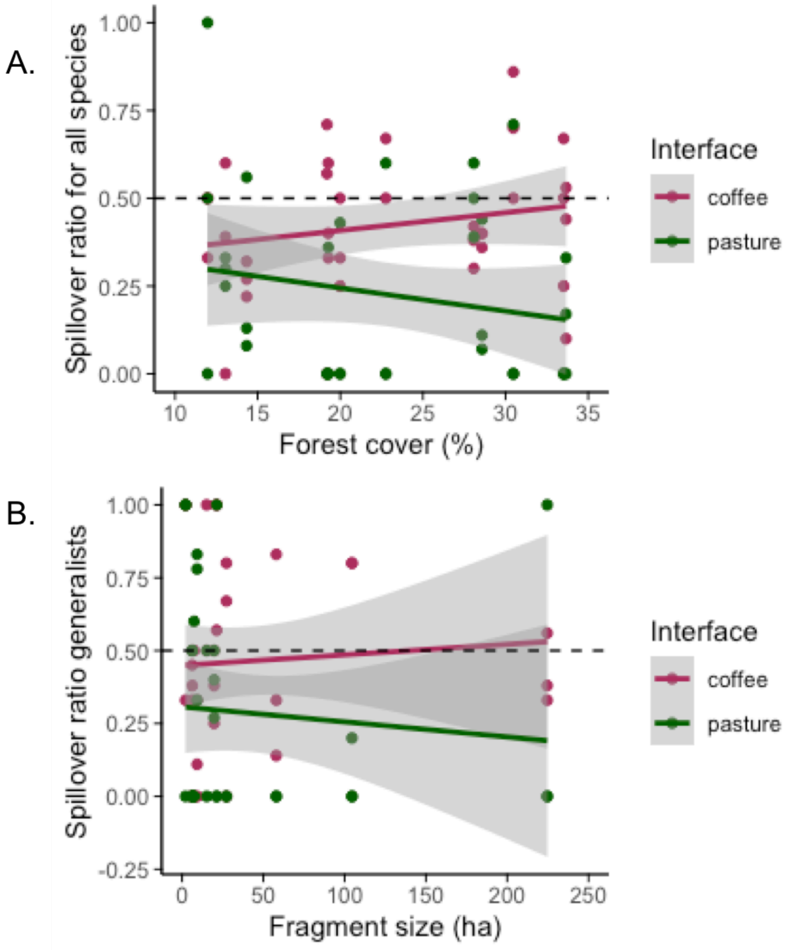

Figure 4. Spillover ratio for A) total bird spillover ratio ($R_{spillover}T$), B) Generalist species spillover ($R_{spillover}G$), including linear tendency regression. A ratio value above 0.5 indicates that birds are leaving the fragments and a value below 0.5 indicates that the birds are entering the forest fragments.

Concerning insectivore degree, the occasional insectivore's spillover was the only case where spillover was not inverse (i.e. more species leaving the forest). $R_{spillover}OI$ was affected by an interaction between interface type and fragment size (Table 1). In coffee matrices, as fragment size increase, the ratio of occasional insectivores increases, i.e. more individuals are leaving the patch than entering. In the pasture interfaces, an opposite pattern was detected, with more individuals entering the forest than leaving (fig. 5A). Results for insectivore guilds indicated that total insectivores' spillover ratio

($R_{\text{spillover}}$TI) as well as restricted insectivores' spillover ratio ($R_{\text{spillover}}$RI) were not influenced by any of the analyzed landscape variables.

The only species responding to landscape structure was *B. culicivorus*, a restricted insectivorous species. The best predictive model of spillover for this species was the interactive model of fragment size and interface (Table 1). In the coffee interfaces, as forest fragments increases, spillover ratio of *B. culicivorus* increased, i.e. more individuals are leaving the patch than entering. Similarly to generalist species, the spillover ratio is balanced around a 100 ha value. In pasture matrices, an opposite pattern was detected, as more individuals are entering when forest fragments increase in size (Fig. 5B).

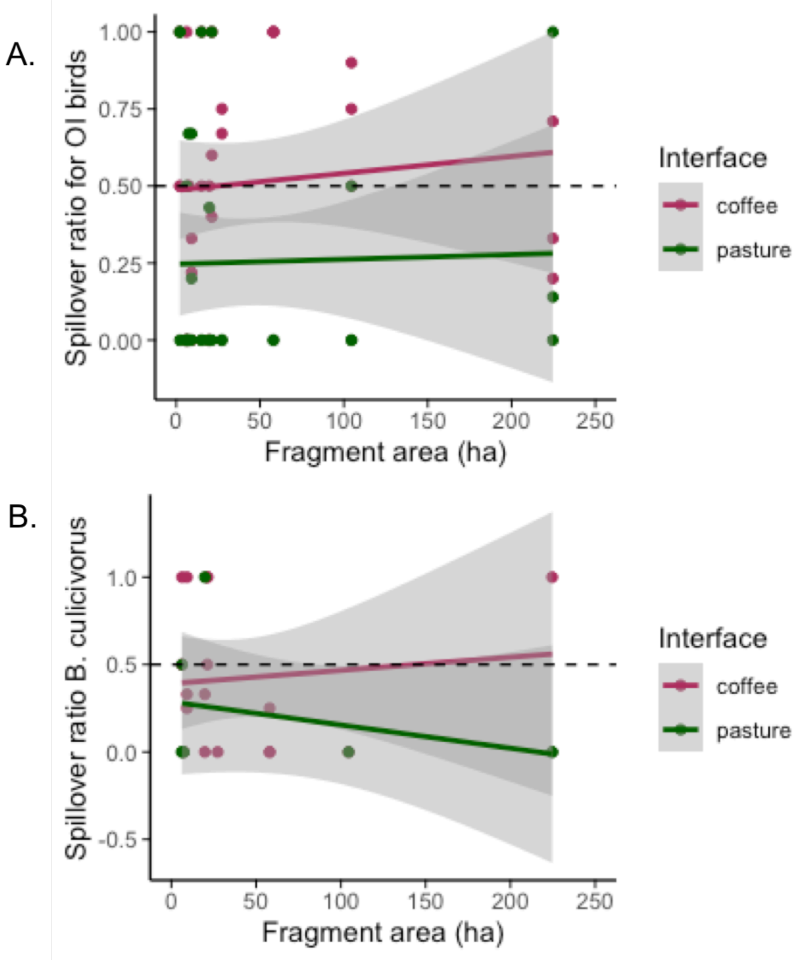

Figure 5. Spillover ratio for A) occasional insectivorous bird spillover ratio ($R_{spillover}OI$), B) *Basileuterus culicivorus* spillover, including linear tendency regression. A ratio value above 0.5 indicates that birds are leaving the fragments and a value below 0.5 indicates that the birds are entering the forest fragments.

We only found support for spillover dissimilarity when evaluating the total bird community ($\beta_{dissimilarity}T$) and restricted insectivores' dissimilarity ($\beta_{dissimilarity}RI$). For $\beta_{dissimilarity}T$, interface type was the best model explaining its variation (Table 1). This means that species entering and leaving forest patches at coffee interfaces are more similar than species that are moving at pasture matrices, which might indicate that the movement is more constant at coffee interfaces and more rare at pasture interfaces (Fig. 6A). Fore restricted insectivores ($\beta_{dissimilarity}RI$), we observed an interaction between interface type and forest cover (Table 1), indicating also that species entering and leaving forest patches at coffee interfaces are more similar than at pasture interfaces, and that this dissimilarity tends to increase with increasing forest cover in coffee interfaces (Fig. 6B) There was no clear predictor model of dissimilarity for generalists ($\beta_{dissimilarity}G$), forest dependent ($\beta_{dissimilarity}FD$), occasional insectivores ($\beta_{dissimilarity}OI$) and total insectivore species ($\beta_{dissimilarity}TI$).

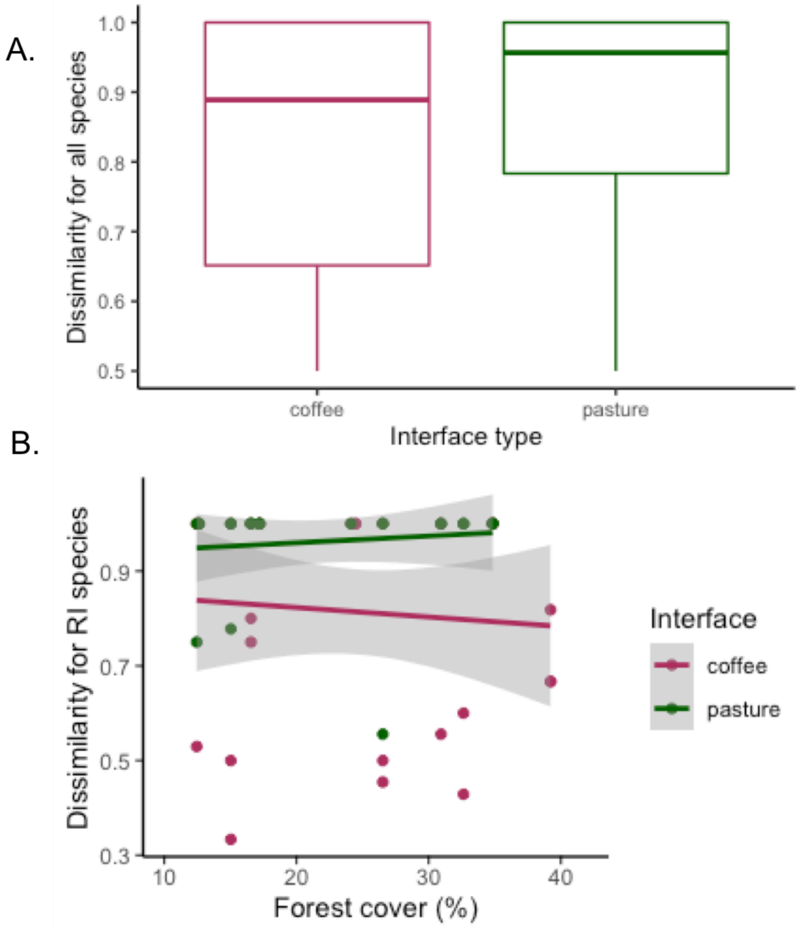

Figure 6. Bray-Curtis dissimilarity for A) total bird community ($\beta_{spillover}$T), B) Restricted insectivorous species ($\beta_{dissimilarity}$RI), including linear tendency regression.

Table 1. Model selection for bird spillover (S) and dissimilarity (β). Only models with AIC < 2 are shown. 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 denotes to 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. $R_{spillover}$T refers to total spillover, $R_{spillover}$G refers to generalist spillover, $R_{spillover}$OI refers to occasional insectivore spillover, $\beta_{dissimilarity}$T refers to total dissimilarity and $\beta_{dissimilarity}$RI refers to restricted insectivore dissimilarity.

