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Dissertação de Mestrado

# Non-random inter-specific encounters between Amazon understory forest birds: what are they and how do they change?

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Porto Alegre, August 2016

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia em Ciências com ênfase em Ecologia.

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‘Il y a autant de voyages que de feuilles  
sur l’arbre du voyageur.’  
*Kenneth White*

‘Carpe diem.’  
*Horace*

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## **ABSTRACT**

Inter-specific associations of birds are complex social phenomena, frequently detected and often stable over time and space. So far, the social structure of these associations has been largely deduced from subjective assessments in the field or by counting the number of inter-specific encounters at the whole-group level, without considering changes to individual pairwise interactions. Here, we look for evidence of non-random association between pairs of bird species, delimit groups of more strongly associated species and examine differences in social structure between old growth and secondary forest habitat. We used records of bird species detection from mist-netting capture and from acoustic recordings to identify pairwise associations that were detected more frequently than expected under a null distribution, and compared the strength of these associations between old-growth and secondary forest Amazonian tropical forest. We also used the pairwise strength associations to visualize the social network structure and its changes between habitat types. We found many strongly positive interactions between species, but no evidence of repulsion. Network analyses revealed several modules of species that broadly agree with the subjective groupings described in the ornithological literature. Furthermore, both network structure and association strength changed drastically with habitat disturbance, with the formation of a few new associations but a general trend towards the breaking of associations between species. Our results show that social grouping in birds is real and may be strongly affected by habitat degradation, suggesting that the stability of the associations is threatened by anthropogenic disturbance.

**Key words:** Mixed-species flocks, tropical forest birds, inter-specific interaction, null models, networks, pairwise co-detection

## **Título**

Encontra interespecífica não aleatória entre aves de sub-bosque amazônico: qual elas são e como elas mudam?

## **Resumo**

Os bandos mistos de aves são agregações sociais complexas estáveis durante o tempo e espaço. Até hoje, a estrutura social dessas espécies foi descrita a partir de estudos subjetivos de campo ou a partir de compilações do número e intensidade das interações a nível de todo o grupo, sem considerar as interações par-a-par individualmente. Nossos objetivos foram buscar evidências de associações não-randômicas entre pares de espécies de aves, delimitar os grupos a partir das espécies com as associações mais fortes e verificar se há diferenças na estrutura social entre os habitat de floresta primária e secundária. Utilizamos dados de ocorrência das espécies coletados a partir de redes de neblina e gravação de vocalizações para identificar pares de espécies que foram co-detectadas mais frequentemente do que o esperado a partir do modelo nulo e comparamos a força dessa interação entre as florestas tropicais primária e secundária Amazônicas. Nós também utilizamos as associações par-a-par para construir as redes de interação social e suas mudanças entre os tipos de habitat. Nós encontramos muitas interações positivas fortes entre as espécies, mas nenhuma evidência de repulsão. As análises das redes de interação revelaram vários grupos de espécies que corroboram com grupos ecológicos descritos na literatura. Além disso, tanto a estrutura da rede de interação como a força da interação se alteraram drasticamente com a perturbação do habitat, com formação de algumas associações novas, mas uma tendência geral para quebra de associações entre as espécies. Nossos resultados mostram que as interações sociais entre essas aves podem ser fortemente afetados pela degradação do habitat, sugerindo que a estabilidade das interações desenvolvida entre espécies é ameaçada pelos distúrbios causados pelo homem.

**Palavras-chave:** bandos-mistos, aves de florestas tropicais, interações inter-específicas, modelos nulos, redes de interações, co-deteccção

# SUMMARY

<b>ABSTRACT</b> .....	<b>V</b>
<b>TITULO</b> .....	<b>VI</b>
<b>RESUMO</b> .....	<b>VI</b>
<b>LIST OF FIGURES:</b> .....	<b>2</b>
<b>LIST OF SUPPLEMENTARY FIGURES:</b> .....	<b>2</b>
<b>LIST OF TABLES:</b> .....	<b>3</b>
<b>LIST OF SUPPLEMENTARY TABLES:</b> .....	<b>3</b>
<b>GENERAL INTRODUCTION</b> .....	<b>4</b>
<b>NON-RANDOM INTER-SPECIFIC ENCOUNTERS BETWEEN AMAZON UNDERSTORY FOREST BIRDS: WHAT ARE THEY AND HOW DO THEY CHANGE?</b> .....	<b>6</b>
<b>INTRODUCTION</b> .....	<b>6</b>
<b>METHODS</b> .....	<b>9</b>
<i>Study area and sampling design</i> .....	<b>9</b>
<i>Study species</i> .....	<b>11</b>
<i>Data organization</i> .....	<b>12</b>
<i>Quantifying pairwise interspecific associations</i> .....	<b>13</b>
<b>RESULTS</b> .....	<b>16</b>
<b>DISCUSSION</b> .....	<b>25</b>
<b>REFERENCES</b> .....	<b>31</b>
<b>ANNEXES</b> .....	<b>35</b>
<b>CLOSING REMARQUES</b> .....	<b>45</b>
<b>REFERENCES</b> .....	<b>46</b>

**LIST OF FIGURES:**

**Fig. 1.** Study area of the Biological Dynamics of Forest Fragments Project..... 11

**Fig. 2.** Interspecific association network based on the combination of audio and capture data from old-growth sites..... 20

**Fig. 3.** Interspecific association network based on the combination of audio and capture data from secondary-forest sites..... 22

**List of supplementary figures:**

**Fig. S1.** Interspecific association network based on the audio recording (A) and mist-net capture (B) data from old-growth sites..... 40

**Fig. S2.** Interspecific association network based on the audio recording (A) and mist-net capture (B) data from secondary forest sites..... 44



**LIST OF TABLES:**

**Table 1.** Group-level association strengths for old-growth forest based on the combination of audio and capture data..... 21

**Table 2.** Triangular matrix of changes in pairwise inter-specific associations from OG to SF habitat..... 24

**List of supplementary tables:**

**Table S1.** Data summary and overview of inter-specific group classifications prior to and including this study..... 35

**Table S2.** Pairwise association strengths and group delimitation based on old-growth audio data.. 37

**Table S3.** Pairwise association strengths and group delimitation based on old-growth capture data..... 38

**Table S4.** Pairwise association strengths and group delimitation based on the combination of audio and capture data from old-growth sites..... 39

**Table S5.** Pairwise association strengths and group delimitation based on secondary-forest audio data..... 41

**Table S6.** Pairwise association strengths and group delimitation based on secondary-forest capture data..... 42

**Table S7.** Pairwise association strengths and group delimitation based on the combination of audio and capture data from secondary forest..... 43

**Table S8.** Group-level association strengths for secondary forest based on combined audio and capture data..... 44

## GENERAL INTRODUCTION

Group living in animals can be composed by one species, e.g. a flock of starling (Morse 1977), so they are conspecific groups. Living in groups provides several benefits to individual participants such as reducing predation risk (e.g. Cresswell and Quinn 2004). However, being with conspecifics may be costly, as it can increase resource competition and the risk of exposure to disease and parasites (e.g. Altizier et al 2003).

Joining mixed-species flocks would be an efficient strategy to reduce competition while keeping anti-predation benefits (Morse 1977, Sridhar et al 2009, Harrison and Whitehouse 2011). These interspecific groups are found in many taxa, including ungulates (Fitzgibbon 1990), primates (Terborgh 1990), fish (Allan and Pitcher 1986), and birds (Moynihan 1962). In tropical forests, there are two main interspecific associations among understory Amazonian birds, which are the mixed-species flocks and the ant-following birds (Bierregaard and Lovejoy 1989, Cohn-Haft et al 1997). Ant following birds are aggregated at swarms of army-ants (e.g. *Eciton burchelli*) (Willis and Oniki 1978). They are following the ants but do not feed on them. Instead, these birds are capturing prey (mainly arthropods) flushed by the flow of ants. Those ants are mainly active during the reproductive or ‘nomadic’ period (i.e. fourteen days in each 35 days, Schneirla 1971 in Willis and Oniki 1978), which will drive the presence of birds in an area (Willis and Oniki 1978). At swarms, we can find birds with two different strategies. There are the species that are exclusively foraging over ant swarms, classified as “professional”, and the birds that will wait at the edges of the swarms and occasionally forage in the center, categorized as “non-professional” (Oniki 1972, Oniki and Willis 1972, Willis and Oniki 1978, Harper 1989, Willson 2004).

Understory mixed-species flocks are groups of insectivorous species that move and forage together all day long, and have the particularity to be stable throughout the year in tropical areas (Morse 1970, Martinez and Gomez 2013). The association between species results in higher foraging efficiency and reduces predation, as well as increases their fitness (Beauchamps 2004). They consist of breeding pairs of six to ten ‘core’ species (i.e. almost exclusively seen in flock), which have together a foraging area that includes all their territories (Munn 1985, Jullien and Thiollay 1998). Among those ‘core’ species, the *Thamnomanes* sp. are species that play the role of leader in the Amazon. Their role consists of rallying the members of the flocks by emitting loud calls early each morning

that continue throughout the day in order to maintain the cohesion of the group during movements. They also give alarm calls when they detect a potential predator, which provides benefits for other species that therefore can decrease their vigilance (Munn and Terborgh 1979, Powell 1985). Martínez and Zenil (2012) demonstrated the dependence on those warnings for the species that attend to flocks. *Thamnomanes* sp. take the opportunity, that those species will stop foraging after emission of an alarm call, to emit false warnings and benefit from the distraction effect to catch prey flushed by other birds (Powell 1985). Those behaviors show the different implications of the acoustic communication within the flock. During day, the ‘core’ species can be joined by up to 50 species, with variation over time in species’ flock attendance (Jullien and Thiollay 1998). Considering this difference in ‘attendance’, flock species have been allocated to different categories from ‘core’ to ‘occasional’ species (see Munn and Terborgh 1979, Jullien and Thiollay 1998 for example of classifications). These definitions highlight the complexity of studying mixed-species flocks in the field and partly explained that many researchers have relied on an ultimately subjective decision like include an individual in the studied group or not.

Tropical forests are subject to high degrees of habitat degradation, which affect the entire avifauna (Bierregaard and Lovejoy 1989). However, whilst the effects of disturbance on non-trophic and social interactions in birds are known to exist, they are not sufficiently studied so far at the entire group structure scale (Mokross et al 2014).

Our first objective is to look for non-random associations within both mixed-species flocks and ant-following birds in undisturbed tropical forests. We then want to be able to delimit sub-groups in old growth forest in order to test the validity of species’ traditional categorizations from the ornithological literature. The second objective is to use these results to compare with the associations and group structure in disturbed forest, and thus be able to highlight any breaking of associations that would explain any changes to the group structure of these groups of bird species.

# NON-RANDOM INTER-SPECIFIC ENCOUNTERS BETWEEN AMAZON UNDERSTORY FOREST BIRDS: WHAT ARE THEY AND HOW DO THEY CHANGE?

## INTRODUCTION

Living organisms are in constant interaction with their environment and with each other. Among these interactions, group living is one of the features adopted across many animal taxa, including mammals, fish, and birds (Moynihan 1962, Allan and Pitcher 1986, Terborgh 1990). Groups are most commonly composed of animals of one species, but there are many striking cases of inter-specific association resulting either from the presence of a common resource or from a social behavior that pulls animals from different species together (Morse 1970, Moriarty 1977, Powell 1979). Inter-specific associations of a social nature may reduce competition between individuals while increasing foraging success and anti-predation effects (Harrison and Whitehouse 2011, Sridhar et al 2009). As important as those ecological interactions may be, they are subject to environmental change (Tylianakis et al 2008), and by human activity, mainly via habitat loss (Thiollay 1992, 1999a, Stouffer and Bierregaard 1995, Maldonado-Coelho and Marini 2000, Van Houtan et al 2006, Knowlton and Graham 2011, Mokross et al 2014).

