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Decay of interspecific avian flock networks along a disturbance gradient in Amazonia

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Our understanding of how anthropogenic habitat change shapes species interactions is in its infancy. This is in large part because analytical approaches such as network theory have only recently been applied to characterize complex community dynamics. Network models are a powerful tool for quantifying how ecological interactions are affected by habitat modification because they provide metrics that quantify community structure and function. Here, we examine how large-scale habitat alteration has affected ecological interactions among mixed-species flocking birds in Amazonian rainforest. These flocks provide a model system for investigating how habitat heterogeneity influences non-trophic interactions and the subsequent social structure of forest-dependent mixed-species bird flocks. We analyse 21 flock interaction networks throughout a mosaic of primary forest, fragments of varying sizes and secondary forest (SF) at the Biological Dynamics of Forest Fragments Project in central Amazonian Brazil. Habitat type had a strong effect on network structure at the levels of both species and flock. Frequency of associations among species, as summarized by weighted degree, declined with increasing levels of forest fragmentation and SF. At the flock level, clustering coefficients and overall attendance positively correlated with mean vegetation height, indicating a strong effect of habitat structure on flock cohesion and stability. Prior research has shown that trophic interactions are often resilient to large-scale changes in habitat structure because species are ecologically redundant. By contrast, our results suggest that behavioural interactions and the structure of non-trophic networks are highly sensitive to environmental change. Thus, a more nuanced, system-by-system approach may be needed when thinking about the resiliency of ecological networks.

1. Introduction

Biological systems are often organized as networks [1–3] and while these networks are nearly ubiquitous, analytical approaches have only recently been applied to identify common properties and understand system-level dynamics. In its simplest form, a biological network can be represented as a graph comprising nodes (individuals or species) and edges (biological interactions). Network theory offers the ideal conceptual framework to understand the structural complexity of biological systems, because it provides metrics to quantify and interpret interactions at the level of individuals or species, and documents the properties of the system as a whole [4]. Ultimately, these approaches have advanced our understanding of a variety of complex biological processes and types of interactions such as mutualisms [5], trophic interactions [6], fitness consequences of social behaviour [7,8], disease transmission [9] and robustness of communities to extinction [10].

Networks of trophic interactions have been the focus of a substantial body of research [6,11]. The structure of these networks can be influenced not only by

intrinsic traits of participating organisms (e.g. phenotype) but also by extrinsic characteristics of the environment (e.g. habitat heterogeneity). For example, habitat modification affects trophic network structure via changes in species richness and frequency of interactions [12]. Previous work has shown that most ecological networks are resilient to environmental change, but that the threshold at which a community collapses is dependent upon the degree to which species are ecologically redundant and the responses of keystone species to habitat loss [5,10,13]. While trophic networks have been fairly well studied, non-trophic interactions, such as the social mutualisms observed in avian mixed-species flocks, have received considerably less attention. Ultimately, by characterizing the roles that species play within ecological networks we can begin to understand the assembly of ecological communities [14], the predisposition for species to engage in non-random spatio-temporal aggregations [15] and how those ecological and evolutionary processes are influenced by environmental change.

Mixed-species flocks are among the most complex multi-species aggregations found in terrestrial vertebrates [16]. Some forms of mixed-species flocking occurs throughout the world, but few reach the temporal stability and interdependency of understory mixed-species flocks in Amazonian rainforests. These flocks of insectivores have a year-round territory and consist of a core of eight to 10 obligate species, each represented by a breeding pair. The territories of these core species overlap in a flock territory of 8–10 ha [16–18]. Cinerous antshrikes (*Thamnomanes caesioides*) play a nuclear role in these mixed-species flocks throughout the Amazon basin [19] by rallying individuals and giving alarm calls [20]. Up to 50 other species, mostly in breeding pairs, are known to join the core flock in varying periodicity [17]. Given that flocks are often species-rich and exhibit both spatial and temporal stability [21], they represent an important component of the Amazonian understory avifauna [22]. Flocks provide direct fitness benefits in participating birds, including improved predator detection and increased foraging efficiency [23], yet these benefits may vary by species and be strongly dependent upon habitat context and flock organization.