Total spillover				**Coefficients**			
Model	**ΔAICc**	**df**	**AICc Wi**	**Intercept (se)**	**Var 1 (se)**	**Var 2 (se)**	**Interaction (se)**
$R_{spillover}$T							
S~interface	0	4	0.44	-0.31 (0.14)	-0.58 (0.19)	-	-
S~Forest cover + interface	1.5	5	0.21	-0.33 (0.14)	0.08 (0.12)	-0.57 (0.19)	-
$R_{spillover}$G							
S~(Fragment area)^2 * interface	0	8	0.7281	-0.31 (0.18)	1.55 (0.68)	-0.30 (0.29)	-4.54 (1.53)
$R_{spillover}$OI							
S~(Fragment area)^2 * interface	0	8	0.58	0.01 (0.35)	3.20 (1.12)	-0.84 (0.34)	-5.19 (1.66)
S~(Forest cover)^2 * interface	1.4	8	0.28	-0.60 (0.42)	0.76 (0.26)	0.08 (0.53)	-0.59 (0.36)
Basileuterus culicivorus							
S~(Fragment area)^2 * interface	0	8	0.524	0.02 (0.94)	-4.57 (2.68)	-18.78 (45.13)	45.28 (53.14)
$\beta_{dissimilarity}$T							
β~interface	0	7.1	0.51	0.66 (0.11)	0.54 (0.18)	-	-
$\beta_{dissimilarity}$RI							
β~Forest cover * interface	0	8.9	0.75	-0.34 (0.23)	2.47 (0.62)	0.02 (0.01)	-0.08 (0.03)

DISCUSSION

We found novel evidence that avian-spillover occurs mostly from crops to native forests in high-deforested landscapes, with 64,2% of bird captures made from crop (coffee or pasture) to forest fragment, characterizing an inverse spillover. At the same time, we found evidence that the opposite movement happens, when there is an increase in forest cover or fragment size at lower contrasting matrices (i.e. coffee), which has important implications in terms of ecosystem services provisioning in agricultural landscapes. Additionally, we encountered that dissimilarity in species composition was lower in coffee plantations than in pastures, indicating that species are very likely moving more often at coffee interfaces. This evidences that resource complementation is happening in such interfaces, while a higher dissimilarity and an indication of more punctual movements occur at pasture interfaces. Besides showing original evidence that the landscape can affect the spillover movement (see chapter 1), these findings highlight the importance of maintaining forest fragments for avian cross-habitat spillover, and the importance of keeping a permeable matrix around those fragments, in order to assure species movement, which in turn can affect pest control provision.

We found strong evidence of an inverse avian spillover at high-deforested landscapes. These findings corroborate Frost et al. (2015), who reported generalist and specialist parasitoids spilling over in greater numbers from plantation to native forest, than in the opposite direction. Spillover direction across the crop/non-crop interface is influenced by the relative productivity and temporal resource availability of each system (Tscharntke et al., 2005), where organisms usually move from the higher productivity habitat to the lower (Oksanen et al., 1992; Polis et al., 1997). In our case, coffee plantations seems to represent a higher-productivity environment, providing habitat for a large variety of arthropod communities, including herbivores, ants, parasitoids, spiders, among others (Perfecto et al., 2014) as well as insect pests, like the coffee berry borer (CBB), *Hypothenemus hampei* (Jiménez-Soto et al., 2013), which might work as complementary resources for birds. Complementary resource use appears as an important mechanism regulating spillover, as crop habitats offer high amounts of food, at least at some times of the year (Tscharntke et al., 2005). Therefore, we can infer that coffee matrices are important sites for birds to forage for insect prey and that they are performing landscape complementary movements between natural and anthropic habitats.

The constant movement in-and-out at coffee matrices elucidated also by spillover similarity, reinforce that the main mechanism driving spillover direction in coffee plantations might be the resource complementation (Dunning et al., 1992). On the other hand, at pasture interfaces, spillover dissimilarity was very high, indicating that the movement is more random, but still, species are overwhelming moving into forest fragments and movement is mostly performed by generalists (70.8%). Two mechanisms might explain this pattern. First, although at a lower rate than in coffee, species are also moving into forest to achieve complementary resources given that pastures are very unproductive environments (Castellón & Sieving, 2006); and second, given that generalist species are able to occupy or move across pastures, this intense movement into forest patches might be due to high-levels of predation (Awade et al., 2017; Biz et al., 2017; Gebauer et al., 2013), obligating species to refuge and forage at forest edges explaining this strong movement into forest patches. Importantly, we captured 57% less individuals in pasture interfaces than in coffee interfaces, which reinforces the importance of matrix permeability (Boesing et al., 2018; Kupfer et al., 2006; Renjifo, 2001).

We also found that fragment size was an important driver for avian spillover, specifically for habitat generalists and for *Basileuterus culicivorus,* but always facilitated by the surrounding matrix. In particular, we found a slightly signal that individuals of the two groups moved into to coffee matrix when fragments where larger than 100 ha. Thus, larger fragments might act as font of individuals (Dunning et al., 1992) in which the fragments are the sources of individuals and the matrix is the sink. Therefore, when larger forest fragments remain in the landscape, spillover movements from the fragments to the matrix are facilitated, especially at lower contrasting matrices that facilitate species movement, like coffee.

Forest cover also acted significantly on avian spillover. Many studies have been showing that spillover from forest into croplands is intensified at higher amounts of forest cover (Boesing et al., 2018; Estavillo et al., 2013). We also demonstrated a trend of spillover ratio increasing with forest cover when the whole assemblage is evaluated together, but only at coffee interfaces, where the contrast of the matrix allows species movement. Given that we surveyed a limited range of forest cover (12 to 34%), in landscapes above this threshold, the spillover from forest into matrix might be increased. The fact that at low values of forest cover many individuals are entering the forest fragments, from both matrices, reflects the scenery of an extremely fragmented landscape, where generalist species are invading forest fragments (Marvier et al., 2004). This increase in spillover can bring deleterious effects for in-patch communities, including increase resource competition at edges (Tscharntke et al., 2005), predation (Rand & Louda, 2006) and even increased parasitism, which seems be happening especially in the pasture matrix.

Occasional insectivores where the only group that clearly presented spillover from the forest fragments into the matrix. Natural habitats are used by natural enemies for finding alternative prey, food resources, better microclimate, refuge and nesting sites (Landis et al., 2000). Therefore, it is clear that forest remnants are sources of natural enemies, like insectivorous birds, that have the potential to invade crops and control pest populations (Tscharntke et al., 2005). A recent review found that pest regulation by birds was often higher in landscapes with higher native habitat cover (Boesing et al., 2017). Particularly, in the same study areas as ours, other authors found that pest control services in coffee plantations is modulated by forest cover (Librán-Embid et al., 2017).

Concluding remarks

We bring novel evidence that spillover is a bi-directional process, especially, that in highly deforested landscapes this process happens mostly from crops into native patches. Our results reinforce that matrix type is a strong determinant of spillover movements in agricultural landscapes; specifically, coffee matrices are permeable to avian spillover movements and pastures are barriers for this process. Also, other landscape features, like forest cover and fragments size are relevant for cross-habitat spillover process. In particular, higher forest cover incentivizes spillover but only in permeable matrices and at larger forest fragments favor spillover movement from fragments to crops. Finally, occasional insectivores are the only group spilling over from fragments to crops, which suggest that spillover of those species can help to control arthropod pests in coffee landscapes. These results suggest that in the case of coffee plantations in the Atlantic Forest, where more than one third of Brazilian coffee is produced, if protection of Atlantic Forest remnants is guaranteed, an abundant complex of natural enemies could be maintained, which could then provide sustainable crop protection.

Supplementary material:

Table S1. Extension of land uses (%) for the four landscapes included in the study, each with a radius of 3 km.

Landscape	Forest	Coffee	Pasture	Water	Eucalyptus	Human settlement	Other	Central geographical location	
								Latitude	Longitude
9	11	23	42	16	1	3	3	-21° 38’	-46° 32’
10	20	23	48	6	1	1	1	-21° 41’	-46° 31’
26	21	27	33	1	12	3	3	-21° 46’	-46° 27’
28	19	12	46	0	1	5	17	-21° 29’	-46° 42’

Table S2. Fragments sizes per landscape

Landscape	Fragment code	Fragment area (ha)
9	F1	15.13
	F2	9.22
	F3	2.18
10	F1	57.97
	F2	21.25
	F3	6.23
26	F1	104.54
	F2	27.27
	F3	7.42
28	F1	224.6
	F2	19.74
	F3	6.32

Table S3. Multi-scale buffer analysis for all groups

Model	Scale (m)	ΔAICc	df	AICc Wi	Intercept (se)	PLAND coefficients
Total spillover	1000	0	4	0.3	-0.92 (0.41)	0.01 (0.01)
Generalist spillover	600	0	4	0.3	-0.70 (0.35)	0.01 (0.01)
Dependent spillover	600	0	4	0.3	-0.61 (0.65)	-0.01 (0.02)
Total insectivores spillover	1000	0	4	0.3	-0.91 (0.31)	0.01 (0.01)
Occasional insectivores spillover	800	0	4	0.4	-2.11 (0.66)	0.07 (0.02)
Restricted insectivores spillover	400	0	4	0.2	-0.45 (0.50)	-0.01 (0.01)
Total dissimilarity	600	0	7.4	0.3	0.57 (0.25)	0.01 (0.01)
Generalist dissimilarity	400	0	7.9	0.3	0.97 (0.59)	-0.01 (0.01)
Dependent dissimilarity	600	0	6.5	0.2	0.46 (0.30)	0.01 (0.01)
Total insectivores dissimilarity	1000	0	4	0.3	1.11 (0.36)	-0.01 (0.01)
Occasional insectivores dissimilarity	400	0	6.4	0.5	0.73 (0.60)	-0.01 (0.01)
Restricted insectivores dissimilarity	800	0	6.7	0.2	0.50 (0.31)	0.01 (0.01)

Table S4. Species captured in the studied landscapes in both pasture and coffee matrices, with habitat association, following del Hoyo et al. (2020) and insectivorous guild, following Wilman et al. (2014). Nomenclature follows del Hoyo et al. (2020).