In the Amazon tropical rainforests that are the setting of this study one can find two main types of inter-specific association between understory forest birds, the social-driven mixed-species flocks (Morse 1970) and the resource-driven army-ant-following flocks (Willis and Oniki 1978). Mixed-species flocks of birds are among the most complex multi-species association of foraging species, present in diverse habitat around the world (Harrison and Whitehouse 2011). Historically, these interspecific associations of birds have been delimited in two main approaches. The first is qualitative, and based on field observations done by experts with recognized authority in the field (e.g. Munn and Terborgh 1979, Cohn-Haft et al 1997, Willis and Oniki 1978). The second is

quantitative and results from mathematical analysis of field observations (e.g. Moynihan 1962, Jullien and Thiollay 1998). Since field observations are at the root of both approaches, it is important to consider two principal difficulties in identifying and following multi-species flocks in the field. First, it is very costly; researchers may spend several hundreds of hours following tens of flocks (e.g. Moynihan 1962, Mokross *et al.* 2014). Second, it is difficult to determine which bird is part of a flock due mostly to difficulty in delimiting the spatial and temporal extent of the observed association. While Moynihan (1962) considered tropical birds to be flocking when they were seen in the same tree or bush, others include only species seen moving together throughout periods of 10, 15 or 30 minutes (Powell 1989, Jullien and Thiollay 1998, Mokross *et al.* 2014). Given the variety of temporal and spatial criteria, it is easy to understand how they can influence perceptions of who associates with whom. Indeed, in the Amazon, many species are rarely detected outside of inter-specific associations, and the detection of mixed-species flocks is usually triggered by the presence of *Thamnomanes* spp. individuals (Munn and Terborgh 1979, Powell 1985). The subsequent step of categorizing what species are more or less involved in the association is also problematic. These categories usually result from a species-level calculation of flocking propensity, sometimes measured as the percentage of all sightings of species that occurred in flocks (Moynihan 1962, Jullien and Thiollay 1998). Studies of the impact of habitat degradation on inter-specific associations usually allude to changes in the abundance and presence of flocking species (Thiollay 1997, Van Houtan *et al.* 2006), but they also use measures of flocking propensity to assess changes from a quantitative perspective (Thiollay 1999b, Mokross *et al.* 2014). The main drawback of propensity measures, however, is that they miss the opportunity to understanding associations at the pairwise level. That is, any re-structuring of inter-specific associations that results in a similar proportion of (unspecified) interspecific encounters for each species will be missed by propensity metrics.

Species interactions in general have for a long time been studied at the entire matrix (or set of species) level (Gotelli and McCabe 2002). The analysis of species co-occurrence on islands elicited

much academic debate through the years, starting with Jared Diamond's studies of bird species co-occurrence on islands in Southeast Asia (1973, 1975, reviewed in Gotelli and MacCabe 2002). Diamond's study focused largely on the assessment of diffuse competition; thus requiring the analysis of co-occurrence patterns among multiple species within an assemblage. Such focus resulted in methods aimed at understanding patterns at the level of the entire assemblage regardless of the specifics of interaction between any two particular pair of species. One important component of such methods is the Null Model approach (synthesis of algorithms and metrics in Gotelli 2000) which help quantify the extent to which a particular observed pattern is different from what could be expected from chance encounters of species that do not seek to interact with each other. Null models have been applied to study possible patterns of co-occurrence in mixed-species bird flocks (Graves and Gotelli 1993) and in ant-following flocks of neotropical forest (Pizo and Melo 2010). More recent applications suggest examining pairwise co-occurrence associations (Sfenthourakis et al 2006, Veech 2006, Gotelli and Ulrich 2010, Pitta et al 2012) with methods that could detect positive, negative or random association between two species (Veech 2013, 2014).

A second, much used approach to understanding inter-specific interactions is the use of social network analysis. Network analysis is still based on matrix-level information (Croft et al 2008, Farine and Whitehead 2015) and it helps one to visually identify social interaction based on a graph representing species by nodes and biological interactions by edges (Wey et al 2008). These networks are ideal to understand the structural complexity of biological processes and types of interactions, such as mutualism (Guimarães et al 2011). They are also helpful to assess the impact of habitat disturbance (Tylianakis et al 2007, Mokross et al 2014) and climate change (Araújo et al 2011) on interactions. Different metrics are used to interpret the interactions represented in a network, with modularity metrics, usually employed for delimiting subunits of a network (Girvan and Newman 2002, Newman 2004, 2006).

In order to identify non-random encounters of Amazon understory forest birds and measure their change with habitat disturbance, we decided to combine the two methodological approaches of null models and network analysis. While doing so, we will focus on pairwise measurements of association between species which will enable us to go beyond the whole ensemble view of the inter-specific interaction. To do so, we create a new pairwise metric of association strength that results from the null model analysis and subsequently informs the construction of network graphs. Once having a network, we perform a modularity analysis for delimiting groups of interacting species above the pairwise approach.

Perhaps the most striking aspect of our study is that we evaluate the association between species through an approach that, at the outset, assumes that such associations might as well not exist. Instead of going to the field and sampling animals that we determine to be part of an association, we sample animals without regard for their association status and let the data inform us of any patterns of co-detection. To strengthen our inference, we sample using two different techniques, automated audio recording and mist-netting. The analyses were first carried out separately by sampling technique and subsequently joined producing a view of interspecific associations that uses different lines of evidence. The results give a robust view of what species are most strongly associated and enable an analysis of how the associations play out in different habitat with different levels of disturbance.

## **METHODS**

### **Study area and sampling design**

This study draws on data collected between 2010 and 2015 at the Biological Dynamics of Forest Fragments Project (BDFFP) area, 70 km north of Manaus, Amazonas, Brazil (2°30'S 60°W; Fig. 1). The area of approximately 300 square kilometers is covered by upland old-growth (OG) and

secondary (SF) tropical rain forest, with an annual rainfall from 1900 to 2500 mm, and a pronounced dry season from June to December (Gascon and Bierregard 2001). The BDFFP started as a landscape manipulation experiment aimed at understanding the effect of habitat removal and isolation on a broad range of organisms and ecological parameters (Bierregaard and Lovejoy 1989). Prior to the project onset, in 1979, the area was covered and surrounded by continuous OG forest. Between 1980 and 1984, three large cattle ranches were established (Stotz and Bierregaard 1989), with pasture established in approximately 20% of the area. The ranches were subsequently abandoned and the present-day landscape consists almost entirely of forest cover, approximately one fifth of which is SF.

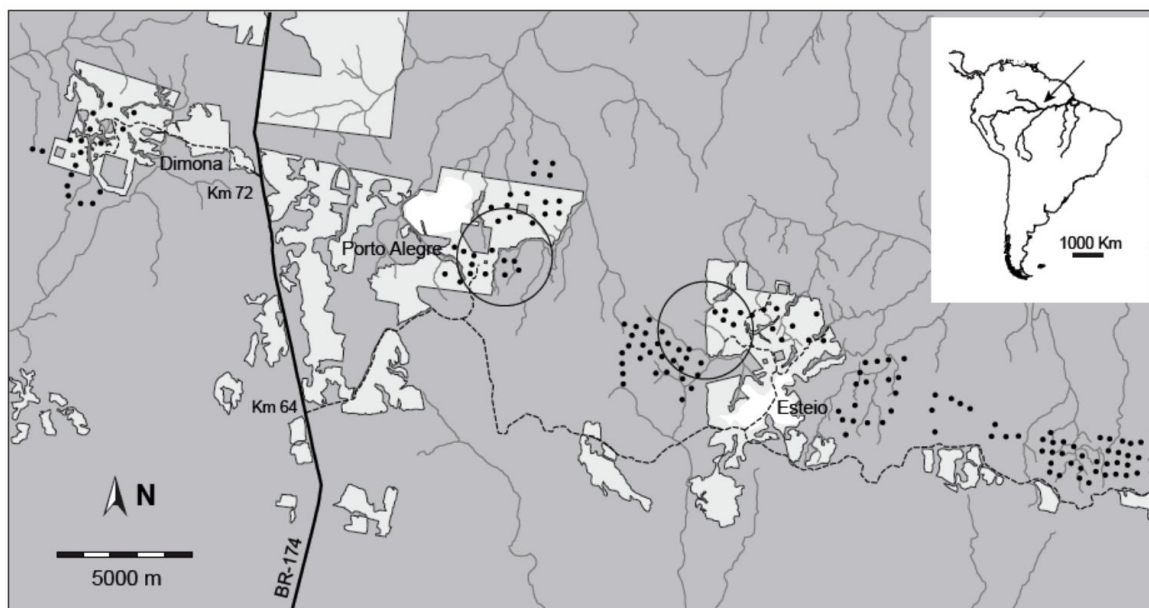


Fig. 1. Study area of the Biological Dynamics of Forest Fragments Project showing our 151 recording sites (filled circles) and approximate location of the 38 mist-netting sites near Porto Alegre (left circle) and Cabo Frio (right circle) camps, Amazonas, Brazil. Sites are distributed through old growth (dark grey) and secondary forest (light grey). Pastures are represented in white, while roads, paved and unpaved, appear as continuous and dashed lines, respectively.

We based our study on two datasets of understory forest bird detections obtained with two different sampling techniques: audio recording and mist-netting. Both the audio recorders and the mist-nets



were placed in the forest understory, but the audio data naturally represents a higher vertical section of the forest, as it can record vocalizations of the loudest birds all the way up to the forest canopy. Mist-nets extended from the ground level up to 2.5 meters high. For logistic convenience, recording quality, and bird safety, we sampled only during dry season months. Mist net captures took place between June 2009 and October 2015 (excluding 2010 and 2012), while audio recording took place between June and November 2010.

The audio dataset comprises 151 sites, 107 in OG and 44 in SF, distributed throughout the study area. Sites were sampled for four to six consecutive days each. The autonomous recorders worked unassisted for three hours per day per site, starting 40 minutes before sunrise (details in Figueira et al 2015). Each three-hour recording was randomly subsampled with five, five-minute, non-overlapping recording cuts that were subsequently processed in the lab by ornithologists with knowledge of the local bird sounds. Each cut produced a list of detected species. Mist-net captures happened over a smaller, central portion of the study area covering 38 OG and SF sites. Lines of 4 to 15 mist-nets were placed monthly (throughout the dry season of the mist-netting years) at a randomly selected subset of sites. The 12-by-3 meter nets were opened from 6 am to 12 pm and checked every 30 minutes. One mist-net sample consists of one mist-net opened for 30 minutes and has an associated species list.

### **Study species**

We focus our study on species that have been previously reported to occur in our study area and to take part in inter-specific associations. Cohn-Haft *et al.* (1997) has the most complete list of the BDFFP avifauna, updated from Stotz and Bierregaard (1989) and including 394 species. Cohn-Haft *et al.* (1997) also provide qualitative information about abundance, preferred habitat, and sociality status of each species. The sociality status is particularly relevant for us, because it lists species as foraging in monospecific flocks, mixed-species flocks of the canopy or understory, solitary or in pairs, and as part of army-ant following flocks. Of these categories, the mixed-species and the ant-

follower flocks comprise inter-specific associations. We therefore built our study species list starting from all species that were listed as understory mixed-species or ant-following flock members by Cohn-Haft *et al.* (1997; Table S1). To complete the list, we obtained information from other studies of BDFFP birds (Harper 1989, Stouffer and Bierregaard 1995) and from elsewhere in the biogeographic region of the Guyana shield (Jullien and Thiollay 1998). As many species classified as being part of canopy flocks can spend many hours per day with understory flocks (Munn 1985), we also included species described as canopy mixed-species flock members by Cohn-Haft *et al.* (1997) that were reported as occasional understory mixed-species flock members by Jullien & Thiollay (1998) and by Munn & Terborgh (1979). In the end, we obtained a list of 37 target species, with hypothetical inter-specific associations listed in table S1.

### **Data organization**

The data sets resulting from the two sampling techniques were split by habitat (OG or SF), resulting in four sub-datasets: OG-audio, OG-capture, SF-audio and SF-capture. Each sub-dataset was organized as an observation matrix with  $i = 1$  to  $R$  rows, and  $j = 1$  to  $C$  columns. Each row of the capture data represents one 30-minute sample with one mist-net, while each row of the audio data represents one five-minute recording cut. Each column represents a species that was detected in the corresponding row, either by captured or audio recording. Entry  $a_{ij}$  of the binary observation matrices represents the detection (1) or non-detection (0) of species  $j$  in sample  $i$ . Summing across rows, one obtains  $S_j$ , which is the total number of detections of species  $j$  across all samples. Once having the four observation matrices, we obtained four associated co-detection matrices. Co-detection matrices listed the observed species as rows and columns and show the number of times that each possible species pair was detected in the same (audio or mist-netting) sample.