The Amazon provides an important setting to examine changes in interspecific avian interactions, because the area is subjected to substantial forest clearing which produces heterogeneous landscapes of primary forest (PF), secondary forest (SF), forest fragments, and interspersed roads [24]. These newly fragmented and regenerating Amazonian forests influence the dynamics [25–27] and diversity of avian communities [28]. Given that mixed-species flocks in the Amazon are largely forest dependent, they are highly susceptible to habitat disturbances. For example, most flock species avoid open areas, show reluctance to cross narrow roads [18], and often disappear in selectively logged forests [29] and small fragments [25,30]. Despite the detrimental effect of forest clearing on these species, depauperate flocks can still be detected in second-growth and small fragments [31]. To date, research on how mixed-species flocks change along disturbance gradients have largely focused on species richness and encounter rates (e.g. number of detections per unit time [32,33]), yet no studies, to our knowledge, have examined how habitat modifications influence interspecific interactions and the stability of flock structure.

Understanding how both species interactions and the subsequent structure of ecological networks change across landscape gradients are important because flocks can affect

community dynamics and the fitness of participating species. To date, accurately characterizing interactions within mixed-species flocks has remained challenging because flock attendance is dynamic (i.e. many individuals join and leave a flock in both time and space). The analytical framework of network theory can advance our understanding of flock dynamics by characterizing changes at multiple levels of organization (species, i.e. node level and flock, i.e. network level). Here, we apply network theory to examine how individual species' interactions and flock-level structure change across a heterogeneous landscape mosaic in the Amazon. First, at the species level, we compare how the number (degree) and frequency (weighted degree) of interspecific interactions within mixed-species flocks varied among PF, 100 ha fragments (100 ha), 10 ha fragments (10 ha), a mix of primary and secondary forest (PSF) and SF. Second, we examine how environmentally induced changes at the species-level scale-up to influence flock-level network properties. In particular, we characterize how the connectedness (the distribution of interactions) and cohesion (clustering of species) of flocks change across a landscape gradient. Third, we examine the relationship between vegetation structure and network cohesion as one possible mechanism for changes in social structure among habitats. Given the changes in flock structure among habitats, we also compared species attendance among habitat types to determine whether network differences were causing species disappearance or reduction in flock attendance. This work builds a framework for understanding how environmental heterogeneity affects the resilience of complex ecological interactions by examining the integrity and stability of flock networks across a habitat mosaic.

2. Material and methods

(a) Study site and data collection

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) in central Amazonia, Brazil. Fragments were isolated between 1980 and 1990 during the settlement of cattle ranches [34,35]. Following initial clear-cutting, some areas were burned to create pastures while others were abandoned. Most pastures were inactive by the 1990s, allowing the matrix around the fragments to regenerate. A buffer of 100 m was cleared around some fragments from the early 1990s to the early 2000s, but these areas have regenerated as well. Different management histories have created a structurally heterogeneous landscape [36], with fragments of different sizes surrounded by SFs varying in structure and age.

Understory mixed-species flocks gather in the same location every day at dawn and move through their territory until about 13 min prior to sunset [17]. Flock activity is conspicuous, allowing birds to be followed on foot from a distance of 10–20 m. Importantly, the mixed-species flocks described here should be differentiated from those observed at army-ant swarms, which comprise solitary species that become spatially aggregated around a resource. We followed 21 flocks for at least 17 h each (mean = 42.1, max. = 121.4, min. = 17.1), totalling 693 h between March and November of 2010 and 2011. We recorded flock composition in 30 min time blocks, generating a total of 12 414 species entries. A species was noted as participating with a flock if it was seen within 15 m of core flock activity for more than 30 min. To assess that we had adequately sampled flocks in each habitat, we constructed 'sample-based' species accumulation rarefaction curves using the program ESTIMATE S [37] (see the electronic supplementary material, figure S1). Based on

flock sampling criteria, we also used the program ESTIMATES and the frequencies of species in the original sampling data to generate a non-parametric estimator of species richness (Chao II) [37,38]. Likewise, we estimated encounter rate as the number of times a species was detected corrected for total sampling time.