Family	**Scientific name**	**Common name**	**Matrix captured**	**Habitat association**	**Insectivorous guild**
Accipitridae	*Rupornis magnirostris*	Roadside Hawk	Pasture	G	OI
Columbidae	*Leptotila verreauxi*	White-tipped Dove	Both	G	OI
Cuculidae	*Piaya cayana*	Common Squirrel-cuckoo	Coffee	G	RI
Trochilidae	*Amazilia lactea*	Sapphire-spangled Emerald	Both	G	OI
	Chlorostilbon lucidus	Glittering-bellied Emerald	Both	G	OI
	Heliomaster squamosus	Stripe-breasted Starthroat	Coffee	G	OI
	Heliothryx auritus	Black-eared Fairy	Both	G	OI
	Phaetornis eurynome	Scale-throated Hermit	Pasture	G	OI
	Phaetornis pretrei	Planalto Hermit	Both	G	OI
	Thalurania furcata	Fork-tailed Woodnymph	Pasture	G	OI
	Thalurania glaucopis	Violet-capped Woodnymph	Coffee	G	OI
Bucconidae	*Malacoptila striata*	Greater Crescent-	Coffee	D	RI

Family	Scientific name	Common name	Matrix captured	Habitat association	Insectivorous guild
		chested Puffbird			
Galbulidae	*Galbula ruficauda*	Rufous-tailed Jacamar	Coffee	G	RI
Picidae	*Campephilus robustus*	Robust Woodpecker	Pasture	D	RI
	Picumnus cirratus	White-barred Piculet	Coffee	G	RI
Furnariidae	*Anabazenops fuscus*	White-collared Foliage-gleaner	Pasture	D	RI
	Cranioleuca pallida	Pallid Spinetail	Both	D	RI
	Dendrocolaptes platyrostris	Planalto Woodcreeper	Pasture	D	RI
	Lepidocolaptes squamatus	Scaled Woodcreeper	Pasture	D	RI
	Sittasomus griseicapillus	Eastern Olivaceous Woodcreeper	Both	D	RI
	Synallaxis frontalis	Sooty-fronted Spinetail	Both	G	RI
	Synallaxis ruficapilla	Rufous-capped Spinetail	Both	D	RI
	Synallaxis spixi	Spix's Spinetail	Both	G	RI
	Syndactyla rufosuperciliata	Buff-browed Foliage-gleaner	Coffee	D	RI
	Xiphorhynchus fuscus	Lesser Woodcreeper	Coffee	D	RI

Family	**Scientific name**	**Common name**	**Matrix captured**	**Habitat association**	**Insectivorous guild**
Thamnophilidae	*Dysithamnus mentalis*	Plain Antvireo	Pasture	D	RI
	Pyriglena leucoptera	White-shouldered Fire-eye	Coffee	D	RI
	Thamnophilus caerulescens	Variable Antshrike	Coffee	D	RI
Conopophagidae	*Conopophaga lineata*	Rufous Gnateater	Coffee	D	RI
Tyrannidae	*Camptostoma obsoletum*	Southern Beardless Tyrannulet	Both	G	RI
	Cnemotriccus fuscatus	Fuscous Flycatcher	Coffee	D	RI
	Colonia colonus	Long-tailed Tyrant	Pasture	D	RI
	Elaenia cristata	Plain-crested Elaenia	Pasture	OA	RI
	Elaenia flavogaster	Yellow-bellied Elaenia	Pasture	G	RI
	Elaenia mesoleuca	Olivaceous Elaenia	Both	D	RI
	Hemitriccus diops	Drab-breasted Bamboo-tyrant	Coffee	G	RI
	Knipolegus cyanirostris	Blue-billed Black-tyrant	Pasture	OA	RI
	Leptopogon amaurocephalus	Sepia-capped Flycatcher	Both	D	RI
	Mionectes rufiventris	Grey-hooded Flycatcher	Coffee	D	RI
	Myiarchus swainsoni	Swainson's	Coffee	G	RI

Family	**Scientific name**	**Common name**	**Matrix captured**	**Habitat association**	**Insectivorous guild**
		Flycatcher			
	Myiophobus fasciatus	Bran-colored Flycatcher	Pasture	G	RI
	Pitangus sulphuratus	Great Kiskadee	Pasture	G	OI
	Poecilotriccus plumbeiceps	Ochre-faced Tody-flycatcher	Coffee	D	RI
	Serpophaga subcristata	White-crested Tyrannulet	Coffee	G	RI
	Todirostrum poliocephalum	Yellow-lored Tody-flycatcher	Coffee	G	RI
	Tolmomyias sulphurescens	Yellow-olive Flatbill	Coffee	D	RI
	Tyrannus melancholicus	Tropical Kingbird	Pasture	G	RI
Tityridae	*Myiobius atricaudus*	Black-tailed Flycatcher	Both	G	RI
Pipridae	*Chiroxiphia caudata*	Blue Manakin	Both	D	OI
Corvidae	*Cyanocorax cristatellus*	Curl-crested Jay	Pasture	G	OI
Hirundinidae	*Stelgidopteryx ruficollis*	Southern Rough-winged Swallow	Coffee	OA	RI
Troglodytidae	*Troglodytes musculus*	Southern House Wren	Pasture	OA	RI
Turdidae	*Turdus albicollis*	White-necked Thrush	Coffee	D	RI
	Turdus amaurochalinus	Creamy-	Both	G	OI

Family	Scientific name	Common name	Matrix captured	Habitat association	Insectivorous guild
		bellied Thrush			
	Turdus leucomelas	Pale-breasted Thrush	Both	G	RI
	Turdus rufiventris	Rufous-bellied Thrush	Both	G	OI
Vireonidae	*Cyclarhis gujanensis*	Rufous-browed Peppershrike	Pasture	G	RI
	Hylophilus amaurocephalus	Grey-eyed Greenlet	Coffee	G	RI
	Hylophilus poicilotis	Rufous-crowned Greenlet	Both	D	RI
Parulidae	*Basileuterus culicivorus*	Stripe-crowned Warbler	Coffee	D	RI
	Myiothlypis leucoblephara	White-rimmed Warbler	Both	D	RI
Thraupidae	*Asemospiza fuliginosa*	Sooty Grassquit	Pasture	OA	NI
	Coereba flaveola	Bananaquit	Both	G	OI
	Conirostrum speciosum	Chestnut-vented Conebill	Pasture	D	RI
	Coryphospingus cucullatus	Red-crested Finch	Coffee	G	OI
	Coryphospingus pileatus	Pileated Finch	Both	G	OI
	Dacnis cayana	Blue Dacnis	Pasture	G	OI
	Haplospiza unicolor	Uniform Finch	Pasture	OA	NI

Family	Scientific name	Common name	Matrix captured	Habitat association	Insectivorous guild
	Saltator fuliginosus	Black-throated Grosbeak	Coffee	D	OI
	Saltator similis	Green-winged Saltator	Both	G	OI
	Sicalis luteola	Grassland Yellow-finch	Both	OA	NI
	Sporophila caerulescens	Double-collared Seedeater	Both	OA	NI
	Tachyphonus coronatus	Ruby-crowned Tanager	Both	G	RI
	Tangara cayana	Burnished-buff Tanager	Both	G	OI
	Tangara cyanoventris	Gilt-edged Tanager	Coffee	D	OI
	Thlypopsis sordida	Orange-headed Tanager	Coffee	G	OI
	Thraupis sayaca	Sayaca Tanager	Coffee	G	OI
	Trichothraupis melanopis	Black-goggled Tanager	Both	D	RI
	Volatinia jacarina	Blue-black Grassquit	Pasture	OA	OI
Cardinalidae	*Cyanoloxia brissonii*	Ultramarine Grosbeak	Both	D	OI
Passerellidae	*Arremon flavirostris*	Saffron-billed Sparrow	Both	D	RI
	Zonotrichia capensis	Rufous-	Both	OA	OI

Family	**Scientific name**	**Common name**	**Matrix captured**	**Habitat association**	**Insectivorous guild**
		collared Sparrow			
Fringillidae	*Euphonia chlorotica*	Purple-throated Euphonia	Coffee	G	NI

D = forest dependent, G = habitat generalist, OA = open-area specialist. RI = restricted insectivorous, OI = occasional insectivorous, NI = not-insectivorous

Table S5. Coefficients from a GLMM with Poisson errors (and log link function) testing whether interface type predicted the number of total captures. Landscape and point were included as random factors. Significant *P* values (α ≤ 0.05) are indicated in bold.

Fiexed effects	Estimate	Std. Error	*z* value	Pr(>|*z*|)
Intercept	2.03	0.19	10.51	< 0.0001
Matrix (pasture)	-0.36	0.08	-4.18	**< 0.0001**

Table S6. Coefficients from a GLMM with Poisson errors (and log link function) testing whether direction type predicted the number of total captures. Landscape and point were included as random factors. Significant *P* values (α ≤ 0.05) are indicated in bold.

Fiexed effects	Estimate	Std. Error	*z* value	Pr(>|*z*|)
Intercept	1.42	0.19	7.40	< 0.0001
Matrix (pasture)	-0.58	0.09	-6.66	**< 0.0001**

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CHAPTER 3

TEMPORAL ASPECTS OF AVIAN SPILLOVER IN ANTHROPOGENIC LANDSCAPES

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Abstract: Cross-habitat spillover is the movement of individuals between different habitat types, which is often coupled with the provision of ecosystem services. Despite the importance of this connectivity process, many aspects of its functioning still need to be better understood. In this work we attempted to test how temporal daily avian spillover is influenced by landscape structure (represented as interface type, fragment size and forest cover), considering bird species with different biological characteristics. We performed mist netting across two interface types (forest/coffee plantations and forest/pastures), and estimated the ratio of birds moving in- and out- forest fragments throughout the day, according to bird habitat association and feeding guilds. We found that temporal spillover follows a bi-modal pattern, occurring mostly in the morning and afternoon hours. Matrix that surrounds forest fragments determines the temporality of spillover. In the coffee matrix birds are moving out of the fragments in the morning hours and coming back in the afternoons, which indicates that coffee plantations might be providing complementary feeding resources. However, birds are still using forest patches of different sizes for roosting and refuge, evidenced by the movement into forest patches in the afternoons. In pasture interfaces individuals are moving in and out all day long, with predominance of movement into the fragment. Those results suggest that birds avoid leaving the fragments, indicating that pasture acts as a barrier for dispersal, not providing complementary alimentary resources, and that forest fragments supply resources and refuge. Forest cover and fragment size have a more limited, and sometimes unexpected influence in temporal spillover. In general, the inward movement happens in pasture matrices, in landscapes with less forest cover and when fragments are small, that is, when landscapes are more disturbed. The most consistent results of this study indicate that for spillover movements to occur along the day in the matrix, it is necessary to have a more permeable matrix, and preferably in landscape conditions of higher forest cover.

Keywords: agricultural landscape, temporal spillover, landscape structure, forest cover, fragment size, matrix type, birds, Brazilian Atlantic forest.

INTRODUCTION

Agricultural landscapes are characterized by habitat loss and modification that result in disrupted animal movement (Doherty & Driscoll, 2018). In such fragmented and altered environments species become confined in isolated patches that are surrounded by contrasting inter-habitat matrices (Driscoll et al., 2013). Some aspects of landscape structure, such as matrix quality, habitat patchiness and habitat amount can predict the balance between the risks and benefits of movement across the landscape (Gadgil, 1971; Hovestadt et al., 2001; Ronce et al., 2000; Travis & Dytham, 1999). Therefore, species that inhabit in landscapes with high habitat cover are predicted to perform longer movement distances than species that inhabit in landscapes with low habitat cover, due to the lower movement cost in habitat than in matrix (Cornelius et al., 2017; Fahrig, 2007). Other aspects that influence movement rates in fragmented landscapes are related to the presence or absence of food resources (Siriwardena, 2010), and the risk of predation (Biz et al., 2017).