## **Quantifying pairwise interspecific associations**

We assess the strength of association between species by measuring the extent to which the observed number of co-detections could result from a simulated observation matrix where the distribution of detections across samples was independent between species. To do this, we use the fixed-equiprobable algorithm of Gotelli (2000), where, for every species, the total number of detections per ( $S_j$ ) is fixed but each detection has the same probability of happening on every sample. Under this algorithm, the simulated number of species per sample (row total) can vary, but all occasions have the same average number of species. Figuratively, this amounts to shuffling detections of each species across sites, independently between species. We employed the randomization algorithm 1,000 times for each sub-dataset, each time simulating one observation and one co-detection matrix. The 1,000 simulated co-detection matrices provide one distribution of co-detection for each pairwise combination of species. In order to quantify the extent to which species associate more than expected under the null model, one only has to look where the observed number of co-detections falls within the simulated distribution.

Our pairwise index of association strength (AS) between two species measures the distance between the observed number of co-detections and the mean number of simulated co-detections, in units of standard deviation of the simulated distribution. Our AS index provides a better description of interspecific association than a raw count of the number of times two species were seen together because it accounts for the inevitable fact that species that are detected more often have a higher chance of being co-detected with others than species that are rarely detected. Thus, the AS index can be used for comparing association strengths between species pairs, between methods and between habitats. High AS values mean that the species were detected together more times than expected under the null model. Near-zero values indicate that observations are compatible with the null expectations. We consider that there is a strong association between two species when AS is greater than 2.576 SDs. Under a normal distribution of simulated co-detections, using this threshold value

amounts to a two-tailed test of the null hypothesis of no association between species, using a p-value of 0.01.

Having the results from all pairwise associations, we built association strength matrices for each habitat and sampling technique. In order to combine results from the two sampling techniques, we simply calculated the arithmetic mean between AS indexes obtained for the same pair under the two techniques. When a pair of species was detected by only one of the sampling techniques, we considered that technique alone in the combined analysis. In the end, we produced six AS index matrices corresponding to OG-audio, OG-capture, OG-combined, SF-audio, SF-capture, and SF-combined data.

### **Visualizing and delimiting groups of interacting species**

Beyond measuring pairwise associations, we wanted to visualize association patterns at the level of the whole set of study species. To do so, we built six weighted networks based on the six AS index matrices using the software *Gephi* and the graph layout algorithm ForceAtlas2 (Jacomy et al 2014). Each node on a network represents a species and the ‘degree’ of a node, illustrated by its size, represents the number of links (or edges) that a species has with all other species. The weighted edges connected pairs of species with strong association ( $AS > 2.576$ ), with edge width representing the magnitude of the association. AS values smaller than or equal to 2.576 were not considered in the network construction.

In order to identify groups of species and measure the extent to which a network is compartmentalized, we performed a modularity analysis based on the function *cluster-louvain* from the R package *igraph* (Blondel et al 2008). This analysis returned a network graph showing the partition of species in groups and a modularity metric  $Q$  that quantifies the extent to which a network shows fewer edges than expected under a model of no compartmentalization (Newman 2006). Overall, species groups defined by the modularity analysis tended to associate amongst themselves

more strongly than with species from other groups. To quantify this tendency, we calculated the average AS values within and between modules, based only on the strong associations. This quantification and previous knowledge of species natural history helped us name each module and compare our findings with the ornithological expectation compiled in table S1.

### **Change in interspecific association between old-growth and secondary-forest habitat**

To study the change in interspecific associations from OG to SF, we computed pairwise differences in the number of co-detections in SF and OG, separately for each sampling technique. Positive differences denote an increase, and negative differences a decrease in pairwise association from OG to SF. Subsequently, in an approach parallel to that used for generating AS values, we simulated 1000 joint-habitat observation matrices for each technique. Each simulation shuffled each species' detections across samples from both habitats, allowing that a detection from OG might be randomly placed in a SF sample. Based on the 1000 simulations, we obtained distributions of SF-OG differences and an index of association change (AC) for each pair of species and sampling technique. Once having the technique-specific AC values, we averaged them across techniques to obtain a combined-data AC matrix. When a AC value is greater than 2.576 we say that the association became significantly stronger in SF; conversely, when AC is smaller than -2.576 we say that the association became significantly weaker. Combining information on AC and AS indices, we obtain the nine possible scenarios for association change listed in Table 2. Broadly, there are three increasing and three decreasing scenarios, plus to scenarios of no change and one scenario without evaluation. We could only evaluate changes with forest type when the two species of a pairwise comparison had sufficient data (> 10 detections) in both habitats for at least one of the observation techniques, when this is not the case, Table 2 cells show an 'NA' value. The two no-change scenarios indicate situations where AS is low (<2.576) in both habitats, with a low AC value (denoted by '0') and where AS is high in both habitats with low AC value ('='). The three decreasing scenarios comprise: a) AS high in both habitats with high negative AC value ('↓'); b) AS high in

OG but smaller than 2.576 in SF with a small negative AC value ('↓↓'); and c) AS high in OG and low in SF with a high negative AC value ('↓↓↓'). Similarly, the three increase scenarios are: a) high positive AC value with high AS in both OG and SF ('↑'); b) low AS in OG and high AS in SF with small positive AC ('↑↑'); and c) low AS in OG and high AS in SF, with high positive AC value.

## RESULTS

### *Data overview*

Our recording data consisted of 3,076 five-minute audio samples, 2,178 from OG and 898 from SF. The aggregate of all audio samples contained 18,072 detections, 34% of which were detections of our target species, corresponding to 4,039 target-species detections in OG and 1,090 in SF. The capture data consisted of 65,230 netting samples, 35,755 in OG and 29,475 in SF. These samples returned a total of 6,455 individual bird captures, 58% of which were from our target species and were split between 2,077 OG and 1,658 SF captures (Table S1). Three of the target species, the flycatchers *Onychorhynchus coronatus*, *Terenotriccus erythrurus* and *Rhynchocyclus olivaceus* were not sampled ten or more times in OG with at least one of the sampling techniques, so they did not fulfill the criterion for inclusion and were dropped from the analysis.

### *Group delimitation based on pairwise association in old growth forest*

All 37 target species occurred in OG but only 34 fulfilled the criterion for inclusion in the analysis. All 34 showed strong associations with at least one other species but some were detected less than ten times with either of the sampling techniques and were excluded from technique-specific analyses. Namely, *Epinecrophylla gutturalis*, *Isleria guttata*, *Dendrocincla merula* and *Mionectes macconnelli* had more than ten mist-net captures each, but were audio-recorded less than ten times in the OG data. Conversely, *Piculus flavigula*, *Lanio fulvus*, *Automolus ochrolaemus*, *Tolmomyias assimilis*, *Sittasomus griseicapillus*, *Dendrocolaptes certhia*, *D. picumnus*, *Hylexetastes perrotii* and

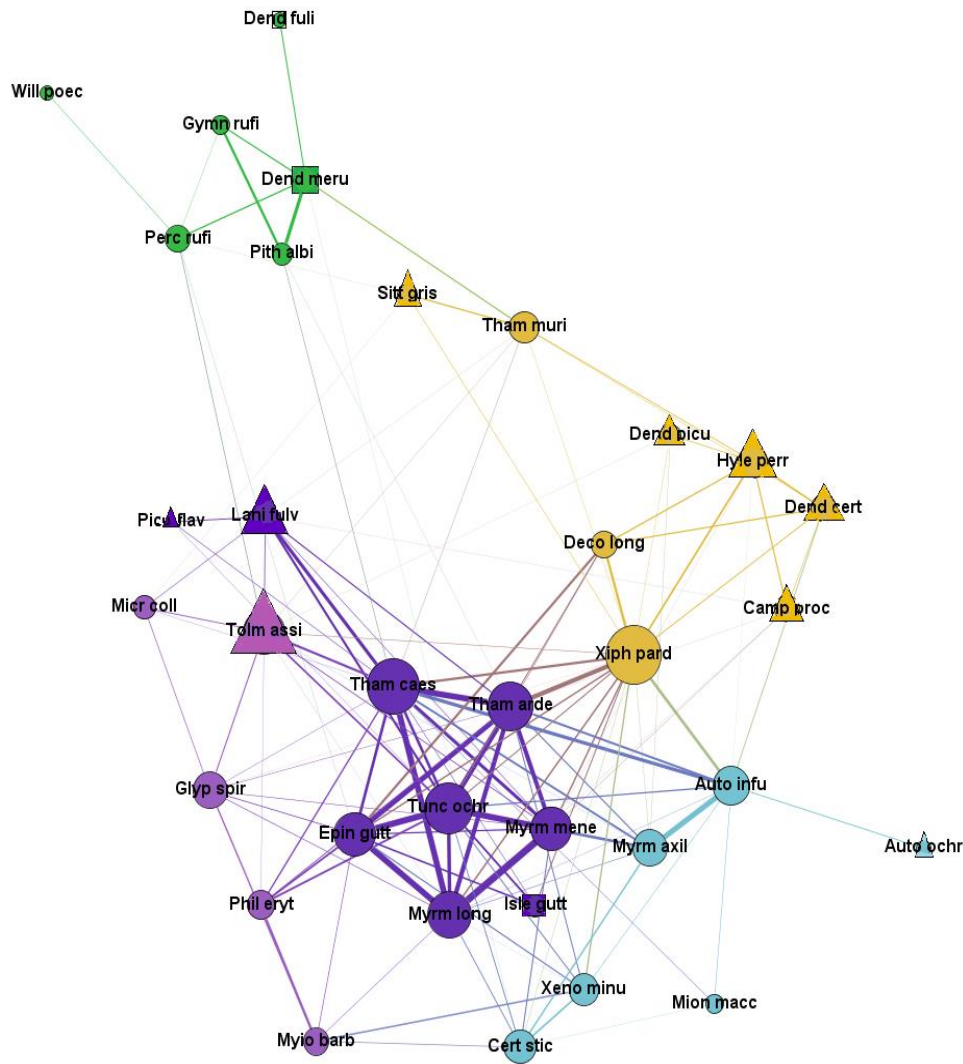
*Campylorhamphus procurvoides* had a sufficient number of audio-recordings but neither had more than ten mist-net captures for inclusion in OG capture-data analyses.

The pairwise analysis of audio samples returned association strengths of -2.49 to 16.32 SDs. There were, in all, 117 strong associations in 406 possible associations (26.35%, Table S2). Pairwise association strengths from capture data ranged from -0.80 to 23.34 SDs, with 88 strong associations in 300 possible associations (29.33%, Table S3). When we combined results from both sampling techniques into one triangular matrix of average association strengths, values ranged from -2.49 to 17.39 SDs, with 132 strong associations over 561 possible associations (25.58%, Table S4). None of the negative values were more than 2.576 SDs away from the mean of the null distribution.