(b) Habitat and vegetation characterization

To measure flock territories, flock positions were recorded at 30 s intervals with a Garmin eTrex Vista HCx unit (approx. 10 m resolution). A quadratic kernel was generated using Geospatial Modeling Environment software [39], 99% isopleth was generated at 1 m resolution, 275 bandwidth at default scaling factor. Vegetation was measured using LIDAR (Light Detection and Ranging) canopy height models provided by Scott Saleska (University of Arizona) and Michael Lefsky (Colorado State University). We generated the zonal statistics for the vegetation located inside the isopleth (see the electronic supplementary material, table S1).

Flock territories were categorized in five habitat types: PF, if flocks used more than half of the territory in continuous PF; 100 ha, if flocks inhabited a 100 ha fragment; 10 ha, these fragments are only large enough for one flock territory; PSF mix, if flocks used more than half of their territory in degraded SF and patches of semi-isolated PF; and SFs, if a territory was exclusively in SF. Mean vegetation height was used as an indication of habitat structure and quality.

(c) Network and statistical analyses

We constructed networks for mixed-species flocks in all five habitat types. Based on species co-occurrences in each time block, we used the cumulative frequency of associations to construct weighted networks for each flock. Specifically, network edges were defined using species co-occurrences within sampling time blocks. As such, any species associated with the flock aggregation is by default associating with all species present in that sampling time block. Hereafter, we use the term 'interspecific association' to describe these interactions. Using spatial proximity to define network associations in this manner is termed the 'gambit of the group' such that all individuals within a spatial and temporal range will have reciprocal ties in the network [40,41]. Although, many species will appear accidentally in flocks, our threshold (30 min sampling time blocks) removes accidental species, which do not accompany the flock for more than a few metres. We chose not to apply filtering techniques to remove low-frequency co-occurrences, because we used weighted network metrics and were interested in how common and rare species influenced network structure across habitat types. Moreover, data from replicates of independent flocks within habitat types should produce more precise measures of network co-occurrence.

At the species level, for each flock, we calculated unweighted and weighted degree metrics using UCINET [42] and the R package tnet [43]. Degree is the number of edges (co-occurrences) one given species (network node) maintains with other species in a flock (i.e. species connectedness). Weighted degree is the sum of the frequency of interspecific associations for each node. Networks were visualized using R package 'network' [44]. We calculated the average network degree following [45], the degree distribution skewness using R package moments [46] and global weighted clustering coefficients following [47] using the tnet package in R. To ensure that interspecific associations and network structure could be differentiated from random, we used iterative permutation procedures (for methods and results, see the electronic supplementary material). Network metrics for replicate flocks were grouped within habitat type for subsequent analyses (see above).

We used a suite of analyses to examine the effect of habitat on species- and flock-level network properties. First, we looked at the

response of species richness and encounter rate to habitat type. To examine how species richness (Chao II estimator) varied by habitat type, we used a GLMM (generalized linear mixed model) with flock as a random effect and habitat as a fixed effect. All GLMM models used Poisson error distributions and log-link functions unless otherwise noted (see below). To examine how encounter rate (detections per unit time) varied by habitat, we used a zero-inflated negative binomial mixed model to account for over-dispersion in the data. The residuals of all models were normally distributed and we compared the effects of habitat type with null models using likelihood ratio tests.