Fahrig (2007) describes as "boundary response" when an animal shows a propensity to stay in a patch when it encounters a patch boundary, instead of crossing and going to the adjacent non-habitat cover types (i.e., the matrix) on the other side of the edge. As a consequence, species that inhabit in landscapes with a "risky" matrix should show a *strong boundary response*, which would take them back whenever they encounter a habitat edge (Cornelius et al., 2017). In contrast, species that inhabit in patchy landscapes with a "low-risk" matrix should show a less intense "boundary response" because the risk of crossing the edge is lower (or perceived as lower). In addition, forest-specialist species, which rely mainly on forest resources, have a tendency to establish their home range inside forested areas and may have reduced movement outside their patch, unless the patch is too small and supplementary resources should be collected in adjacent habitat patches (Kuefler et al., 2010). In contrast, habitat generalists use a broader scope of resources and are expected to use a variety of habitat types, including those under intensive human use (Hansbauer et al., 2008). Consequently, we would expect forest dependent and generalist species to have a differentiated response to habitat edges, avoiding or not, respectively, habitat gap crossings.

Fragment size, forest cover percentage and matrix type are landscape structure features that can affect animal abundance and dispersal movements (Boesing et al., 2018; Kupfer et al., 2006; Renjifo, 2001; Ries et al., 2004), but to date there is no information on how those features affect foraging movement behaviors along the daytime. Usually, birds show a bi-modal pattern of circadian activity, being typically more active in the mornings and in the afternoons or early evenings (Bonter et al., 2013). In human altered landscapes, where small forest fragments become embedded in highly contrasting matrices like cattle pastures, bi-modal spillover movements can be altered, because the level of matrix quality can be perceived by animals, which in turn can modify their movement behavior in order to maximize benefits and minimize risks (Cornelius et al., 2017; Zollner & Lima, 2005). For example, Cornelius et al. (2017) found that birds from fragmented landscapes show a strong boundary response, but are more successful at crossing the matrix when compared to continuous forest birds. Likewise, Suarez-Rubio et al., (2015) found that migrant bird species were less reluctant to cross the matrix, compared to resident, understory bird species.

Even though animals perform different kinds of movements throughout their life cycles, like dispersal and migration, in this study we focus on daily foraging movements, which are typically performed repeatedly within a home range and several times per day (Jeltsch et al., 2013). Specifically, we will consider cross-habitat spillover, which is the movement of organisms among different habitats (Blitzer et al., 2012; Tscharntke et al., 2012). This is a bi-directional process occurring from native habitats into agricultural landscapes or from agricultural landscapes into native patches (Rand et al., 2006). We aim to test avian spillover movements across daytime and how different landscape features (including patch size, forest cover and interface type, coffee or pasture) affect this temporal movement. We will test these relationships for species with different habitat specificity and also different degrees of insectivory. We hypothesize that forest-dependent birds (both forest specialists and generalists) will use the coffee matrix to forage (resource complementation), resulting therefore in periodic movements at the interface of two environments. More specifically, we expect two patterns of movement: A) When the matrix has a high supply of resources and is safer, we expect forest birds to explore these environments longer throughout the day, possibly leaving the forest fragments in the morning and returning in the late afternoon; B) When the matrix is more inhospitable and unsafe, we expect birds to explore these environments faster and more punctually, entering and exiting the forest fragments throughout the day. The first behavior pattern should occur when the matrix is more permeable, when there is more habitat in the landscape, or when the forest fragment is smaller (forcing birds to have a more active behavior of complementing resources). The second pattern should occur under opposite conditions, when there is a greater risk of displacement in the matrix, that is, when the matrix is less permeable, there is less habitat in the landscape, or when the forest fragment is larger (not justifying the risk of going out to seek more resources). We also expect that generalist species or those with broader food preferences will tend to present behavior pattern A, while strict forest-dependent species or those with more restricted food preferences will tend to present behavior pattern B (more close to a *strong boundary response*). The combination of these conditions results in the set of hypotheses that we indicate in Figure 1.

Bird spillover ratio

Group	Fragment size		Forest cover	
	Small	Med-large	< 30	> 30
Generalist in coffee	╲	—	—	╲
Generalist in pasture	—	—	—	—
Dependent in coffee	╲	—	—	╲
Dependent in pasture	—	—	—	—
Occasio. insect. in coffee	╲	—	—	╲
Occasio. insect. in pasture	—	—	—	—
Rest. insect. in coffee	╲	—	—	╲
Rest. insect. in pasture	—	—	—	—

Time of day

Figure 1. Expected relationships between time of day (x axis) and bird spillover (y axis; high values indicate spillover going out the habitat fragment, and low values spillover going into habitat fragment), mediated by fragment size, forest cover and matrix type, for two habitat

dependency categories (habitat generalists and forest dependent) and two alimentary guild categories (occasional and restricted insectivores). The downward line indicates that species tend to leave the fragment in the morning and enter back in the late afternoon (spillover behavior pattern A; see text). The horizontal line indicates that species enter the fragment throughout the day (spillover behavior pattern B).

METHODS

Study region

The study region is located in the limit between the states of São Paulo and Minas Gerais, in the region known as *Sul de Minas*. This region is highly important for coffee production, giving that nearly one third of the whole Brazilian production is harvested there (EMBRAPA, 2020). Moreover, Brazil produces almost 35% of the worldwide-commercialized coffee (USDA, 2020). This high-productive region is embedded within the Brazilian Atlantic Forest domain, a highly biodiverse hotspot and extremely threatened biome (Myers et al., 2000), of which only 28% to 16% of its original forest cover remains (Rezende et al., 2018). Nowadays, the *Sul de Minas* region is characterized as an agricultural coffee landscape that displays a heterogeneous mosaic of patches of native forest and extensively sun-coffee farms (fig. 1). Other land use types are also present, such as pastures, *Eucalyptus* and urban settlements, but in a lesser proportion (Table S1).

Landscapes selection

We selected four 3 km radius “focal landscapes” ranging from 11% to 21% of forest cover remaining (Fig. 1; table S1), with similar abiotic conditions (i.e. soil type, altitude) and at least 6 km away from each other in order to avoid spatial overlap.

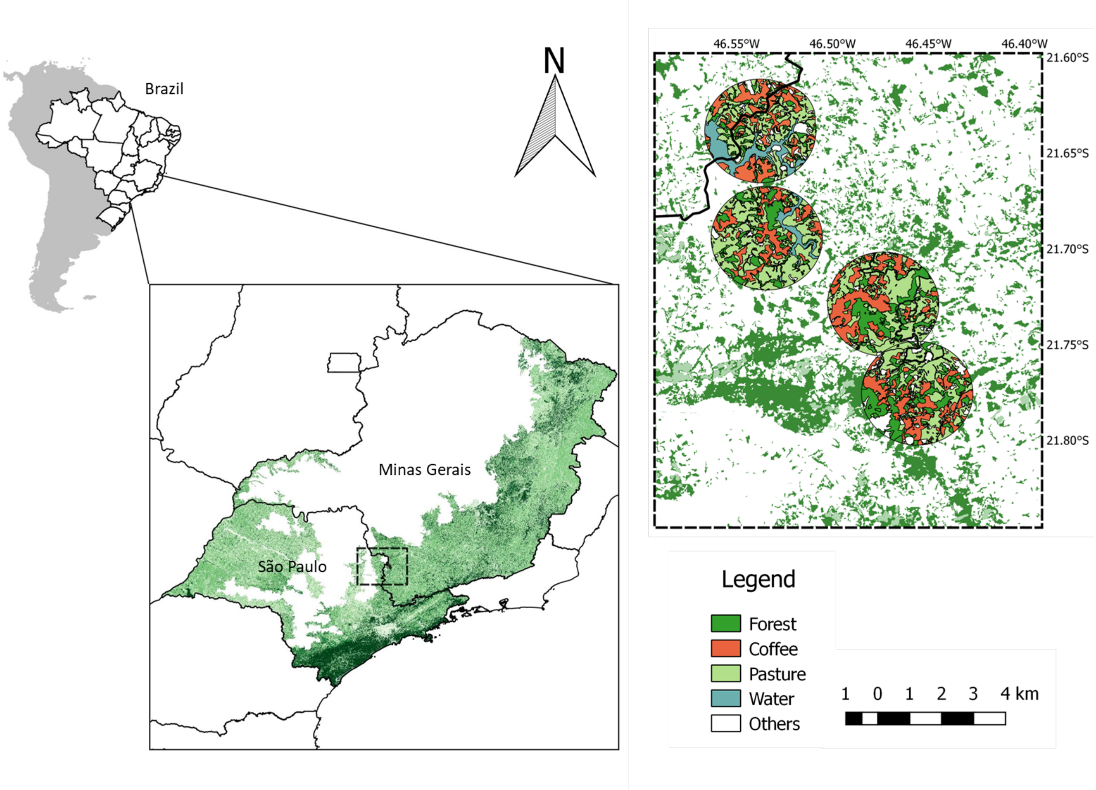


Figure 1. Study areas in the Brazilian Atlantic Forest biome between the states of São Paulo and Minas Gerais, and geographical location of the four (3 km radius) landscapes used in this study.

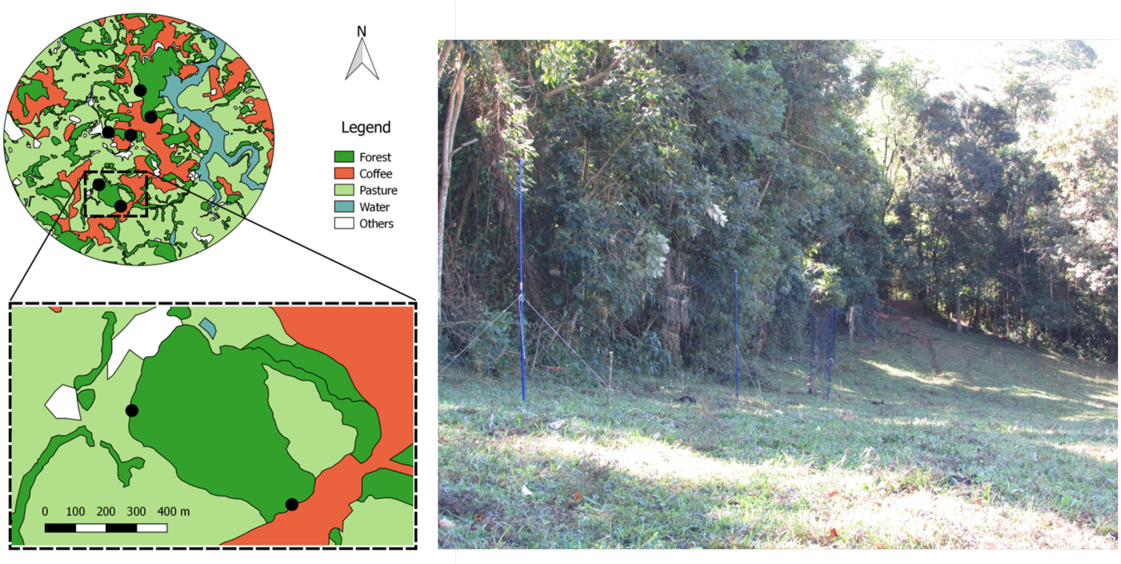


Figure 2. Experimental sampling design applied to collect field data. At each focal landscape, three forest patches of different sizes were sampled. For each fragment, we placed sampling sites in contact with pasture, on the one hand, and with coffee, on the other. For each interface (fragment-coffee and fragment-pasture) a line of five mist nets (~ 60 m) was placed.