The two networks based on the association strengths for each sampling technique were broadly coincident (Fig. S1). The audio-data network partitioned the 29 analyzed species in three modules composed of twelve, ten and six species, with a modularity metric of  $Q = 0.209$  (Fig. S1A). The same analysis applied to the capture data produced a network with 25 species divided in four groups of nine, five, four and seven species. Here, the modularity metric was slightly higher, at  $Q = 0.237$  (Fig. S1B). There are two sets of species that appear in the same group in both the audio- and the capture-data networks. One set, at the center of the networks, is the quintet *Thamnomanes ardesiacus*, *T. caesius*, *Myrmotherula longipennis*, *M. menetriesii* and *Tunchiornis ochraceiceps*; and the second, always clearly separated from the first, is the trio *Pithys albifrons*, *Gymnopithys rufifigula* and *Percnostola rufifrons*. The combination of audio and capture data into one triangular matrix of interaction strengths, offers a single graphical representation of the associations in our data. (Table S4, Fig. 2). The modularity analysis of this joint-data network resulted in five modules with a metric  $Q = 0.248$ . Individual modules contained between five and eight species, with seven to 25 strong associations within the module. We designate as ‘core’, the module of eight species with 25 strong associations among them and a ratio of 3.13 strong associations per species (Table 1). The core module had the highest ratio of strong associations per species and the highest—although extremely

variable—association strengths. The two modules designated as ‘Attendant 1’ and ‘Attendant 2’ had higher average association strength within the module than with any other module, as did the Core and the ‘Ant Follower’ modules. Nonetheless, the two ‘Attendant’ modules have higher average association strength with the ‘Core’ than with any module other than themselves, which justifies their name. The ‘Ant follower’ module had the lowest average association strength with the ‘Core’ and is composed by species that are well known to forage around moving army-ant swarms. Finally, there was only one module whose average association strength within the module was not higher than all average association strengths between itself and other modules. We designate this weaker module as ‘Unknown’ (Table 1).





Core	Attendant 1	Attendant 2	Uncertain	Ant-followers
<i>Piculus flavigula</i> *	<i>Myrmotherula axillaris</i>	<i>Glyphorhynchus spirurus</i>	<i>Thamnomphilus murinus</i>	<i>Percnostola rufifrons</i>
<i>Thamnomanes ardesiacus</i>	<i>Certhiasomus stictolaemus</i> *	<i>Philydor erythrocerum</i> *	<i>Sittasomus griseicapillus</i>	<i>Pithys albifrons</i>
<i>Thamnomanes caesioides</i>	<i>Xenops minutus</i>	<i>Tolmomyias assimilis</i>	<i>Deconychura longicauda</i> *	<i>Gymnopithys rufigula</i>
<i>Isleria guttata</i> *	<i>Automolus ochrolaemus</i>	<i>Myiobius barbatus</i>	<i>Dendrocolaptes certhia</i>	<i>Willisornis poecilinotus</i>
<i>Epinecrophylla gutturalis</i>	<i>Automolus infuscatus</i>	<i>Microbates collaris</i>	<i>Dendrocolaptes picumnus</i> *	<i>Dendrocincla merula</i>
<i>Myrmotherula longipennis</i> *	<i>Mionectes macconnelli</i>		<i>Hylexetastes perrotii</i> *	<i>Dendrocincla fuliginosa</i>
<i>Myrmotherula menetriesii</i>			<i>Xiphorhynchus pardalotus</i>	
<i>Tunchiornis ochraceiceps</i> *			<i>Campylorhamphus procurviroides</i> *	
<i>Lanio fulvus</i> *				

Fig. 2. Interspecific association network based on the combination of audio and capture data from old-growth sites. Eight-letter codes indicate species listed on the bottom of the figure. Circles represent species that were detected more than ten times by both sampling techniques, triangles show those recorded but not captured, and squares show those captured but not recorded. Symbol size is proportional to the number of edges connecting focal species with other species. Edge width is proportional to the association strength. The colors represent species groups given by the network modularity analysis: Core (Dark Blue), Attendant 1 (Light Blue), Attendant 2 (Purple), Uncertain (Yellow), and Ant-follower (Green). Species names on the bottom give the composition of each group. Those species marked with ‘\*’ were detected fewer than 10 times in secondary forest.

Table 1. Group-level association strengths for old-growth forest based on the combination of recording and mist-netting data. Values in the triangular matrix are the arithmetic mean and variance (in parentheses) of strong associations within and between the groups listed as row and column labels. The meaning of abbreviated row labels is given in the expanded column labels. The three columns on the right show group-specific values for the number of species (N), the number of strong associations within group (SL), and the ratio of strong associations per species (SL/N).

	Core	Attendant 1 (A1)	Attendant 2 (A2)	Unknown (U)	Ant Follower (AF)	sps (N)	strong links (SL)	SL/N
Core	9.20 (23.21)					8	25	3.13
A1	5.24 (3.46)	5.87 (14.46)				6	7	1.17
A2	4.54 (1.98)	4.49 (3.00)	4.74 (2.67)			5	7	1.40
U	4.84 (5.87)	4.40 (4.29)	3.10 (0.31)	4.80 (1.67)		8	15	1.88
AF	3.00 (0.11)	2.83 (0.00)	3.73 (0.00)	3.77 (2.39)	5.64 (5.59)	6	7	1.17

### *Inter-specific associations in the secondary forest*

Twenty-three of our target species crossed the threshold of ten or more detections in secondary forest by at least one of the sampling techniques. Among these, eighteen crossed the threshold with audio data, eighteen with capture data, and thirteen with both. One third (32.35 %) of the target species detected in OG were not detected in SF but 21 of the 23 species detected in SF showed at least one strong pairwise association with some other species (Table S7). *Microbates collaris* and *Sittasomus griseicapillus* did not show strong associations at all, so they were not included in the network analysis.

The pairwise analysis of audio samples returned association strengths of -1.32 to 11.32 SDs. These included 34 strong associations over 153 possible associations (22.22%; Table S5). The analysis of capture data returned association strengths from -0.99 to 16.07 SDs, with 42 strong associations in 153 possible associations (27.45%, Table S6). The combination of the two sampling techniques returned a slightly lower proportion of strong links (52 / 253 or 20.55%, Table S7) than either technique taken in isolation. A few of the combined-data associations were negative, but none had an absolute value greater than 2.576 SDs away from the mean of the null distribution. Comparing the

combined results from OG and SF, we see a decrease of nearly one fifth (19.66%) in the proportion of strong associations in SF relative to OG.

As in the OG, the technique-specific network analyses of SF data produced broadly coinciding results ( $Q_{\text{capture}}=0.258$ ,  $Q_{\text{sound}}=0.201$ , Fig. S2); for simplicity, we focus on the combined-data network (Fig. 3). It is noteworthy that even though the proportion of strong links decreases relative to that in OG, the modularity metric goes up, from  $Q = 0.248$  to  $Q = 0.296$ . The 21 species were distributed in three modules with three to nine species, and three to 21 strong associations per module (Fig. 3, Table S7). Some of the SF modules mirror those in OG, with, for example, *T. caesius* and *M. menestriesii* strongly associated and present in the same group. Likewise, *P. albifrons*, *G. rufigula* and *Willisornis poecillinotus*, were once again found together in the same module.

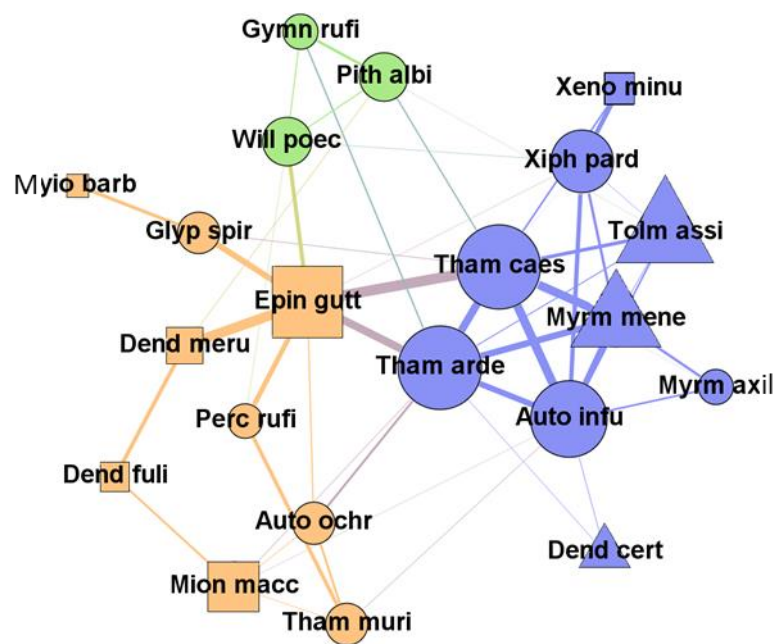


Fig. 3. Secondary-forest interspecific association network, based on the combination of recording and mist-netting data. Eight-letter codes, symbol, symbol size, and edge width as in Fig. 2. Colors represent groups formed in the network modularity analysis: SF-Core (Blue), SF-Attendant (Orange), and SF-Ant-follower (Green). Species names on the bottom give the composition of each group.

The analysis of association strengths within and between SF modules reflects the similarity between OG and SF networks (Table S8). Unlike in the OG data, here there is higher average association strength within them between modules for all modules, i.e. no ‘Unknown’ group. We again designate as ‘Core’, or ‘SF-Core’, the module with the highest average and variability of association strengths. Once again, this was the only module with a ratio of more than two strong links per species. Ranking the remaining modules in decreasing order of average association to the ‘SF-Core’, the second module still had more than one strong link per species and showed a relatively high average association with the ‘SF-Core’; we designated this module as ‘SF-Attendant’. Finally, we gave the name ‘SF-Ant-follower’ for the last group containing only three ant-following species (Table S8, Fig. 3).

Table 2 summarizes changes in pairwise association strength from OG to SF. It first becomes clear that some of the species in the OG network of Figure 2 are not present in the comparison, because they were not sufficiently detected in SF. The twenty-three species present in both habitats, potentially produced 253 pairwise comparisons; we can only evaluate 223 of these because some species pairs did not have sufficient data for both species under one single sampling technique—a condition for comparison. In all, 24 (~11%) associations that were strong in OG, were broken (or ceased to be strong) in SF. Twenty-two (~10%) were either weaker than expected under the null model but still strong, or showed a numerical reduction that was no bigger than expected under the null model of no change between habitats. On the opposite end of the spectrum, there were eight (<4%) new associations, which were strong in SF but absent in OG, and thirteen (~6%) which were already present in OG and increased significantly in SF, or just increased from OG to SF albeit no more than predicted by the null model. Finally, seventeen associations were present in both habitats without any significant change and 139 were absent in both habitats without significant change. Looking within the OG modules, the vast majority of changes are negative, with only two exceptions

for a significant increase in the associations *W. poecillinotus* - *G. rufigula* and *W. poecillinotus* - *P. albifrons* associations, which were already present in the OG habitat.

Table 2. Changes in pairwise inter-specific associations from OG to SF habitat. Symbols represent the whole range of responses to habitat change, from the complete loss to the formation of a new and strong association in SF. Old-growth modules are outlined by bold black lines. Species within a module are ranked by decreasing order of average association strength to other species in the same module. Old-growth species that were detected fewer than 10 times in secondary forest are not represented in this table.