Second, we used GLMMs to examine how habitat influenced species-level network metrics (i.e. degree and weighted degree). Given that network data are not independent [48], we used flock replicates within each habitat type and included flock identity as a random effect and habitat as a fixed effect to explain variation in degree and weighted degree. To compare across networks in different habitats, we accounted for the number of possible species interactions and sampling time using a log (n or t) offset [49] where n represents the number of possible interspecific associations within the network ($n - 1$, number of nodes) and t represents sampling time. These corrections enabled us to compare networks with different number of species (nodes) and sampling effort, which is a common problem in network analyses [40]. Hereafter, we report the corrected values of normalized degree [50] and weighted degree (i.e. frequency of associations are corrected by sampling time). Maximum-likelihood estimates of β coefficients and p -values for fixed effects from each model are reported.

Third, to examine how flock-level network properties varied by habitat type, we compare the distribution of species interspecific associations (degree distributions) using Wilcoxon sign-rank tests (see the electronic supplementary material). In addition, given that there was substantial variation in habitat structure among replicates (see the electronic supplementary material, table S1) we used least-squares regression to examine how a continuous measure of habitat, vegetation height, influenced flock attendance and cohesion as measured by weighted clustering coefficients. We used the base package of program R for regressions and lme4 [51] and glmmADMB [52] for GLMMs. Graphs were generated using gplot2 [53].

Finally, we estimated changes in species participation by using detections within each flock. We used PF as the template for comparison under the assumption that it represents baseline flock species composition and attendance rates. To differentiate between species disappearance and decreased attendance, we compared presence/absence and attendance data from altered habitat (100 ha, 10 ha, PSF and SF) to those observed in PF. We used all possible pairwise combinations of PF flocks and those in other habitats. For example, the comparison of PF (nine flocks) and SF (three flocks) would generate 27 values. We report percentages of species that disappeared (if only one species was present in a determined habitat type) or decreased attendance (if both species were present in both habitat types) relative to PF. Because some novel species appear in certain habitats and other increase in attendance, reported values do not sum to 100%. The magnitude of change in attendance is reported as averages across flocks sampled in each habitat type where negative values represent decreases.

3. Results

We sampled 21 flocks across five habitat types with each habitat type receiving a minimum of 86 h (table 1 and electronic supplementary material, S1). Habitat was a good predictor of both species richness ($\chi^2 = 15.85$, $p = 0.003$) and encounter rate ($\chi^2 = 11.92$, $p = 0.017$) as evidenced by those models being better fit than null models (see the electronic supplementary