Mist-net sampling

In each focal landscape, we selected three forest fragments (one small-sized < 10 ha, one medium-sized 10-50 ha, and one large-sized > 50 ha; Table S2), which had both pastures or coffee plantations in its adjacencies, composing a paired sampling design (hereafter sampling site). Therefore, for the same fragment we sampled both interfaces (N = 24 interfaces in total, 12 interfaces per matrix: pasture and coffee) simultaneously. Each sampling site was composed by two mist-net lines (5 mist-nets of 12 m. x 2.6 m; 60 m. aprox. in each line), one at a forest-coffee interface and another one at a forest-pasture interface, distant from each other 377.75 ± 166.74 (mean ± SD). Mist-nets were operated along 3 consecutive days, from 06:00 am to 12:00 m and from 14:00 pm to 18:00 pm (totaling 3600 net-hours, 300 per fragment). This number of days was estimated considering the time that resident birds learn to identify mist-net placements (Dunn & Ralph, 2004). The sampling was done during the dry season of 2018 (March, April, May), before coffee harvesting in the region. Whenever a bird was captured, the direction of entry or exit to/from the fragment was recorded, species identity recorded and each bird was marked with nail polish in a unique color combination in order to identify recaptures.

We classified species according to habitat specificity (forest-specialist and forest-generalists) and foraging habits. Forest specialists were defined as species that are mostly found in the interior of native forest and require forest areas for breeding and surviving (del Hoyo et al., 2020). Generalists were defined as species with a higher plasticity to use different forest types and agricultural areas (del Hoyo et al., 2020). Feeding guilds were obtained in Wilman et al., (2014) that identify numerically the contribution of different feeding items in birds' diet. Thus, we ended up with two insectivorous categories: *occasional insectivorous*, defined as species that occasionally feed on insects, but other feeding resources (fruit, nectar, seeds) are the most important; *restricted insectivorous* were defined as species that are predominantly insectivorous, but feed on other resources occasionally.

Spillover indicators

We used the information regarding birds entering or leaving the fragment as spillover indicator. A similar method was used by Frost et al., (2015) to evaluate spillover of generalist and specialist flying-insect predators of lepidopteran larvae across the edges of managed plantations and native forest. We used two approaches for measuring spillover. First an in/out spillover ratio ($R_{spillover}$) using birds' abundance was calculated using the following formula:

$$\boxed{\textbf{Ratio} = \frac{\text{\# of individuals leaving fragment}}{\text{\# of individuals leaving fragment} + \text{\# of individuals entering fragment}}}$$

This equation results in a ratio that ranges between 0 and 1: Values higher than 0.5 indicate more individuals moving out of the fragment (leaving); values lower than 0.5 indicate more individuals moving into the fragment (entering). Values of 0.5 indicate that the number of individuals leaving or entering the fragment was the same.

Second, we used a spillover Bray-Curtis index ($\beta_{dissimilarity}$) to assess the dissimilarity between the number of individuals of different species that entered and left the interfaces. We estimated both Spillover ratios ($R_{spillover}$) and Bray-Curtis index ($\beta_{dissimilarity}$), according to birds' habitat specificity: forest-dependent ($R_{spillover}FD$, $\beta_{dissimilarity}FD$), habitat generalists ($R_{spillover}G$, $\beta_{dissimilarity}G$), total ($R_{spillover}T$, $\beta_{dissimilarity}T$) and according to insectivore degree: i.e. occasional insectivorous ($R_{spillover}OI$, $\beta_{dissimilarity}OI$), restricted insectivorous ($R_{spillover}RI$, $\beta_{dissimilarity}RI$) and total insectivorous

($R_{spillover}$TI, $\beta_{dissimilarity}$TI). Finally, spillover movement was also assessed for the four most abundant species.

Data analysis

To test our hypothesis that time of day determines bird spillover and that this is affected by fragment size, forest cover and interface type, we modeled spillover ratios (for all groups), as a function of time of the day (from 06:00 to 18:00 in intervals of two hours), fragment size (small=<20 ha and medium-large=>20 ha, which is the mean forest fragments value; range: min = 2.2, max = 224.6), forest cover in the surrounding landscape (600 m around mist-net lines; <30 % and >30%, threshold found in studies like Pardini et al., 2010) and interface type (coffee, pasture) in generalized lineal models (GLMM), using a Binomial distribution and LogLik function. We competed models considering models only with the variable of time, and others with both additive and interactive models of time with landscape variables (i.e. interface type, fragment size, and forest cover). Finally, AIC model selection analysis was performed to identify the best predictive model (Burnham & Anderson, 2002) considering models with ΔAICc ≤2 as equally probable. All analyses were performed in R environment (RStudio Team, 2015) using the “lme4” (Bates et al., 2015), “bbmle” (Bolker & R Development Core, 2019) "AICcmodavg" (Mazerolle, 2019) packages.

RESULTS

Overall, 559 captures were performed, 394 at mornings (between 6 and 8 am) and 165 at afternoons (between 2 and 6 pm) (Fig. 4). There is a clear pattern that more captures were made during the mornings (mean = 11.3, standard deviation = 8.1) than in the afternoons (mean = 5.1, standard deviation = 4.6; Z = 0.80, P < 0.001, Table S3). In general, more captures were performed at coffee interfaces (329 individuals, mean =

9.13 ± 6.21) compared to pastures interfaces (230 individuals, mean = 6.39 ± 6.16; Z = -0.36, p < 0.001; Table S4), regardless the time of the day or the species characteristics (Fig. 4).

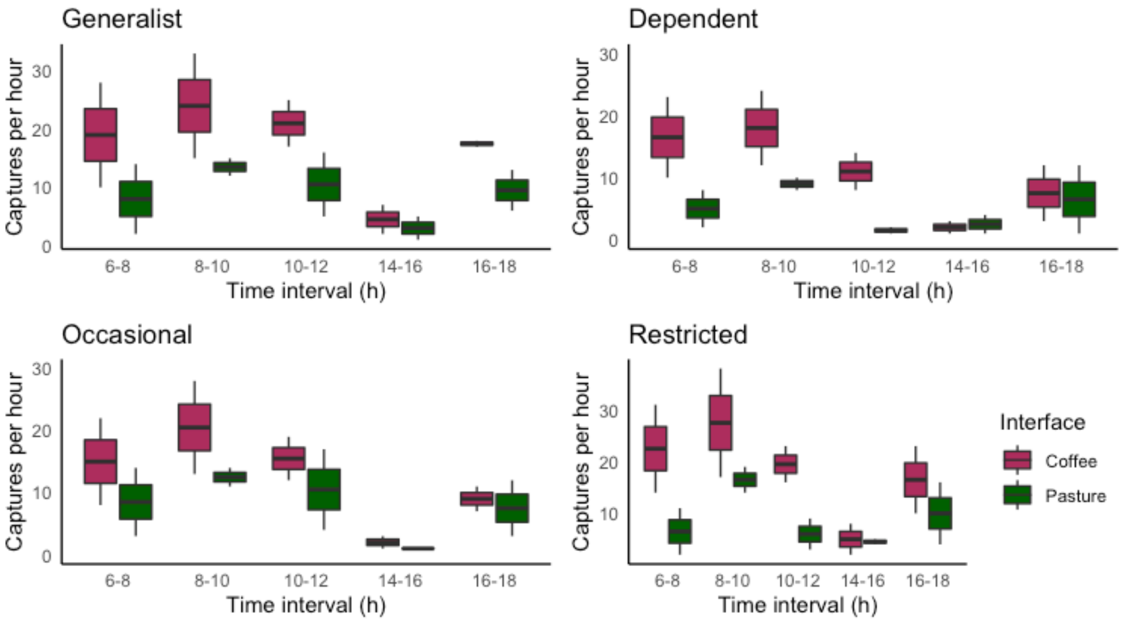


Figure 4. Mean number of captures per two-hour interval in coffee and pasture interfaces for generalist, dependent, occasional insectivores and restricted insectivore species.

We found evidence that landscape structure modulates the spatiotemporal spillover in agricultural matrices, and habitat generalist and forest dependent species showed different patterns across time and according to interface. For habitat generalist species, both the additive and interactive model of time and interface type were selected as the best predictive models (Table 1). We found a clear evidence of spillover movement type A in coffee plantations, i.e. more birds leaving than entering the forest patches in early mornings, and the opposite pattern in the late afternoon (Fig. 5). In pasture interfaces, spillover is more constant along the day (more close to spillover behavior B), but always into patches (Fig. 5).

For forest dependent species, we found another pattern: the interaction between time of day, interface type and fragment size was the best predictor of spillover ratio (Table 1). In coffee plantations, forest-dependent species were moving exclusively into forest patches along the day regardless fragment size, with intensification in the late afternoon. A similar pattern of bird entering the patches along the day was detected when patches were smaller at pasture interfaces, but a total opposite (and unexpected) pattern was observed at larger fragments, with individuals entering the larger fragments in the mornings and leaving in the afternoons (Fig. 6).

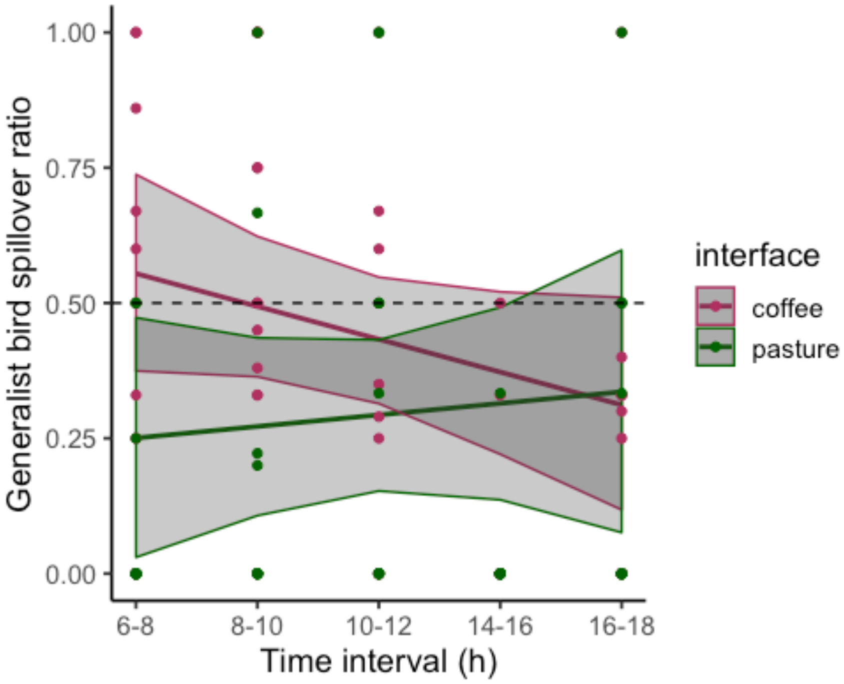


Figure 5. Predicted spillover ratio for habitat generalists, using an interactive model between time interval and interface type. A ratio value above 0.5 indicates that birds are leaving the fragments and a value below 0.5 indicates that the birds are entering the forest fragments.