	Tham caes	Epin gutt	Myrm mene	Tham arde	Auto infu	Myrm axil	Xeno minu	Auto ochr	Mion macc	Tolm assi	Glyp spir	Micr coll	Myio barb	Xiph pard	Dend cert	Tham muri	Sitt gris	Gymn rufi	Pith albi	Dend meru	Perc rufi	Dend fuli	
Epin gutt	=																						
Myrm mene	↓	NA												↑↑↑	New, significantly stronger association in SF (8)								
Tham arde	↓	↓	↓											↑↑	New but not significantly stronger association in SF (2)								
Auto infu	=	0	=	=										↑	Significant increase in an already strong association (11)								
Myrm axil	↓	0	↓	↓↓↓	↓									=	Association present without significant change (17)								
Xeno minu	↑↑↑	↓↓↓	NA	↓↓↓	↓↓↓	0								↓	Significant decrease in association that stayed strong (13)								
Auto ochr	0	NA	0	0	↓↓↓	0	NA							↓↓	Association lost without significant decrease (9)								
Mion macc	↓↓↓	0	NA	↑	=	0	0	NA						↓↓↓	Association lost with significant decrease (24)								
Tolm assi	↓	NA	=	↑	↑	↓↓↓	NA	0	NA					0	Association is still absent (139)								
Glyp spir	=	↑↑	↓↓	=	0	0	0	↑↑↑	0	↓↓↓				NA	Change could not be evaluated due to lack of data (30)								
Micr coll	↓↓↓	NA	0	↓↓↓	0	0	NA	0	NA	↓↓↓	↓↓												
Myio barb	0	↓↓↓	NA	0	0	0	↓↓↓	NA	0	NA	=	NA											
Xiph pard	↓	=	↓	↓↓↓	=	=	↓	↑	0	=	↓↓	0	0										
Dend cert	0	NA	0	↑	↓	0	NA	0	NA	0	0	0	NA	↓↓↓									
Tham muri	↓↓	0	↓↓	0	↑	0	0	↑↑↑	↑↑↑	↓↓↓	0	0	0	↓↓	↓↓↓								
Sitt gris	0	NA	0	0	0	0	NA	0	NA	0	0	↓↓↓	NA	↓↓↓	0	↓↓↓							
Gymn rufi	0	0	0	↑	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Pith albi	=	0	0	↓↓	0	0	0	0	0	↑	0	0	0	0	0	0	0	0	=				
Dend meru	0	↑↑↑	NA	0	0	0	0	NA	0	NA	0	NA	0	0	NA	↓↓↓	NA	↓↓↓	↓				
Perc rufi	0	↑↑	0	0	0	0	0	0	0	↓↓↓	0	0	0	0	0	↑↑↑	↓↓	↓↓	0	↓↓↓			
Dend fuli	0	0	0	0	0	0	0	0	↑↑↑	0	0	0	0	0	0	0	0	0	0	=	0		
Will poec	0	↑↑↑	0	0	0	0	0	0	0	0	0	0	0	↑	0	0	0	↑	↑	0	=	0	

## DISCUSSION

Our study confirms the existence of strong patterns of interspecific co-detection among Amazon understory forest birds. The evidence of interspecific association conveyed by this patterns is particularly strong for three main reasons: i) it uses two different observation techniques, ii) it accounts for variations in the number of detections across species, and iii) it does not involve any subjective decisions by field observers about whether two species are or are not part of the same group. AS index values revealed that approximately one fourth of all possible species pairings in old growth show strong, non-random association. Moreover, we found no evidence of repulsion, i.e. strong negative AS values, suggesting the absence of interference competitive interactions that are strong enough to result in inter-specific avoidance among the species in our study. Previous studies of interspecific associations in our study region (e.g. Jullien and Thiollay 1998, Mokross et al 2014) focused on individual species rather than pairwise interactions, measuring ‘mixed-species flocking propensity’ as the proportion of times a species was detected in an observer-defined ‘mixed-species’ group out of the total number of detections for that species. With our approach, we can assess inter-specific association at a pairwise level and combine the pairwise information for all species into a representation of interactions among all species in the study set.

The analysis of the network diagram based on association strengths between species in old-growth forest showed two distinct aggregates of species. One, aggregate, the ant-follower species was particularly well separated from the other species. The other aggregate, which we termed ‘Core’ mixed-species flocking species had a high variance but also a high AS value. Three intermediate groups—Attendant 1, Attendant 2, and unknown—were less clearly defined. These groups, resulting from the modularity analysis had a modularity metric  $Q$  between 0.2 and 0.3. Following Newman (2004),  $Q$ -values greater than 0.3 suggest the group structure is strong, therefore our network should be described as diffuse. Nonetheless, except for a few odd associations (i.e. species not considered from the same class based on previous studies), the members of the modules based on the joint-data

network coincide well with traditional categorizations of mixed-species flocks and ant-followers in the central amazon (Table S1, Jullien and Thiollay 1998, Harper 1979); which means that our group delimitation supports pre-existing ecological expectations.

In total, sixteen species in our study fell on groups that are coincident with those defined in the previous literature. Five species, including *Thamnomanes caesius*, *T. ardesiacus*, *Myrmotherula longipennis*, *M. menestriesii* and *Epinecrophylla gutturalis* were considered as ‘constant flock members’ by Jullien & Thiollay (1998) and were defined as ‘Core’ in our analyses. Two species, *Xenops minutus* and *Automulus infuscatus*, classified as ‘permanent members’ (less than constant) by Jullien & Thiollay (1998), were classified as ‘Attendant 1’ in our study. And likewise, three other species—*Glyphorynchus spirurus*, *Mionectes macconelli* and *Myobius barbatus*—that were classified as ‘frequent but not permanent members’ by Jullien & Thiollay (1998) appear as ‘Attendant 2’ in our study. Finally, six species of ant-following birds already classified as such by Harper (1979) were isolated from the other species in our analysis and appeared as ‘Ant-followers’ in our network division. These last species are generally aggregated at swarm of army ants (Willis and Oniki 1978, Harper 1979), so it makes sense to have them here all together in the same module. Consequently, we found our group delimitation relevant and consistent with previous expert knowledge, using simple co-detection matrices which do not require any a priori decision as to whether two species are or are not interacting in the field.

The analysis of SF data revealed a substantial loss of species and loss of associations among the remaining species. In all, one third of the species studied in OG did not have sufficient data for analysis in SF. At the same time, among those species that remained, there was a 20% reduction in the number of strong associations. These results agree with the tendency for decreased species richness and abundance found in previous analyses of disturbed forest habitat (Thiollay 1997, Lee et al 2005, Sodhi et al 2008, Sridhar and Sankar 2008, Mokross et al 2014). Nonetheless, we still found many strong associations in SF, revealing that several mixed-species flock members and ant-



following birds are still appearing together more than expected under the null model. Indeed, it is striking that even though more connections were lost than formed in the transition from OG to SF, the modularity metric  $Q$  was slightly higher in SF ( $Q_{OG} = 0.248$  and  $Q_{SF} = 0.296$ ), albeit still characteristic of a diffuse network. As in the OG, the modularity of the SF network clearly separates two sets of mixed-species flocking and ant-following species.

Looking across all species, there are more than twice as many cases of decreased association (46) than of increased association (21; Table 2). If, however, we look at changes in pairwise associations within the modules defined based on OG data, all evidence of change is negative, except for two pairwise increases among ant-following species. This suggests that, 30 years after the onset of SF regrowth, the interaction between mixed-species flocking species may be more seriously disrupted than the aggregation of ant-followers around army-ant swarms. We can only speculate about the reasons behind the overall reduction in association. Perhaps some changes are due to differences in canopy height and vegetation density, which might influence flock attendance due to changes in exposure to predators (Thiollay 1997) or in prey availability (Develey and Peres 2000). The reduction in resource availability may constrain species to extend their space use and consequently reduce their flock attendance. These results support the idea that understory forest bird inter-specific associations are fragile and vulnerable to disappearing as a result of habitat disturbance (Mokross et al 2014). It is an open question whether the weakening of inter-specific associations has any measurable effect on the fitness of the involved species.

Our study does not refute any previously held belief about interspecific association of Amazon understory forest birds, but it improves quantitative detail and robustness of the existing ideas about group delimitation and association changes with habitat disturbance. The key methodological choices behind this improvement are the use of two different field sampling techniques, and the integration of a null model approach with the network representation of pairwise associations. The main advantage of combining two sampling techniques

is the potential for reducing technique bias. Audio recording is an efficient approach for sampling bird presence across a broad range of vertical positions in dense, low-visibility tropical rainforests (Terborgh et al 1990). Furthermore, autonomous audio recording, which we used in this study, makes it possible to sample birds without the interference of a human observer (Acevedo and Villanueva-Rivera 2006, Brandes 2008). The second technique, mist-net capture, makes it possible to detect secretive and non-vocalizing birds (Blake and Loiselle 2001). Mist-nets do span a limited portion of the vertical profile of the forest, as they extend up to three meters in height at most. The species in our study move in a variety of heights throughout the forest, but with the exception of a few mixed-species flocking birds that tend to forage above the mist-net level (e.g. *Myrmotherula menestriesii*, Munn and Terborgh 1979), they tend to concentrate in the understory, within reach of the mist-nets.

Three caveats should be considered when evaluating our methodological choices and constraints. First, our data were constrained by broadly non-overlapping spatial distribution of audio recording and mist-net samples. This makes it difficult to directly compare the performance of each technique without explicitly modeling detection probability; nonetheless, our finding of many similar associations under both techniques strengthens our confidence in the findings. It is noteworthy, too, that the combined data network showed an increase, albeit a slight one, of the modularity metric (i.e. highest Q based on combined data). We conclude that even with difference spatial distribution of the sampling effort, the two techniques complement each other in an informative way.

A second caveat relates to the idea that falling in the same mist-net within a period of 30 minutes or calling within 5 minutes within the proximity of a recording device are not undisputable evidence of social interaction. This is particularly true when species have coincident and narrow schedules of vocal activity. Nonetheless, it is also true that social interaction will necessarily increase the probability of calling together or falling in the same net. Species moving as a group will make constant contact calls to stay grouped together or warn each other about the proximity of a predator,

a behavior that is well document for core mixed-species flocking species such as *Thamnomanes sp.* (Munn and Terborgh 1979, Martinez and Zenil 2012). Indeed, behavioral ecologists often use the ‘gambit of the group’ to define animal associations based on spatial proximity (Franks et al 2010). We apply this reasoning in our interpretation of co-detection data. Despite its probabilistic nature, the use of indirect evidence of interaction is useful for contrasting with previous work, because it does not rely on subjective judgment of who is interacting with whom in the field. Whatever patterns we identify with our approach are not influenced by prior expectation about social interaction and thus fulfill our objective of trying to detect hypothetical associations under the presumption that they do not exist.

The third and final caveat relates to the use of degenerate matrices in our null model algorithms (Gotelli 2000, Connor and Simberloff 1983). Degenerate matrices include rows (or columns) that are filled with zeros and they may not always be helpful in inferring associations. In our case, however, we believe it is more appropriate to use degenerate than non-degenerate matrices. One row of zeros in our detection matrices represents an occasion where none of our target species was detected (an empty column would represent a species that is never detected). We did not include non-detected target species in any of our analysis, but the empty rows (i.e. occasions without detection) represent a biologically meaningful situation as it is possible that some nets have no captures or some recordings have no vocalizations because the individuals that could possibly be sampled there are concentrated elsewhere. That is why we decided to develop our analysis using degenerate observation matrices, a decision that finds support in the null model literature (Haefner 1988, Gotelli 2000).

Mixed-species flocks and ant-follower birds in tropical forest are a real phenomenon of non-random associations that can be found either from direct observations in the field or from indirect sampling techniques. The groups that we delimited are ecologically meaningful as confirmed by direct observations in previous studies. However, the associations between species are not stable when faced with habitat disturbance; many of the associations observed in old-growth forest break down in

secondary forest. In addition, some species were detected less or not at all in secondary forest.

Associations between species are clearly evident from the data, but we know next to nothing about the extent to which they influence the fitness of the involved species. Future work should focus on developing experimental or creative observation approaches to understand the extent to which the associations that we report here are being subject to natural selection.

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## ANNEXES

Table S1. Data summary and overview of inter-specific group classifications prior to and including this study. Numerical columns show the data summary for audio recordings and mist-net captures. ‘Audio Recordings’ show number of 5-min tracks where species was detected in old growth (OG) and secondary forest (SF); ‘Mist-net Captures’ show number of individual captures. Shading highlights sampling technique and habitat combinations that had fewer than ten detections for the corresponding species, these detections were not included in our analyses. The four columns on the right show classification of study species in inter-specific groups according to three prior studies and to our own classification based on the combination of audio and mist-netting data from the undisturbed old-growth habitat. Species are ranked according to the South American Classification Committee list.