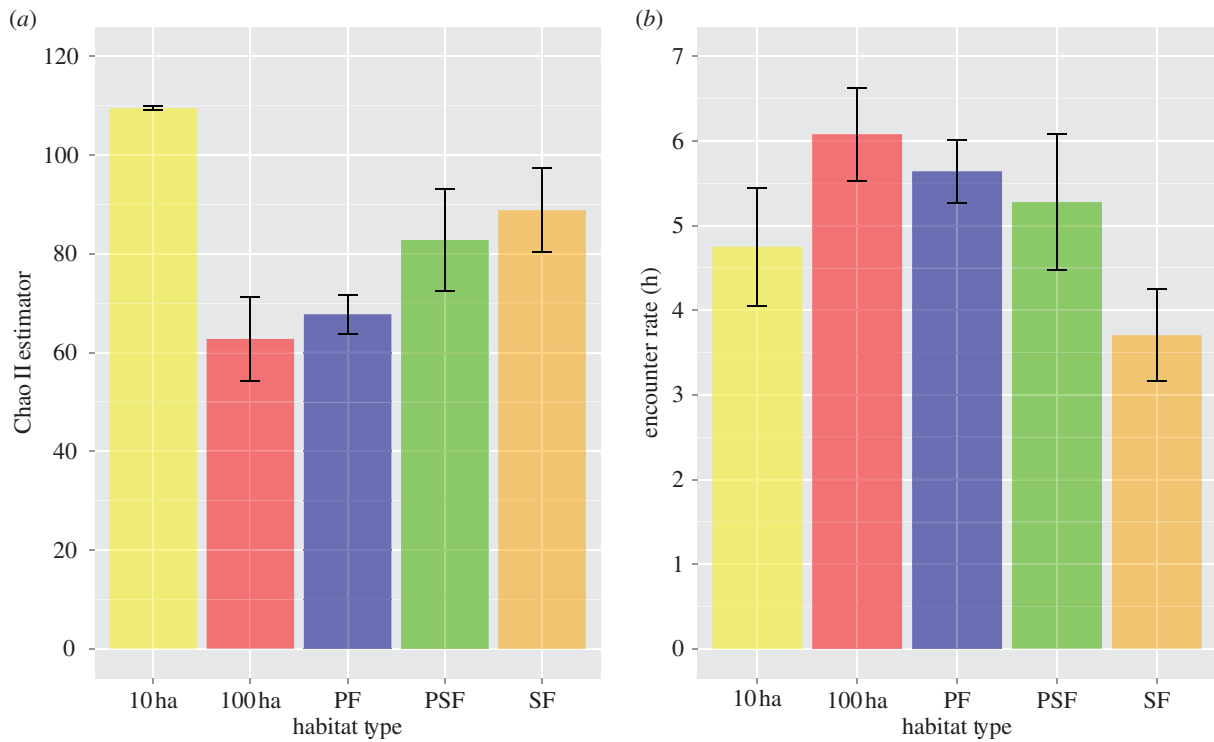


Figure 1. Mixed-species flocks showed substantial variation in both (a) species richness and (b) encounter rate across a habitat gradient in the Brazilian Amazon. Bars represent mean \pm s.e. (Online version in colour.)

Table 1. Summary of sampling for mixed-species flocks in five habitat types at the BDFFP in central Amazonian Brazil.

habitat type	<i>n</i> flocks	canopy		sampling time (h) ^a	attendance	no. spp. ^b
		max. ht. (m)	avg. ht. (m)			
primary forest	9	45.7 \pm 1.5	23.8 \pm 0.35	304.0	851.9 \pm 51.1	109
100 ha fragment	5	46.3 \pm 1.3	21.4 \pm 1.2	151.5	918.0 \pm 60.5	88
10 ha fragment	2	45.0 \pm 5.6	16.4 \pm 1.8	134.5	717.3 \pm 22.2	103
primary-secondary	2	40.4 \pm 3.7	16.8 \pm 0.90	86.0	797.0 \pm 19.9	79
secondary forest	3	39.1 \pm 5.5	14.4 \pm 1.97	88.0	559.5 \pm 121.4	82

^aTotal sampling time.

^bCumulative number of species observed during sampling.

material, table S2). Species richness was significantly higher in 10 ha fragments than in intact habitats ($\beta_{100\text{-ha}} = -0.56$, $p = 0.0003$; $\beta_{\text{PF}} = -0.48$, $p = 0.0001$; figure 1a). By contrast, more intact forest environments (e.g. PF and 100 ha) had higher encounter rates than 10 ha fragments and SF after controlling for sampling effort ($\beta_{100\text{-ha}} = 0.88$, $p = 0.003$; $\beta_{\text{PF}} = 1.01$, $p = 0.0002$; figure 1b).

Models constructed to test for the effect of habitat type on interspecific associations showed that environmental heterogeneity influenced species-level network metrics. Specifically, models that included habitat were a significantly better fit than null models for both normalized degree ($\chi^2 = 22.28$, $p = 0.0002$) and weighted degree ($\chi^2 = 15.69$, $p = 0.003$; see the electronic supplementary material, table S3). Flocking species in PF and 100 ha fragments associated with a proportionately greater number of other species (normalized degree) than did species in degraded habitats (table 2 and figure 2a). Likewise, flocks in less disturbed areas also had a higher frequency of interspecific associations (weighted degree) than did flocks in

degraded habitats (table 2 and figure 2b). Flock identity (random effect) explained only a small portion of the variance in our models, suggesting that results are consistent across habitat-type replicates.