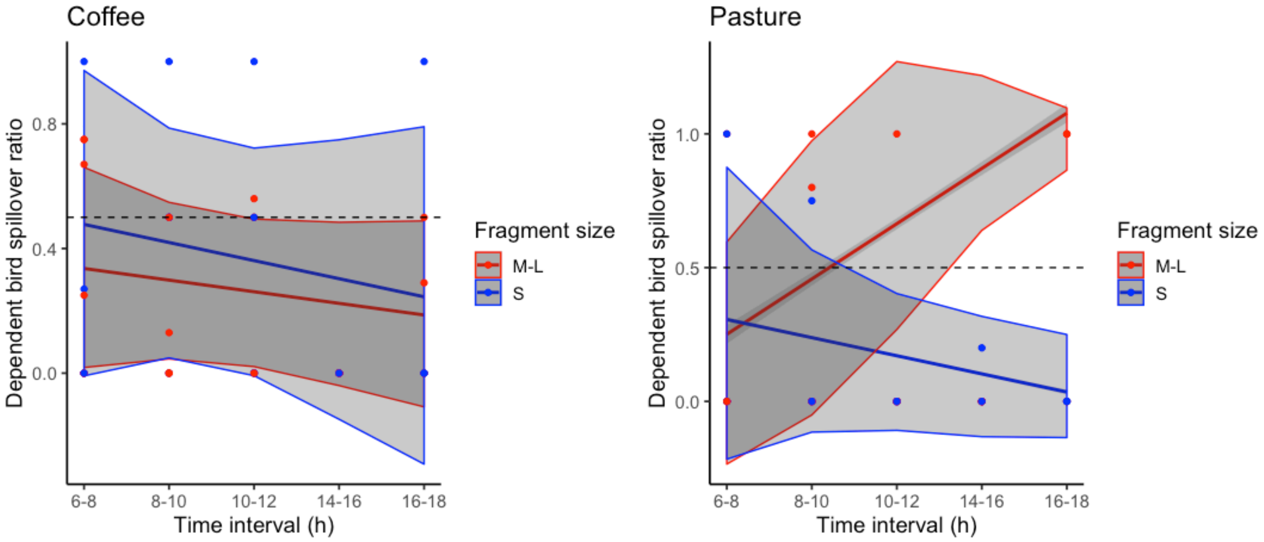


Figure 6. Predicted spillover ratio for forest dependent birds, using the interactive model of time interval, matrix and fragment size. A ratio value above 0.5 indicates that birds are leaving the fragments and a value below 0.5 indicates that the birds are entering the forest fragments.

Regarding the feeding guild, different patterns were detected as well. Occasional insectivores responded to an additive model of time of day and forest cover (Table 1). In this case, spillover ratio was higher in the mornings at higher amounts of forest cover (>30%), and decreased in the afternoon, indicating that birds were leaving the fragments early and coming back in the afternoon regardless interface type (spillover behavior type A; Fig. 7).

Restrictive insectivores responded to an interaction between time of day, interface type and forest cover (Table 1). In general, most movement of restrictive insectivores was from matrix into patches. There was a decrease in spillover ratio along the day at more deforested landscapes (<30%) in both matrices, with an exception of a higher spillover ratio in the morning at coffee interfaces (i.e. birds leaving patches). In the most forested landscapes, the opposite happened at both interfaces: there was an increase in spillover ratio across the day. However, movement was almost absent (zero captures) at higher amounts of forest cover at pasture interfaces (Fig. 8).

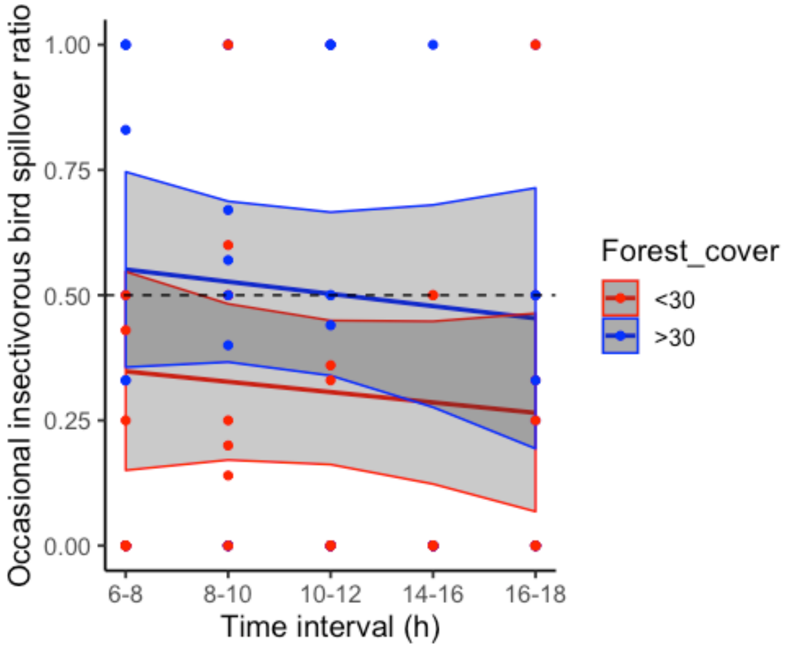


Figure 7. Predicted spillover ratio for occasional insectivore birds, using the additive model of time interval and forest cover %. A ratio value above 0.5 indicates that birds are leaving the fragments and a value below 0.5 indicates that the birds are entering the forest fragments.

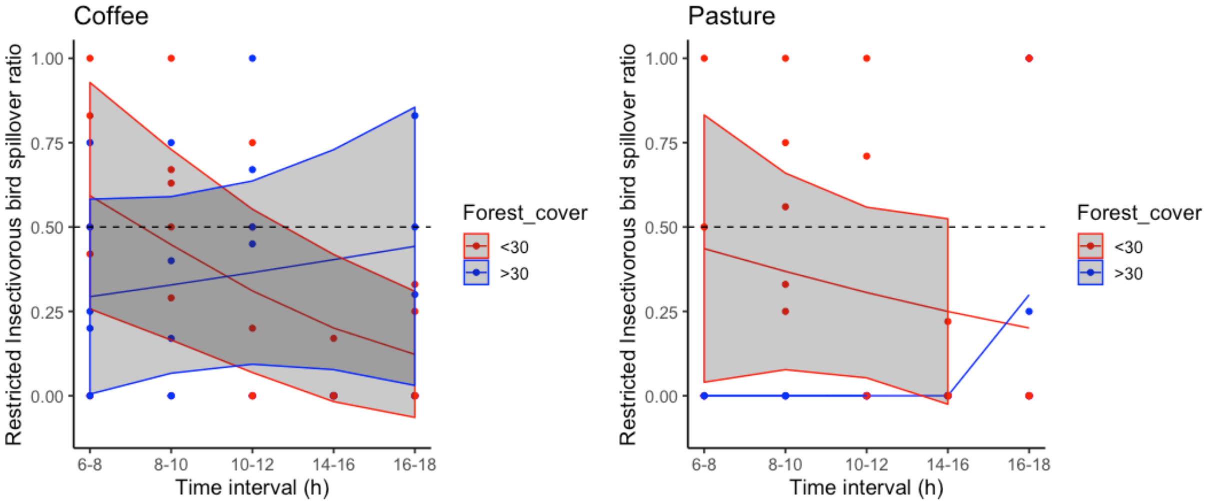
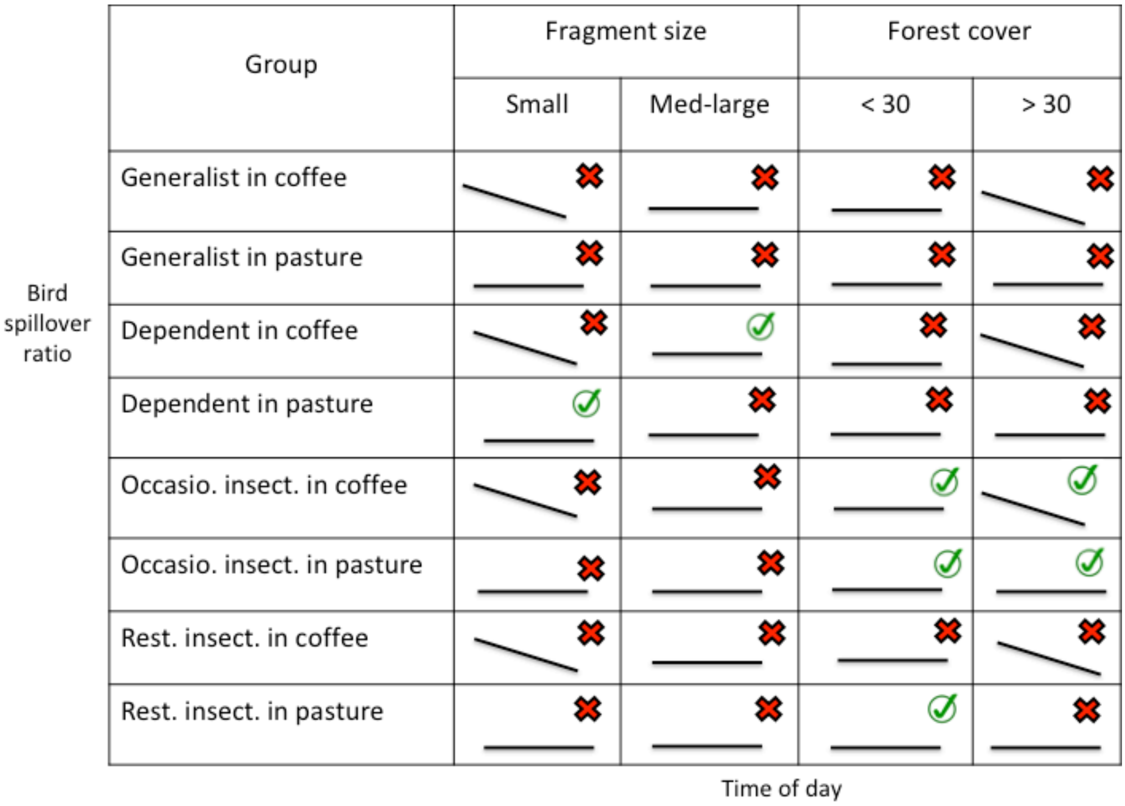


Figure 8. Predicted spillover ratio for restricted insectivore birds, using the interactive model of time interval, interface and forest cover %. A ratio value above 0.5 indicates that birds are leaving the fragments and a value below 0.5 indicates that the birds are entering the forest fragments.

Table 1. Model selection for bird spillover. Only models with AIC < 2 are shown. 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 denotes to 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, Var 3 corresponds to the third predictor variable, Interactions 1, 2 and 3 represent the interaction between the two variables and Triple interaction represent an interaction between three variables.