Species name	Number of Detections				Inter-specific group classifications			
	Audio Recordings		Mist-net Captures		Harper 1989	Cohn-Haft <i>et al.</i> 1997	Jullien <i>et al.</i> 1998	This study
	OG	SF	OG	SF				
<i>Piculus flavigula</i>	47	6	0	0		c,u	f	c
<i>Thamnophilus murinus</i>	423	169	22	37		u,s		u
<i>Thamnomanes ardesiacus</i> *	164	39	128	45		u	c	c
<i>Thamnomanes caesi</i> us*	333	84	137	108		u	c	c
<i>Iseria guttata</i>	4	0	20	0		u,s		c
<i>Epinecrophylla gutturalis</i> *	8	3	59	49		u	c	c
<i>Myrmotherula axillaris</i>	79	33	10	46		u,s		a1
<i>Myrmotherula longipennis</i> *	52	1	78	4		u	c	c
<i>Myrmotherula menetriesii</i> *	138	27	23	6		u	c	c
<i>Percnostola rufifrons</i> *	395	205	64	94	f	s,a		af
<i>Pithys albifrons</i> *	161	43	360	482	o	a		af
<i>Gymnopithys rufigula</i> *	48	13	167	150	o	a		af
<i>Willisornis poecilinotus</i> *	125	33	209	122	f	s,a		af
<i>Certhiasomus stictolaemus</i>	11	4	48	0		u		a1
<i>Sittasomus griseicapillus</i> †	164	18	0	0		c,u,s		u
<i>Deconychura longicauda</i>	52	3	12	4		u,c	p	u
<i>Dendrocincla merula</i> *	2	0	72	38	o	a		af
<i>Dendrocincla fuliginosa</i> *	78	12	22	18	f	u,a,s		af
<i>Glyphorhynchus spirurus</i> *	158	83	264	190		u,s	f	a2
<i>Dendrocolaptes certhia</i>	206	46	9	7	f	a,s		u
<i>Dendrocolaptes picumnus</i>	51	9	1	2	f	a		u
<i>Hylexetastes perrotii</i>	93	3	4	1	f	a,s		u
<i>Xiphorhynchus pardalotus</i>	425	86	82	50	f	u	c	u
<i>Campylorhamphus procurvoldes</i>	30	2	1	0		u	p	u
<i>Xenops minutus</i> *	54	4	25	12		u	p	a1
<i>Philydor erythrocerum</i>	26	1	15	1		u	c	a2
<i>Automolus ochrolaemus</i>	27	35	4	36		u,s		a1
<i>Automolus infuscatus</i> *	96	33	35	50		u	p	a1
<i>Mionectes macconnelli</i> *	0	0	71	58		f	f	a2
<i>Rhynchocyclus olivaceus</i>	5	4	9	15		u		-
<i>Tolmomyias assimilis</i> †	304	78	0	2		c		a2
<i>Onychorhynchus coronatus</i>	0	0	4	3		u		-
<i>Myiobius barbatus</i> *	0	0	40	16		u	f	a2
<i>Terenotriccus erythrurus</i>	2	1	6	5		s,u		-
<i>Tunchiornis ochraceiceps</i>	90	0	46	1		u	p	c
<i>Microbates collaris</i>	132	12	24	5		s,u		a2
<i>Lanio fulvus</i> †	56	0	6	1		c	f	c
<b>TOTAL DETECTIONS</b>	4039	1090	2077	1658				

\*Species with similar results across group classifications.

†Species that occasionally switch from canopy to understory flocks according to Munn & Terborgh (1979).

Key for inter-specific group classes: : Harper 1979 - 'o'=obligate ant-follower, 'f'=facultative ant-follower; Cohn-Haft *et al.* 1997 - 'c' = canopy flock member, 'u' = understory flock member, 'a' = ant-follower s' = solitary, 'f' = in mixed-species aggregations at fruiting trees; Jullien & Thiollay 1998 - 'c' = constant flock member, 'p' = permanent flock member, 'f' = frequent but not permanent member; This study, based on modularity analysis of combined old growth data network - 'c' = core member, 'a1' = attendant 1, 'a2' = attendant 2, 'u' = uncertain, 'af' = ant-follower, '-' = insufficient data in old growth.

Table S2. Pairwise association strengths and group delimitation based on old-growth audio data. Groups resulting from the modularity analysis are outlined in black. *Dendrocincla fuliginosa* is not part of any group because its audio data did not reveal a strong association with any of the other species.

	Picu flav	Tham arde	Tham caes	Myrm axil	Myrm long	Myrm mene	Will poec	Cert stic	Xeno minu	Phil eryt	Tunc ochr	Lani fulv	Tham muri	Sitt gris	Deco long	Dend cert	Dend picu	Hyle perr	Xiph pard	Camp proc	Auto ochr	Auto infu	Perc rufi	Pith albi	Gym rufi	Glyp spir	Tol assi	Micr coll	
Tham arde	0.81																												
Tham caes	3.66	16.32																											
Myrm axil	1.79	10.33	13.73																										
Myrm long	1.79	10.63	12.66	7.51																									
Myrm mene	1.87	16.23	15.42	9.42	11.43																								
Will poec	-1.71	0.87	2.55	1.21	-1.82	0.80																							
Cert stic	-0.50	1.36	1.14	2.62	-0.52	4.12	0.50																						
Xeno minu	0.82	6.16	3.03	2.28	0.64	4.29	-0.06	1.36																					
Phil eryt	0.62	4.67	6.81	2.25	4.46	3.68	0.49	-0.35	1.73																				
Tunc ochr	3.04	11.86	14.23	7.36	10.48	13.31	0.39	0.81	3.32	5.94																			
Lani fulv	4.46	5.03	9.60	2.16	2.34	3.64	1.02	-0.54	-0.35	0.46	7.35																		
Tham muri	0.72	2.28	2.88	1.10	1.39	2.80	1.83	0.67	-1.21	0.08	-0.12	2.78																	
Sitt gris	1.40	0.50	2.32	0.03	1.12	1.91	1.27	-0.95	1.00	0.11	-1.12	1.42	5.45																
Deco long	-0.14	2.61	3.08	2.25	0.68	0.38	1.75	-0.53	-0.29	3.11	0.55	1.47	0.26	-0.51															
Dend cert	-0.69	0.42	1.04	1.01	-0.43	0.95	0.08	-1.07	2.32	1.86	-2.01	-1.04	3.46	0.75	5.27														
Dend picu	-1.05	1.13	0.11	3.21	0.71	1.64	-0.58	-0.51	0.66	-0.78	1.36	-1.18	0.76	-1.51	-0.22	2.07													
Hyle perr	-0.01	0.38	-0.90	0.35	0.52	2.71	-0.17	-0.70	0.46	0.95	-0.45	1.10	4.27	-0.38	5.40	5.93	4.14												
Xiph pard	1.45	8.15	7.94	6.67	6.76	7.02	-0.04	3.74	2.29	3.64	6.63	2.44	6.62	3.64	1.70	4.58	3.25	6.47											
Camp proc	0.42	2.61	1.28	0.91	2.76	3.15	-0.56	2.14	1.48	-0.60	-1.16	2.56	1.93	-0.19	0.30	3.90	1.57	5.25	1.97										
Auto ochr	0.54	-1.49	-0.59	-1.01	1.70	-0.55	1.20	-0.38	0.42	-0.57	-0.11	-0.85	-0.12	-1.49	0.42	-1.01	-0.82	0.84	1.85	-0.62									
Auto infu	-0.76	5.09	5.08	4.81	2.52	4.66	2.46	-0.73	0.43	1.85	0.53	-0.96	4.39	-0.07	3.18	4.27	0.51	2.51	5.68	0.60	4.44								
Perc rufi	0.95	0.66	0.77	1.97	0.95	0.26	0.81	0.00	1.52	-0.78	0.48	-0.41	2.52	2.67	-0.21	0.22	0.99	0.30	1.23	-0.21	1.05	0.69							
Pith albi	0.86	3.66	4.01	0.54	0.09	-0.03	0.98	0.21	0.03	0.12	0.15	-0.06	2.70	1.27	1.12	-1.14	1.21	-0.76	1.85	1.27	1.47	2.79	3.20						
Gym rufi	0.94	0.19	0.68	1.76	-1.10	-0.61	0.80	-0.50	-0.18	-0.75	0.01	1.66	1.75	0.24	-0.16	-1.26	-1.09	-0.75	-0.47	-0.83	0.50	-0.07	2.78	4.20					
Glyp spir	0.31	3.47	5.49	1.88	1.20	2.77	1.36	1.41	2.14	2.48	1.43	0.49	3.40	1.31	-0.46	-0.50	0.71	0.52	3.01	0.60	-0.70	0.43	2.04	2.65	1.42				
Tolm assi	2.35	1.19	7.42	2.97	2.74	4.33	0.97	0.42	0.59	3.17	6.35	4.35	3.06	1.26	1.05	-1.77	2.82	0.96	3.81	1.50	-1.00	-0.40	3.73	1.13	-1.13	4.96			
Micr coll	1.33	3.35	6.30	2.03	3.46	1.72	1.72	0.43	2.15	1.26	3.40	3.74	2.14	2.77	-0.70	-1.97	-0.06	-2.49	0.33	-1.38	-0.53	0.97	-0.67	2.53	-0.55	3.28	4.58		
Dend fuli	-0.54	-0.38	0.05	0.10	0.09	-1.36	0.26	0.99	0.77	2.30	-1.84	-0.71	0.27	-0.79	1.56	1.87	2.39	0.98	1.99	0.89	-1.01	0.32	1.15	1.43	1.77	-1.19	0.71	-0.83	

Table S3. Pairwise association strengths and group delimitation based on old-growth capture data. Groups resulting from the modularity analysis are outlined in black.

	Tham arde	Tham caes	Isle gutt	Epin gutt	Myrm long	Myrm mene	Deco long	Xiph pard	Tunc ochr	Myrm axil	Cert stic	Xeno minu	Auto infu	Mion macc	Glyp spir	Phil eryt	Myio barb	Micr coll	Tham muri	Perc rufi	Pith albi	Gymn rufi	Will poec	Dend meru
Tham caes	13.18																							
Isle gutt	-0.25	3.58																						
Epin gutt	13.17	8.55	5.99																					
Myrm long	13.70	17.67	-0.19	14.98																				
Myrm mene	7.06	3.22	-0.11	5.18	23.34																			
Deco long	4.85	-0.20	-0.07	7.51	-0.15	-0.09																		
Xiph pard	15.19	7.22	4.78	5.72	5.10	4.51	13.77																	
Tunc ochr	15.32	2.26	6.68	15.33	10.15	16.77	9.07	3.14																
Myrm axil	-0.19	-0.19	-0.07	-0.12	-0.14	-0.08	-0.06	-0.13	9.27															
Cert stic	2.07	1.99	-0.15	-0.28	9.23	5.61	-0.12	2.90	7.93	8.61														
Xeno minu	3.28	-0.29	-0.11	5.06	4.53	-0.12	-0.10	8.72	6.01	-0.09	10.81													
Auto infu	8.91	14.49	-0.13	-0.23	3.71	-0.14	-0.11	11.47	10.13	23.09	-0.21	6.73												
Mion macc	1.59	3.56	-0.18	-0.34	-0.36	-0.21	-0.15	-0.37	-0.30	-0.14	3.00	-0.22	3.66											
Glyp spir	3.44	1.19	2.47	4.27	6.59	4.61	3.22	2.06	3.16	-0.26	2.96	-0.42	-0.48	0.74										
Phil eryt	4.36	4.38	-0.07	6.70	-0.16	-0.08	-0.07	-0.17	7.56	-0.06	-0.14	-0.10	-0.11	-0.16	2.88									
Myio barb	-0.37	-0.37	-0.14	3.91	3.47	-0.16	-0.11	-0.29	-0.23	-0.11	4.13	6.04	-0.18	-0.26	5.44	7.70								
Micr coll	-0.27	-0.28	-0.10	-0.18	-0.20	-0.11	-0.08	-0.20	-0.16	-0.08	-0.17	-0.12	-0.14	-0.20	4.85	-0.09	-0.14							
Tham muri	-0.26	3.55	-0.09	-0.17	-0.19	-0.11	-0.08	-0.20	-0.15	-0.06	-0.17	-0.12	-0.14	-0.19	-0.37	-0.09	-0.15	-0.10						
Perc rufi	1.74	3.75	-0.17	2.87	-0.35	-0.20	-0.14	-0.36	-0.27	-0.13	-0.29	-0.20	-0.24	-0.35	0.90	-0.15	-0.26	-0.18	-0.18					
Pith albi	1.86	2.74	-0.40	0.73	1.82	-0.45	-0.33	-0.80	1.01	2.99	2.45	-0.47	-0.54	-0.79	1.92	-0.36	-0.58	1.90	-0.42	0.63				
Gymn rufi	-0.70	2.05	-0.27	1.63	3.28	-0.30	-0.22	1.31	-0.42	-0.20	-0.44	-0.32	2.37	-0.53	1.01	-0.24	-0.38	-0.29	-0.29	3.43	11.35			
Will poec	2.77	1.48	-0.33	-0.57	2.56	-0.35	-0.26	0.89	1.57	-0.24	-0.52	-0.38	-0.43	-0.62	0.48	-0.28	-0.48	-0.35	-0.33	6.04	3.97	0.18		
Dend meru	-0.49	1.52	-0.19	-0.33	-0.36	-0.22	-0.16	-0.38	-0.29	-0.13	2.83	-0.21	-0.27	2.30	-0.69	-0.16	-0.27	-0.20	4.81	5.32	9.77	5.14	-0.64	
Dend fuli	-0.27	-0.28	-0.10	-0.19	-0.20	-0.13	-0.09	-0.21	-0.17	-0.07	-0.17	-0.12	-0.15	-0.21	4.63	-0.09	-0.15	-0.11	-0.11	-0.20	-0.44	-0.29	-0.35	4.81

Table S4. Pairwise association strengths and group delimitation based on the combination of recording and capture data from old-growth sites. Groups defined by the modularity analysis are outlined in black. NAs are due to a lack of detection of both species with the same method, so it was not possible to measure this association index. Species within groups are ranked by phylogeny order.