Organization of flock networks differed across different habitat types (figure 3). A consistent group of core species, particularly *Thamnomanes caesius*, *Xyphorhynchus pardalotus* and *Myrmotherula axillaris*, was present across all habitat types, but the complexity of the network was far greater in PF than in 10 ha fragments and SF. An examination of cumulative degree distributions revealed habitat-specific differences in global network structure (figure 4). Networks in degraded forest habitats were composed of many weakly associated birds (low degree) with few well-connected species (high degree), which resulted in flocks with low median normalized degree and degree distributions with strong positive skew (i.e. long-tail to the distribution; figure 4c–e; electronic supplementary material, table S4). In comparison, networks in PFs and 100 ha fragments had a higher median normalized

Table 2. Parameters estimates and p -values from models examining the effect of habitat type on mixed-species flock network structure at the BDFFP in central Amazonian Brazil.

habitat	normalized degree		weighted degree	
	β	p -value	β	p -value
100 ha	0.57	0.0001	0.88	0.003
primary forest	0.45	0.0002	1.01	0.002
primary-secondary	0.25	0.11	0.70	0.05
secondary forest	-0.004	0.98	-0.06	0.84

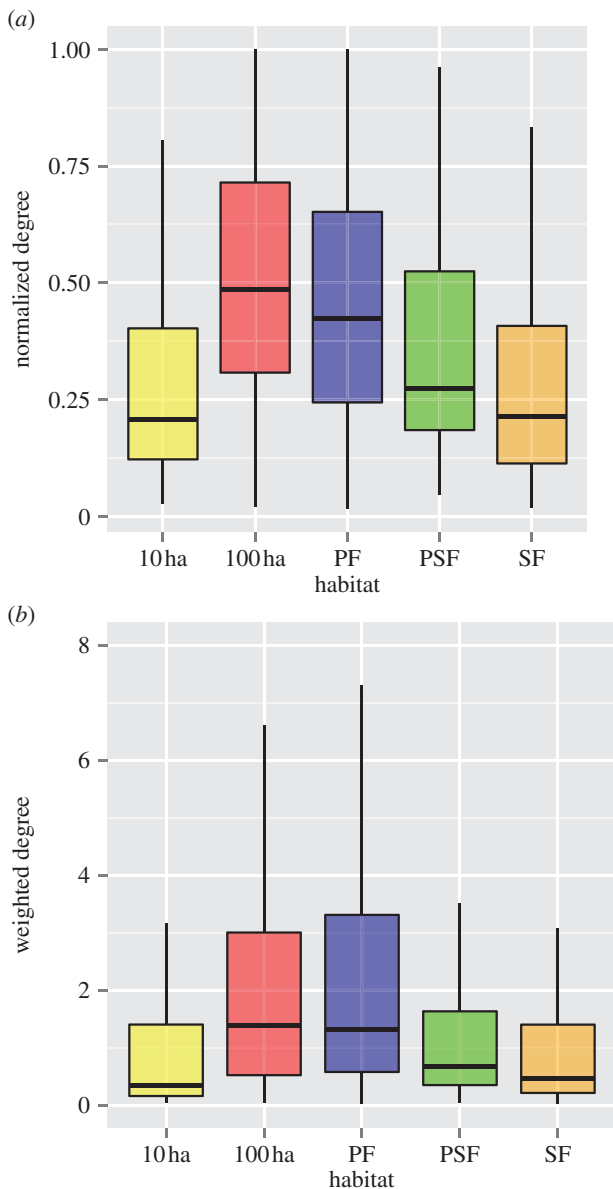


Figure 2. Box plots show that species in mixed-species flocks in more preserved habitats (PF and 100 ha) (a) had a greater number of interspecific interactions (normalized degree) and (b) a higher frequency of interactions (weighted degree) than in degraded forest habitats (SF, PSF and 10 ha). (Online version in colour.)

degree and weaker positive skew (figure 4*a,b*; electronic supplementary material, table S4). Differences in social structure at the level of the flock appear to be in part, driven by

vegetation characteristics. Vegetation height was positively correlated with flock cohesion as measured by species attendance patterns ($r^2 = 0.37$, $F_{1,19} = 11.08$, $p = 0.003$; figure 5*a*) and global clustering coefficients ($r^2 = 0.50$, $F_{1,19} = 19.07$, $p = 0.0003$; figure 5*b*).