Model	**ΔAICc**	**df**	**AICc Wi**	**Intercept (se)**	**Var 1 (se)**	**Var 2 (se)**	**Var 3 (se)**	**Interaction 1 (se)**	**Interaction 2 (se)**	**Interaction 3 (se)**	**Triple interaction (se)**
Habitat generalist											
Time interval * interface	0	6	0.47	0.47 (0.34)	-0.25 (0.11)	-1.67 (0.63)	-	0.35 (0.19)	-	-	-
Time interval + interface	1.1	5	0.27	0.16 (0.29)	-0.13 (0.09)	-0.66 (0.27)	-	-	-	-	-
Forest dependent											
Time interval * interface * fragment class	0	10	0.72	-0.47 (0.60)	-0.19 (0.19)	-2.40 (1.52)	0.65 (1.07)	1.55 (0.66)	-0.06 (0.36)	2.03 (2.01)	-1.82 (0.82)
Occasional insectivores											
Time interval + forest cover	0	5	0.39	-0.52 (0.37)	-0.09 (0.11)	0.83 (0.29)	-	-	-	-	-
Restricted insectivores											
Time interval * interface * forest cover	0	10	0.62	0.96 (0.59)	-0.58 (0.18)	-0.93 (0.84)	-2.00 (0.79)	0.30 (0.28)	0.74 (0.24)	-40.79 (397)	7.91 (79.35)
Time interval * forest cover	1.3	6	0.32	0.619 (0.47)	-0.47 (0.14)	-1.92 (0.70)	-	0.65 (0.20)	-	-	-

DISCUSSION



Group	Fragment size		Forest cover	
	Small	Med-large	< 30	> 30
Generalist in coffee	╲ ✗	— ✗	— ✗	╲ ✗
Generalist in pasture	— ✗	— ✗	— ✗	— ✗
Dependent in coffee	╲ ✗	— ✓	— ✗	╲ ✗
Dependent in pasture	— ✓	— ✗	— ✗	— ✗
Occasio. insect. in coffee	╲ ✗	— ✗	— ✓	╲ ✓
Occasio. insect. in pasture	— ✗	— ✗	— ✓	— ✓
Rest. insect. in coffee	╲ ✗	— ✗	— ✗	╲ ✗
Rest. insect. in pasture	— ✗	— ✗	— ✓	— ✗

Figure 9. Summary of the main results indicating the support or absence of evidence for each of the hypotheses initially considered.

In general, we found that birds present a bi-modal peak of activity during the day, being more active in the early mornings and in the afternoons, and less active around noon. Also, this study highlights that interface type is a key factor influencing birds' daily movement across forest edges. In coffee matrix, the general spillover pattern follows a type A response, where birds clearly leave forest patches for foraging outside patches in the morning and in the afternoon move back into patches for roosting. At pasture interfaces, the general pattern is more similar to type B response, with a more constant in and out throughout the day, but with a greater inflow into the forest fragments than outflow. We also found additional, but limited, effect of both forest cover and fragment size modulating the temporal spillover (Fig. 9). These findings highlight that birds are more active early in the morning, and that there is a temporal pattern in spillover movements, which is particularly affected by the type of adjacent matrix, and secondarily by forest cover and fragment size.

Clearly more individuals were captured in the mornings and in the afternoons than around noon. Authors have predicted daily foraging patterns of birds to be balanced between the risk of starvation and the risk of predation, because these two factors pose opposite effects in delimiting optimal energy reserves (Houston & McNamara, 1993; Lima, 1986; Pravosudov & Lucas, 2001). In birds, the optimal foraging behavior often predicts a bimodal pattern in feeding during the day: in the morning birds replenish energy that has been diminished during the previous night, reducing the risk of starvation. After this morning peak birds remain in a period of relative inactivity, avoiding exposure to predators. Finally, in the afternoon a second foraging peak is predicted, in order to accumulate reserves for the coming night (Bednekoff & Houston, 1994; Mcnamara et al., 1994). Although this dynamics have been studied in temperate ecosystems for resident birds, a similar pattern was also observed in sub-tropical ecosystems (Banks-Leite et al., 2012).

Our results show that the matrix around the forest fragments determines bird movement throughout the day. This applies for generalists, given that in the most permeable matrix this group of birds performed a type A movement, while in pasture they perform a type B movement. This might occur through two main mechanisms: refuge and resource. In coffee they find more refuge sites and more feeding resources (Librán-Embid et al., 2017). In pasture they do not find any of those elements, given that pastures are very unproductive environments (Castellón & Sieving, 2006), and therefore they are forced to enter into the forest fragments. Regarding forest dependents in coffee matrices, individuals are only entering, more in the afternoon than in the mornings. In small fragments they do not find enough resources and they rarely enter in the morning hours. In the afternoon, the movement into the fragment intensifies, given that birds are searching for fragments as a refuge. In pasture, dependent birds may try to leave, but the observed pattern is consistent with a strong boundary response, moreover in the medium to large fragments. We probably captured birds when they were evaluating external conditions to disperse, but not necessarily as they left the forest fragments. Dependent species captured "leaving" forest fragments are mostly sensitive to fragmentation (e.g. *Chiroxiphia caudata, Basileuterus leucoblepharus, Synallaxis ruficapilla*, *Arremon flavirostris;* (Banks-Leite et al., 2014; Martensen et al., 2012). On the other hand, dependent species captured entering the patches are ones with high dispersal capacity and that can cross larger inter-habitat gaps (e.g. *B. culicivorous, Trichothraupis melanopis*, *Cyanocompsa brissonii;* (Awade & Metzger, 2008). Different cover types in the landscape present different levels of risk and benefit (Bélisle, 2005)and since these risks and benefits may vary among species and functional groups, optimal movement parameters will be highly species-specific (Fahrig 2007).

Forest cover also determined spillover along the day, but in a lesser proportion. Forest cover percentage was important for temporal spillover of occasional and restricted insectivorous species. We expected that birds would present spillover pattern A in more forested landscapes because in this condition the isolation between the fragments is smaller, making it easier and faster to move through the matrix (Perović et al., 2010). This expectation was only partially confirmed. In the case of occasional insectivores, they are leaving forest fragments in the mornings and returning in the afternoons, in the contexts of forest cover of more than 30%, like it was expected. Occasional insectivorous bird species captured leaving forest fragments are not too sensitive to habitat fragmentation (e.g. *Zonotrichia capensis, Amazilia lactea, Leptotila verreauxi*). In the case of restricted insectivores, birds performed type A movements in the coffee matrices when forest cover is lower (< 30%); in this case, bird species captured leaving can cross gaps, for example, the Golden-crowned Warbler (*Basileuterus culicivorus*), a frequently captured species at edges, might easily cross gaps of non-habitat as large as 55 m (Awade & Metzger, 2008). Therefore, as in the case of matrix type, response to forest cover is also group or even species-specific (Fahrig 2007).

Fragment size was a driver of temporal spillover, but also to a lesser extent. An interesting and unexpected result was found regarding forest-dependent: in coffee matrices individuals only entered the forest fragments, regardless the fragment size, suggesting that the forest functions as a refuge for these birds. Meanwhile in the pasture matrices, birds entered into small forest fragments and left the larger fragments. This movement of birds leaving large fragments on the pasture is completely unexpected. Our results do not show that forest dependent species are using pasture matrices; instead, what they reveal is that birds try to leave, but present a strong boundary response, as explained above. Also, some of the dependent species that we captured (which are forest-dependent species that live in forest edges) are able to traverse gaps across pasture matrices, in the search of other forest fragments to forage. This ability has been reported for other forest dependent species in fragmented landscapes in the Atlantic Forest (Cornelius et al., 2017; Biz et al., 2017). So captured individuals are not necessarily leaving the forest fragments, but could be performing movements and foraging along the fragment edge.

Concluding remarks

Our results reinforce that avian temporal spillover follows a bi-modal pattern, occurring more frequently in the morning and afternoon hours. We bring new evidence that temporal spillover is highly influenced by the matrix type that surrounds forest fragments, following two types of movement: type A in coffee matrices, where birds leave forest fragments in the mornings, forage in the matrix and come back to roost on the fragments in the afternoons; and type B movement in pasture matrices, where birds try to get out of the forest fragments, perceive a hostile matrix and keep foraging on the fragment edge. This indicates that the coffee matrix provides some sort of feeding complementary resource throughout the day, and that birds, in pasture matrix, are finding alimentary resources and refuge inside forest patches and not in the matrix, which is acting as a barrier for dispersal. Also, other landscape features, like forest cover and fragments size are relevant for temporal spillover process. In general, the inward movement happens in pasture matrices, in less forest cover contexts and when fragments are small, that is, when landscapes are more disturbed. Therefore, in those cases, forest fragments act as refuges for avifauna, for generalist, forest dependent and insectivores alike. Our results highlight that preservation of Atlantic Forest remnants can contribute to cross-habitat spillover movements throughout the day, a process that aids in pest control services carried out by biodiversity.

Supplementary material:

Table S1. Extension of land uses (%) for the four landscapes included in the study, each with a radius of 3 km.

Landscape	Forest	Coffee	Pasture	Water	Eucalyptus	Human settlement	Other	Central geographical location	
								Latitude	Longitude
9	11	23	42	16	1	3	3	-21° 38’	-46° 32’
10	20	23	48	6	1	1	1	-21° 41’	-46° 31’
26	21	27	33	1	12	3	3	-21° 46’	-46° 27’
28	19	12	46	0	1	5	17	-21° 29’	-46° 42’

Table S2. Fragments sizes per landscape

Landscape	Fragment code	Fragment area (ha)
9	F1	15.13
	F2	9.22
	F3	2.18
10	F1	57.97
	F2	21.25
	F3	6.23
26	F1	104.54
	F2	27.27
	F3	7.42
28	F1	224.6
	F2	19.74
	F3	6.32

Table S3. Coefficients from a GLMM with Poisson errors (and log link function) testing whether time of day predicted the number of total captures. Landscape and point were included as random factors. Significant *P* values (α ≤ 0.05) are indicated in bold.

Fiexed effects	Estimate	Std. Error	*z* value	Pr(>|*z*|)
Intercept	1.54	0.21	7.17	< 0.0001
Time of day (morning)	0.80	0.09	8.67	**< 0.0001**

Table S4. Coefficients from a GLMM with Poisson errors (and log link function) testing whether interface type predicted the number of total captures. Landscape and point were included as random factors. Significant *P* values (α ≤ 0.05) are indicated in bold.