	Picu flav	Tham arde	Tham caes	Isle gutt	Epin gutt	Myrm long	Myrm mene	Tunc ochr	Lani fulv	Myrm axil	Cert stic	Xeno minu	Auto ochr	Auto infu	Mion macc	Glyp spir	Phil eryt	Tolm assi	Myio barb	Micr coll	Tham muri	Sitt gris	Deco long	Dend cert	Dend picu	Hyle perr	Xiph pard	Cam proc	Perc rufi	Pith albi	Gym rufi	Will poec	Dend meru		
Tham arde	0.81																																		
Tham caes	3.66	14.75																																	
Isle gutt	NA	-0.25	3.58																																
Epin gutt	NA	13.17	8.55	5.99																															
Myrm long	1.79	12.16	15.17	-0.19	14.98																														
Myrm mene	1.87	11.64	9.32	-0.11	5.18	17.39																													
Tunc ochr	3.04	13.59	8.24	6.68	15.33	10.31	15.04																												
Lani fulv	4.46	5.03	9.60	NA	NA	2.34	3.64	7.35																											
Myrm axil	1.79	5.07	6.77	-0.07	-0.12	3.69	4.67	8.31	2.16																										
Cert stic	-0.50	1.71	1.57	-0.15	-0.28	4.35	4.86	4.37	-0.54	5.62																									
Xeno minu	0.82	4.72	1.37	-0.11	5.06	2.58	2.08	4.67	-0.35	1.10	6.08																								
Auto ochr	0.54	-1.49	-0.59	NA	NA	1.70	-0.55	-0.11	-0.85	-1.01	-0.38	0.42																							
Auto infu	-0.76	7.00	9.79	-0.13	-0.23	3.11	2.26	5.33	-0.96	13.95	-0.47	3.58	4.44																						
Mion macc	NA	1.59	3.56	-0.18	-0.34	-0.36	-0.21	-0.30	NA	-0.14	3.00	-0.22	NA	3.66																					
Glyp spir	0.31	3.46	3.34	2.47	4.27	3.89	3.69	2.29	0.49	0.81	2.18	0.86	-0.70	-0.02	0.74																				
Phil eryt	0.62	4.51	5.60	-0.07	6.70	2.15	1.80	6.75	0.46	1.09	-0.24	0.82	-0.57	0.87	-0.16	2.68																			
Tolm assi	2.35	1.19	7.42	NA	NA	2.74	4.33	6.35	4.35	2.97	0.42	0.59	-1.00	-0.40	NA	4.96	3.17																		
Myio barb	NA	-0.37	-0.37	-0.14	3.91	3.47	-0.16	-0.23	NA	-0.11	4.13	6.04	NA	-0.18	-0.26	5.44	7.70	NA																	
Micr coll	1.33	1.54	3.01	-0.10	-0.18	1.63	0.80	1.62	3.74	0.98	0.13	1.02	-0.53	0.41	-0.20	4.07	0.58	4.58	-0.14																
Tham muri	0.72	1.01	3.21	-0.09	-0.17	0.60	1.35	-0.13	2.78	0.52	0.25	-0.66	-0.12	2.13	-0.19	1.51	0.00	3.06	-0.15	1.02															
Sitt gris	1.40	0.50	2.32	NA	NA	1.12	1.91	-1.12	1.42	0.03	-0.95	1.00	-1.49	-0.07	NA	1.31	0.11	1.26	NA	2.77	5.45														
Deco long	-0.14	3.73	1.44	-0.07	7.51	0.26	0.15	4.81	1.47	1.09	-0.32	-0.19	0.42	1.54	-0.15	1.38	1.52	1.05	-0.11	-0.39	0.09	-0.51													
Dend cert	-0.69	0.42	1.04	NA	NA	-0.43	0.95	-2.01	-1.04	1.01	-1.07	2.32	-1.01	4.27	NA	-0.50	1.86	-1.77	NA	-1.97	3.46	0.75	5.27												
Dend picu	-1.05	1.13	0.11	NA	NA	0.71	1.64	1.36	-1.18	3.21	-0.51	0.66	-0.82	0.51	NA	0.71	-0.78	2.82	NA	-0.06	0.76	-1.51	-0.22	2.07											
Hyle perr	-0.01	0.38	-0.90	NA	NA	0.52	2.71	-0.45	1.10	0.35	-0.70	0.46	0.84	2.51	NA	0.52	0.95	0.96	NA	-2.49	4.27	-0.38	5.40	5.93	4.14										
Xiph pard	1.45	11.67	7.58	4.78	5.72	5.93	5.77	4.89	2.44	3.27	3.32	5.50	1.85	8.58	-0.37	2.53	1.74	3.81	-0.29	0.06	3.21	3.64	7.73	4.58	3.25	6.47									
Camp proc	0.42	2.61	1.28	NA	NA	2.76	3.15	-1.16	2.56	0.91	2.14	1.48	-0.62	0.60	NA	0.60	-0.60	1.50	NA	-1.38	1.93	-0.19	0.30	3.90	1.57	5.25	1.97								
Perc rufi	0.95	1.20	2.26	-0.17	2.87	0.30	0.03	0.10	-0.41	0.92	-0.14	0.66	1.05	0.23	-0.35	1.47	-0.47	3.73	-0.26	-0.43	1.17	2.67	-0.18	0.22	0.99	0.30	0.44	-0.21							
Pith albi	0.86	2.76	3.38	-0.40	0.73	0.96	-0.24	0.58	-0.06	1.76	1.33	-0.22	1.47	1.13	-0.79	2.29	-0.12	1.13	-0.58	2.22	1.14	1.27	0.40	-1.14	1.21	-0.76	0.53	1.27	1.92						
Gym rufi	0.94	-0.26	1.36	-0.27	1.63	1.09	-0.46	-0.21	1.66	0.78	-0.47	-0.25	0.50	1.15	-0.53	1.22	-0.49	-1.13	-0.38	-0.42	0.73	0.24	-0.19	-1.26	-1.09	-0.75	0.42	-0.83	3.11	7.78					
Will poec	-1.71	1.82	2.01	-0.33	-0.57	0.37	0.22	0.98	1.02	0.49	-0.01	-0.22	1.20	1.02	-0.62	0.92	0.11	0.97	-0.48	0.69	0.75	1.27	0.74	0.08	-0.58	-0.17	0.42	-0.56	3.43	2.47	0.49				
Dend meru	NA	-0.49	1.52	-0.19	-0.33	-0.36	-0.22	-0.29	NA	-0.13	2.83	-0.21	NA	-0.27	2.30	-0.69	-0.16	NA	-0.27	-0.20	4.81	NA	-0.16	NA	NA	NA	-0.38	NA	5.32	9.77	5.14	-0.64			
Dend fuli	-0.54	-0.33	-0.12	-0.10	-0.19	-0.06	-0.74	-1.00	-0.71	0.01	0.41	0.33	-1.01	0.08	-0.21	1.72	1.11	0.71	-0.15	-0.47	0.08	-0.79	0.74	1.87	2.39	0.98	0.89	0.89	0.48	0.49	0.74	-0.05	4.81		

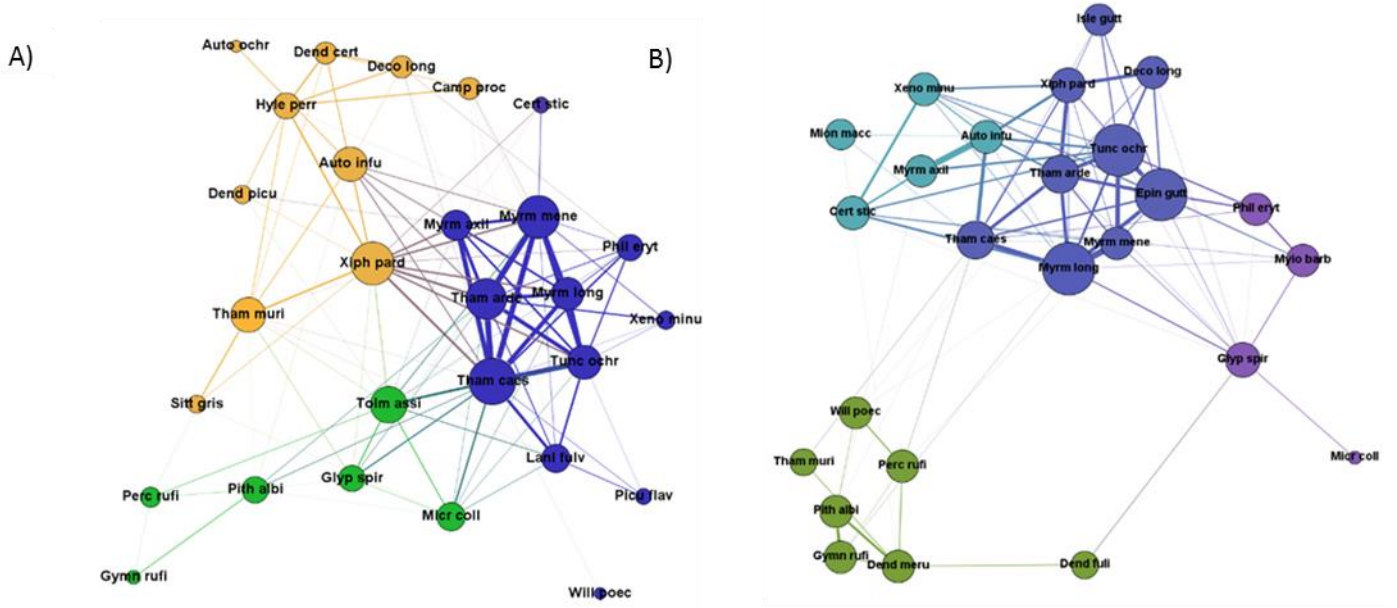


Fig. S1. Interspecific association network based on the audio recording (A) and mist-net capture (B) data from old-growth sites. Eight-letter codes indicate species listed in Figure 3. Network nodes are interacting species and are represented by circles with size proportional to the number of edges connecting the node species with other species. Edge width is proportional to the association strength. The colors represent species groups given by the network modularity analysis.

Table S5. Association strengths and group delimitation for secondary forest based on audio data. Modules are delimited by the black rectangles. Species with gray shading were not included in the modularity analysis. Ranking within groups follows the South American Classification Committee list.