A comparison of presence/absence data and species attendance between disturbed and PF habitats shows that decreased attendance rather than disappearance is the primary driver of differences in network structure (table 3). Specifically, a relatively small proportion of species were absent in disturbed habitats (2–12%), whereas nearly half of species detected in both habitats decreased attendance rates (47–56%) relative to PFs. The magnitude of change was largest in the two most degraded habitat types (e.g. 10 ha and SF; table 3).

4. Discussion

Interspecific interactions in communities are an essential component of ecosystem function and have important implications for the ecological and evolutionary dynamics of species [54]. To date, research on trophic interaction networks has shown that habitat changes can affect interspecific networks, yet their structure is often resilient to habitat change because species are ecologically redundant [10,55,56]. Our results corroborate that the interspecific associations which comprise flock networks are also affected by habitat degradation. While little is known about the functional roles of species within flocks, our results suggest that flock social structure may be comparatively more sensitive than other ecological networks studied to date. Here, we document changes in species richness, encounter rates, species connectedness and the frequency of interspecific associations within mixed-species flocks along a habitat mosaic. Our results suggest that habitat modification and changes in vegetation structure alter flock attendance and subsequent interspecific associations resulting in reduced flock cohesion and stability. Given that mixed-species flocks host a diversity of understory insectivorous birds, these results highlight the potential negative impact of habitat alteration on the dynamics of species interactions.

(a) Species- and flock-level changes in network structure

Multi-species interactions form the basis of ecological networks, and changes in species presence or behaviour can have profound impacts on network structure and ecosystem function [57]. Research on food webs suggests that habitat