Fiexed effects	Estimate	Std. Error	*z* value	Pr(>|*z*|)
Intercept	2.03	0.19	10.51	< 0.0001
Matrix (pasture)	-0.36	0.08	-4.18	**< 0.0001**

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General Discussion

Agroecosystems are the largest and most managed terrestrial ecosystem, covering nearly 40 percent of the global landmass (Foley et al., 2011). Agriculture is fundamentally dependent on ecosystem services, in particular on regulating ones (e.g. pollination and pest control), as the foundation of sustainability (Abson et al., 2014). Conversion of natural habitats to agriculture causes biodiversity and services losses; for example, landscape simplification and increased pesticide use are associated with the loss of pest control services (Meehan et al., 2011). Most regulating services are provided by organisms that move between habitats (Kremen et al., 2007), which is an essential feature of the ecology of many species (Tscharntke et al., 2012). The principal reason for this movement is that organisms often exploit resources that are spatially separated (Dunning et al., 1992). However, the extent of movement will be determined by landscape structure, particularly by the amount of remaining habitat (Goodwin & Fahrig, 2002; Holzschuh et al., 2010; Ricketts, 2001; With & Crist, 1995). With habitat loss, both species and services risk being lost. Here we tried to better understand the relationships between the landscape structure and avian cross-habitat spillover, a process that can potentially underpin the provision of services in sub-tropical agroecosystems.

In chapter one we found that spillover studies are largely limited to temperate regions and a few crop types. Also, spillover is more frequently assessed in an indirect way (i.e. without detecting directly the movements across edges), therefore, most of the studies evaluated spillover through patterns, and not by measuring the process in itself. To estimate the effect of landscape structure on spillover movements, we compared two methods: vote-counting and effect size calculation. With the first method we demonstrate that adjacent habitat type contrast affects spillover of both natural enemies and pollinators, which determines that landscapes with less contrasting edges between natural areas and crop fields, are more favorable for spillover movements from natural to anthropic covers, and can then enhance the provision of pollination and pest control services. With the second method we did not find any relationship between landscape structure and spillover. This lack of relationship may be due to three reasons: (i) studies are still scarce to obtain a clearer pattern on the effect of landscape on spillover; (ii) the methods used to infer indirectly the spillover are not sufficiently consistent, and thus we need to measure more directly the movement; and (iii) there is no single or consistent effect of the landscape on the different pollinators and natural enemies that make spillover movements.

In chapter two, using bird capture data in agroforestry systems, we found novel evidence that in high-deforested landscapes avian-spillover occurs mostly from crops to native forests. Most bird captures (64,2%) where made from crop (coffee or pasture) to forest fragment, characterizing an inverse spillover. We also found evidence that the opposite movement happens, particularly in landscapes with high forest cover, with large fragments and at lower contrasting matrices (i.e. coffee). Particularly, species composition dissimilarity was lower in coffee plantations than in pastures, indicating that species are very likely moving more often at coffee interfaces. These results have important implications in terms of ecosystem services provisioning in agricultural landscapes, highlighting the importance of maintaining forest fragments for avian cross-habitat spillover, likewise the importance of keeping a permeable matrix around those fragments, in order to assure species movement, which in turn can affect pest control provision.

In chapter three we found that daily temporal spillover presents a bi-modal peak of activity. In general, birds are more active in the early mornings and in the afternoons, and less active around noon. This study highlights that interface type is a key factor influencing birds' daily movement across forest edges. In the coffee matrix birds are moving out of the fragments in the morning hours and coming back in the afternoons, which indicates that coffee plantations might be providing complementary feeding resources. However, birds are still using forest patches of different sizes for roosting and refuge, evidenced by the movement into forest patches in the afternoons. In pasture interfaces individuals are moving in and out all day long, with predominance of movement into the fragment. Those results suggest that birds avoid leaving the fragments, indicating that pasture acts as a barrier for dispersal, not providing complementary alimentary resources, and that forest fragments supply resources and refuge. Forest cover and fragment size have a more limited, and sometimes unexpected influence in temporal spillover. In general, the inward movement happens in pasture matrices, in landscapes with less forest cover and when fragments are small, that is, when landscapes are more disturbed. Our results indicate that for spillover movements to occur along the day in the matrix, it is necessary to have a more permeable matrix, and preferably in landscape conditions of higher forest cover, therefore highlighting that the conservation of Atlantic Forest remnants can contribute to cross-habitat spillover movements of species that provide pest control.

In general we found that landscape structure affects cross-habitat spillover. Specifically, a greater permeability of the matrix that surrounds forest fragments is fundamental for spillover, both of insects and birds, two groups that are important pest controllers. Matrix permeability can be increased through the implementation of stepping-stones or corridors (Boscolo et al., 2008; Uezu et al., 2008) or by the enhancement of crop diversity (Perfecto & Vandermeer, 2010). The conservation of Atlantic Forest remnants can help also in the spillover of birds, because they find refuge and alimentary resources inside fragments. Especially, keeping the biggest forest remnants encourages spillover to occur in the direction from the fragments to the coffee matrix, which promotes avian pest control. Nevertheless in the Atlantic Forest more than 80 percent of the fragments are smaller than 50 ha (Ribeiro et al., 2009), which makes it essential to maintain the largest fragments, as well as forest restoration initiatives that expands the current fragments. Finally, we stress the importance of managing the matrix, making it more permeable to facilitate spillover and, consequently, the provision of regulation ecosystem services like pest control and pollination.

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Abstract

Bolstering biodiversity within human-dominated landscapes in order to maintain ecosystem service provision is a major challenge. The movement of species across habitat edges (i.e. cross-habitat spillover) is an essential process linking different environments, often motivated by resource use that are spatially separated. The main objective of this thesis is to advance our current knowledge on how the avian cross-habitat spillover is affected by landscape structure. The thesis is comprised by three chapters that integrate both theoretical and empirical research. In the first chapter we performed a meta-analysis of landscape structure effects on pollinators and natural enemies. After analyzing the empirical results of 50 articles, we found evidence that adjacent habitat type contrast affects negatively spillover of both natural enemies and pollinators. Our results suggest that landscapes with less contrasting edges between natural areas and crop fields are more favorable for spillover movements. In the second chapter we performed bird surveys across a forest cover gradient and at different agricultural interfaces in the Brazilian Atlantic forest, to test how landscape structure features affect bird spillover and community dissimilarity. We found strong evidence of an inverse spillover in highly deforested landscapes (i.e. birds moving from crop fields into forest patches), and that interface type is a key driver of spillover, given that most of individuals where performing spillover from lower-contrasting matrices (i.e. coffee plantations) compared to high-contrasting matrices (i.e. pastures). Also, interface type interacted with forest cover and fragment size. We found evidence of a trend of spillover ratio increasing with forest cover at low-contrasting matrices, and that larger fragments acted as sources of individuals in less contrasting matrices (i.e. more individuals going to the coffee plantations when fragments are larger). Dissimilarity

between individuals coming in and out of the fragments was lower at coffee matrices, demonstrating a regular movement in and out, while it was higher at pasture matrices, evidencing that cross-habitat spillover is more rare in such matrix. Finally, in chapter three we explore how spillover direction changes across the time of day and its interaction with landscape structure. Our results indicate that interface type is a key factor influencing birds' daily movement across forest edges. The general pattern found is a bimodal pattern, with movements occurring mostly in the morning and afternoon hours. At coffee interfaces birds clearly leave forest patches for foraging outside patches in the morning and in the afternoon move back into patches for roosting, while at pasture interfaces, the general pattern is a constant movement in and out all day long, with predominance of movement into the forest fragments. These findings highlight the role that landscape structure has on bird temporal spillover and also that in more permeable matrices birds are able to explore the resources in the matrix over a longer period of time, contrary to more hostile matrices like pasture. In general, our results suggest that bird spillover in anthropogenic landscapes depends on landscape structure and that this has to be taken into account when planning agricultural landscapes in order to ensure ecosystem service provision.

Resumo

Aumentar a biodiversidade nas paisagens antrópicas a fim de manter a provisão de serviços ecossistêmicos é um grande desafio. O *cross-habitat spillover*, o movimento de espécies através das bordas entre ambientes nativos e antrópicos (frequentemente traduzido como 'transbordamento'), é um processo ecológico essencial motivado por diferentes mecanismos, incluindo o uso de recursos que estão espacialmente separados. O objetivo desta tese foi avançar o conhecimento atual de como o processo de *spillover* é afetado pela estrutura da paisagem, integrando pesquisas teóricas e empíricas ao longo de três capítulos. O primeiro capítulo é composto por uma meta-análise dos efeitos da estrutura da paisagem sobre polinizadores e inimigos naturais. A meta-analise resultou em 50 artigos revisados, na qual encontramos evidência que o contraste entre habitats adjacentes tem um efeito negativo no *spillover* de polinizadores e inimigos naturais. Nossos resultados sugerem que paisagens com bordas menos contrastantes entre áreas naturais e culturas são mais favoráveis para o *spillover*. No segundo capítulo, avaliamos o *spillover* de aves ao longo de um gradiente de cobertura florestal e em diferentes interfaces agrícolas na Mata Atlântica do Brasil, para testar se a estrutura da paisagem afeta o *spillover* e a dissimilaridade de assembleias de aves nas bordas. Nossos resultados indicam um *spillover* inverso (i.e. aves se movimentando da matriz para o interior dos fragmentos florestais) em paisagens altamente desmatadas e que o tipo de interface (i.e. matriz adjacente) é um fator chave para o spillover: uma intensificação do processo se deu em matrizes menos contrastantes (i.e. café), enquanto o movimento é mais ocasional em matrizes altamente contrastantes (i.e. pastagens). Por fim, encontramos uma interação entre o tipo de interface com a cobertura florestal e o

tamanho dos fragmentos. Evidenciamos um incremento do *spillover* com o aumento da cobertura florestal em matrizes pouco contrastantes, assim como um aumento do *spillover* em fragmentos maiores nas matrizes de menor contraste, o que pode indicar que estas áreas atuam como fonte de indivíduos em matrizes menos contrastantes (mais indivíduos saindo para os cafezais quando os fragmentos são grandes). A dissimilaridade entre o *spillover* para dentro ou para fora dos fragmentos foi menor nas interfaces de café, demonstrando um movimento mais regular, enquanto nas matrizes de pastagem foi detectada uma maior dissimilaridade, demonstrando que o *spillover* é um evento mais raro nessa matriz. Finalmente, no terceiro capitulo exploramos como a estrutura da paisagem modula a direcionalidade do *spillover* temporal. Nossos resultados indicam diferentes padrões de spillover temporal de acordo com o tipo de matriz. De uma forma geral, o padrão de atividade é bimodal, ocorrendo principalmente de manhã e à tarde. Nas interfaces de café as aves saem dos fragmentos de manhã, provavelmente para forragear nos cafezais, e retornam ao fim do dia, provavelmente para se refugiar nos fragmentos. Por outro lado, nas interfaces de pastagem, o padrão geral é de um movimento mais constante de entrada e saída ao longo de todo o dia, com predomínio de entrada nos fragmentos, independente da hora do dia. Nossos resultados ressaltam que a estrutura da paisagem afeta o *spillover* temporal das aves, sendo que em particular nas matrizes mais permeáveis as aves conseguem explorar os recursos na matriz durante um período de tempo mais longo, contrario ao que acontece em matrizes mais hostis como as pastagens. Em geral, nossos resultados sugerem que o *spillover* de aves em paisagens agrícolas depende da estrutura da paisagem e isto deve ser levado em conta na hora de planejar paisagens agrícolas a fim de assegurar a provisão de serviços ecossistêmicos.