	Tham arde	Tham caes	Myrm axil	Myrm mene	Dend cert	Auto infu	Tolm assi	Tham muri	Perc rufi	Glyp spir	Xiph pard	Auto ochr	Pith albi	Gymn rufi	Will poec	Sitt gris	Dend fuli
Tham caes	10.53																
Myrm axil	4.79	5.90															
Myrm mene	9.32	11.32	5.19														
Dend cert	3.08	1.97	-0.52	1.36													
Auto infu	9.02	7.12	5.75	8.86	3.29												
Tolm assi	3.67	6.34	0.09	3.32	-0.01	4.34											
Tham muri	-0.98	0.40	1.65	0.94	0.97	2.52	-0.46										
Perc rufi	0.11	0.01	-0.18	-1.01	-1.25	0.31	-1.35	6.69									
Glyp spir	3.70	2.54	0.59	1.70	0.36	2.87	2.34	2.13	0.63								
Xiph pard	3.00	5.57	1.69	5.35	1.89	3.46	3.01	3.19	0.44	1.64							
Auto ochr	1.19	-1.39	-0.29	-1.09	0.89	-1.13	-0.61	4.63	0.42	2.86	3.25						
Pith albi	2.39	2.17	-0.52	1.52	-0.18	2.80	2.84	0.78	2.33	-1.05	0.47	-0.53					
Gymn rufi	-0.74	1.70	-0.68	-0.63	-0.84	-0.68	-0.12	0.39	0.72	0.73	0.69	-0.75	3.14				
Will poec	0.51	0.57	0.73	0.03	-0.55	0.68	0.72	0.87	-0.24	0.64	-0.08	-1.14	0.25	3.69			
Sitt gris	0.28	0.27	-0.84	-0.75	0.15	-0.84	0.35	1.00	0.50	-0.54	0.20	0.34	-1.02	-0.52	-0.79		
Dend fuli	-0.79	0.91	0.89	1.08	0.52	2.48	0.00	0.55	-0.48	-0.09	-0.17	-0.66	0.55	-0.42	-0.67	1.42	
Micr coll	0.67	0.89	-0.69	1.05	-0.83	-0.72	-1.09	2.06	1.59	1.97	-1.16	-0.67	2.05	2.01	0.83	-0.50	2.09

Table S6. Association strengths and group delimitation for secondary forest based on capture data. Modules are delimited by the black rectangles. Species ranking within groups follows the South American Classification Committee list.

	Tham caes	Myrm axil	Xiph pard	Xeno minu	Auto infu	Tham muri	Tham arde	Perc rufi	Auto ochr	Mion macc	Epin gutt	Dend meru	Dend fuli	Glyp spir	Myio barb	Pith albi	Gymn rufi
Myrm axil	-0.42																
Xiph pard	-0.43	3.20															
Xeno minu	4.45	-0.15	7.38														
Auto infu	16.07	3.37	10.54	-0.11													
Tham muri	-0.33	-0.22	-0.25	-0.12	3.76												
Tham arde	10.60	-0.27	-0.24	-0.11	8.23	4.31											
Perc rufi	2.89	2.18	-0.38	-0.20	-0.39	6.05	-0.37										
Auto ochr	2.38	-0.23	-0.25	-0.13	3.76	5.10	8.77	2.73									
Mion macc	-0.46	-0.29	-0.32	-0.16	2.95	3.24	3.18	-0.43	3.32								
Epin gutt	13.27	-0.24	2.97	-0.14	-0.26	-0.23	10.64	7.70	3.89	-0.33							
Dend meru	-0.38	-0.25	-0.27	-0.13	-0.25	-0.20	-0.23	-0.35	-0.18	-0.27	12.98						
Dend fuli	-0.26	-0.13	-0.19	-0.06	-0.16	-0.16	-0.15	-0.23	-0.15	4.83	-0.16	6.66					
Glyp spir	4.08	1.35	-0.50	-0.26	-0.56	1.73	1.51	0.56	1.72	0.96	8.76	-0.47	-0.30				
Myio barb	-0.23	-0.18	-0.15	-0.07	-0.14	-0.11	-0.17	-0.23	-0.16	-0.17	-0.16	-0.13	-0.12	6.13			
Pith albi	6.08	-0.82	1.52	-0.41	1.62	0.75	1.99	2.46	2.08	-0.90	0.34	3.23	-0.48	-0.99	-0.47		
Gymn rufi	0.89	-0.41	-0.45	-0.22	-0.44	-0.34	9.25	0.99	2.15	-0.50	-0.46	2.19	-0.29	0.26	-0.27	7.59	
Will poec	-0.65	-0.40	6.21	-0.22	4.22	-0.34	-0.38	6.37	2.06	-0.45	6.66	2.14	-0.25	2.75	-0.25	7.31	3.82



Table S7. Association strengths and group delimitation for secondary forest based on the combination of audio and capture data. Modules are delimited by the black rectangles. Species with gray shading were not included in the modularity analysis. We could only analyze species pairs where both species of the pair had ten or more detections for at least one of the sampling techniques. When this happened, we wrote ‘NA’ in the corresponding cell and excluded this association from the network analysis. Species within groups are ranked according to the South American Classification Committee list.

	Tham arde	Tham caes	Myrm axil	Myrm mene	Dend cert	Xiph pard	Xeno minu	Auto infu	Tolm assi	Tham muri	Epin gutt	Perc rufi	Dend meru	Dend fuli	Glyp spir	Auto ochr	Mion macc	Myio barb	Pith albi	Gymn rufi	Will poec	Sitt gris	
Tham caes	10.56																						
Myrm axil	2.26	2.74																					
Myrm mene	9.32	11.32	5.19																				
Dend cert	3.08	1.97	-0.52	1.36																			
Xiph pard	1.38	2.57	2.44	5.35	1.89																		
Xeno minu	-0.11	4.45	-0.15	NA	NA	7.38																	
Auto infu	8.62	11.60	4.56	8.86	3.29	7.00	-0.11																
Tolm assi	3.67	6.34	0.09	3.32	-0.01	3.01	NA	4.34															
Tham muri	1.67	0.04	0.72	0.94	0.97	1.47	-0.12	3.14	-0.46														
Epin gutt	10.64	13.27	-0.24	NA	NA	2.97	-0.14	-0.26	NA	-0.23													
Perc rufi	-0.13	1.45	1.00	-1.01	-1.25	0.03	-0.20	-0.04	-1.35	6.37	7.70												
Dend meru	-0.23	-0.38	-0.25	NA	NA	-0.27	-0.13	-0.25	NA	-0.20	12.98	-0.35											
Dend fuli	-0.47	0.32	0.38	1.08	0.52	-0.18	-0.06	1.16	0.00	0.20	-0.16	-0.36	6.66										
Glyp spir	2.60	3.31	0.97	1.70	0.36	0.57	-0.26	1.15	2.34	1.93	8.76	0.60	-0.47	-0.19									
Auto ochr	4.98	0.49	-0.26	-1.09	0.89	1.50	-0.13	1.32	-0.61	4.86	3.89	1.58	-0.18	-0.40	2.29								
Mion macc	3.18	-0.46	-0.29	NA	NA	-0.32	-0.16	2.95	NA	3.24	-0.33	-0.43	-0.27	4.83	0.96	3.32							
Myio barb	-0.17	-0.23	-0.18	NA	NA	-0.15	-0.07	-0.14	NA	-0.11	-0.16	-0.23	-0.13	-0.12	6.13	-0.16	-0.17						
Pith albi	2.19	4.13	-0.67	1.52	-0.18	1.00	-0.41	2.21	2.84	0.76	0.34	2.40	3.23	0.03	-1.02	0.77	-0.90	-0.47					
Gymn rufi	4.26	1.29	-0.54	-0.63	-0.84	0.12	-0.22	-0.56	-0.12	0.03	-0.46	0.86	2.19	-0.36	0.49	0.70	-0.50	-0.27	5.37				
Will poec	0.07	-0.04	0.16	0.03	-0.55	3.07	-0.22	2.45	0.72	0.27	6.66	3.07	2.14	-0.46	1.69	0.46	-0.45	-0.25	3.78	3.75			
Sitt gris	0.28	0.27	-0.84	-0.75	0.15	0.20	NA	-0.84	0.35	1.00	NA	0.50	NA	1.42	-0.54	0.34	NA	NA	-1.02	-0.52	-0.79		
Micr coll	0.67	0.89	-0.69	1.05	-0.83	-1.16	NA	-0.72	-1.09	2.06	NA	1.59	NA	2.09	1.97	-0.67	NA	NA	2.05	2.01	0.83	-0.50	

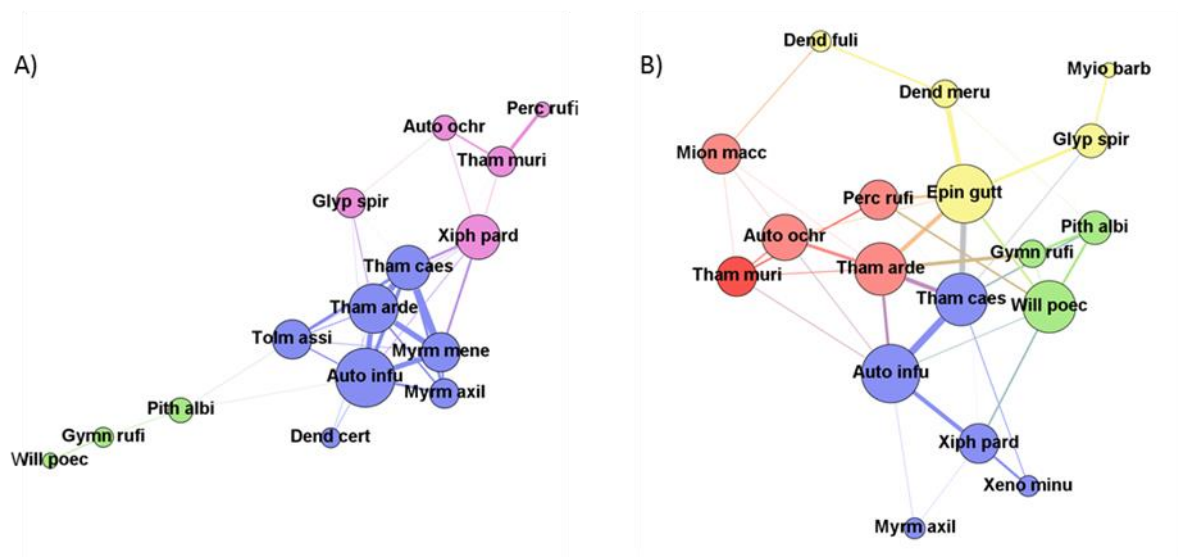


Fig. S2. Interspecific association network based on audio (A) and capture (B) data from secondary forest sites. Eight-letter codes indicate species listed in Fig. 3. Circle (node) size is proportional to the number of edges connecting focal species with other species. Edge width is proportional to the association strength. The colors represent species groups given by the network modularity analysis.

Table S8. Group-level association strengths for secondary forest based on combined audio and capture data. Black and gray numbers show, respectively, the arithmetic mean and variance of strong associations within and between the groups listed on the sides of the triangular matrix. Group labels correspond to the SF-Core (SF-C), SF-Attendant (SF-A), and SF-Ant-follower (SF-AF) groups defined by the modularity analysis. The three columns on the right show group-specific values for the number of species (N), the number of strong associations within group (SL), and the ratio of strong associations per species (SL/N).

	SF-Core (SF-C)	SF-Attendant (SF-A)	SF-Ant Follower (SF-AF)	sps (N)	strong links (SL)	SL/N
SF-C	6.03 (16.20)			9.00	21.00	2.33
SF-A	5.23 (15.42)	6.25 (8.10)		9.00	11.00	1.22
SF-AF	3.57 (0.52)	4.32 (4.32)	4.30 (0.85)	3.00	3.00	1.00

## **CLOSING REMARQUES**

The results that succeed from this work suggest that we are able to study group structure of social associations between understory birds in Amazonian forest from indirect observations. Indeed, we were able to find the evidence of non-random inter-specific encounter within bird species based on data collected with automated sound recording and mist-netting capture. We found many strong associations between species. From those, we were able to delimit groups of species more often associated than by chance with ecological meanings. Those groups were confirmed by previous classifications from other studies.

In addition, our second objective was to be able to observe a change in association with habitat disturbance, and that is what we successfully observed. We found that some species were detected less or not at all in secondary forest. Also, many of the associations between species observed in old-growth forest breaks down in secondary forest; which was a proof of a non-stability of those associations. In the end, our work show that social associations between understory Amazonian bird species was highly sensitive to habitat disturbance.

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