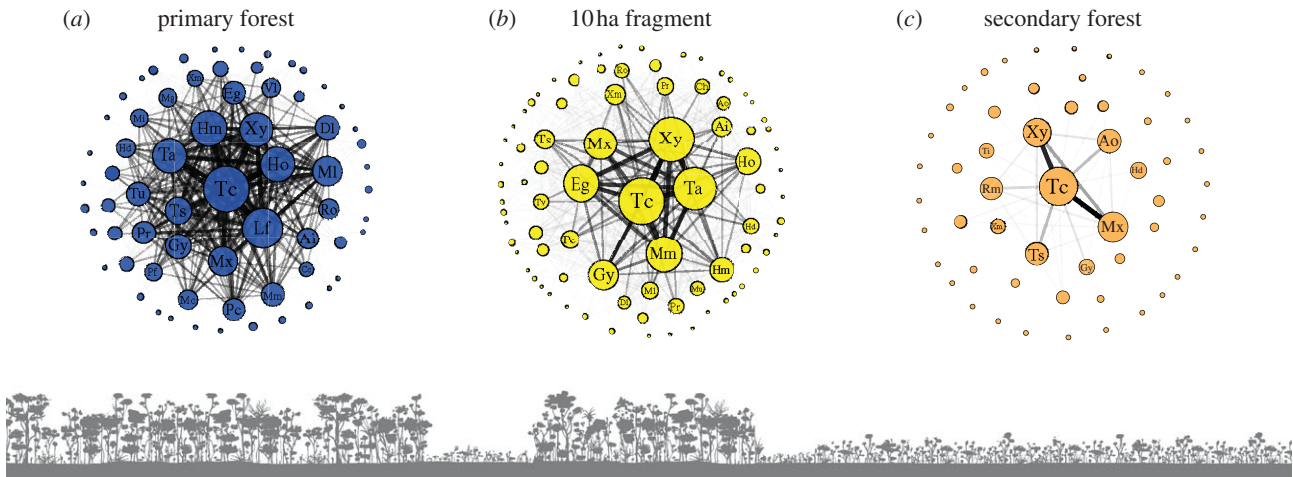


Figure 3. Example of networks and habitat configurations for three flocks found in PF, 10 ha fragment and SF habitat types in the Brazilian Amazon. Differences in network structure reflect the decay of interspecific interactions in mixed-species flocks across a disturbance gradient. Edge thickness and transparency in each network are proportional to numbers of interactions. Interaction values at the lowest 10% are set to transparent. Nodes sizes are proportional to flock attendance. Legends for species with participation above 6% are given. Ai, *Automolus infuscatus*; Ao, *Automolus ochrolaemus*; Cc, *Cariothraustes canadensis*; Ch, *Cacicus haemorrhous*; Dl, *Deconychura longicauda*; Eg, *Epinecrophylla gutturalis*; Gy, *Glyphorhynchus spirurus*; Hd, *Herpilochmus dorsimaculatus*; Hm, *Hylophilus muscicapinus*; Ho, *Hylophilus ochraceiceps*; Lf, *Lanio fulvus*; Mg, *Myiopagis gaimardii*; Mi, *Mionectes* sp.; Ml, *Myrmotherula longipennis*; Mm, *Myrmotherula menetriesii*; Mu, *Myrmotherula brachyura*; Mx, *Myrmotherula axillaris*; Pc, *Piprites chloris*; Pf, *Piculus flavigula*; Pr, *Philydor erythrocerum*; Rm, *Ramphocaenus melanurus*; Ro, *Rhynchocyclus olivaceus*; Ta, *Thamnomanes ardesiacus*; Tc, *Thamnomanes caesius*; Ts, *Tolmomyias assimilis*; Tu, *Tachyphonus surinamus*; Tv, *Trogon viridis*; Vl, *Vireolanus leucotis*; Xm, *Xenops minutus*; Xy, *Xiphorhynchus pardalotus*. (Online version in colour.)

degradation tends to promote homogenization (loss of species) resulting in reduced network complexity and stability [12,58, 59]. Our results, from a non-trophic flock network, corroborate the idea that extrinsic environmental features, like habitat, can affect interspecific social structure. At the species level, our results indicate that flocking birds in small fragments and degraded SFs associated with fewer species (degree) and did so less frequently (weighted degree) than individuals in intact habitats. Structural differences among networks at the level of the flock are best illustrated by habitat-specific degree distributions, which show the cumulative effect of changes in species associations across habitat types. In particular, the majority of associations in 10 ha fragments and SFs were driven by a few remaining core species, while associations were more evenly distributed across species in intact forest environments.

Our results also highlight that habitat configuration can influence patterns of species richness. Specifically, species richness was higher in some of the more degraded habitats than in large intact forests tracts. These results differ from previous studies in the old world tropics, which found decreases [32] or no changes in species richness [33] in mixed-species flocks along disturbance gradients. Increases in species richness in 10 ha fragments were not altogether surprising given the available habitat matrix and community composition. In particular, the proximity of fragment borders and SF probably enabled canopy and edge specialists to interact with understory flocks, thereby increasing diversity. Despite high richness and the addition of novel species in degraded habitats, species were encountered less frequently and had reduced flock attendance in 10 ha fragments and SFs. These results are consistent with the idea that flocking species are disproportionately affected by habitat disturbance when compared with other guilds [29,33]. Ultimately, increases in species richness do not appear to have meaningfully modified flock social dynamics.

Our results suggest that changes in flock attendance rather than species loss across the habitat gradient is probably

driving changes in flock social structure. Differences in attendance may result from either reduced bird density in fragmented and sub-optimal habitats [29,60] and/or changes in propensity to join flocks [20,60–62]. Previous work in this system and our data suggest that these flocking species may have lower densities but are not completely absent in degraded habitats [25,63]. Comparisons of flock participation show that a large proportion of species appear to alter their behaviour by reducing flock attendance. Moreover, such changes in behaviour also suggest that the costs and benefits of flocking behaviour may vary with environmental context [32]. While we have no data on the mechanisms for decreases in flock attendance, we believe that arthropod prey abundance declines in more degraded environments [25,64,65]. Many permanent flock species are known to have specialized foraging niches, and a reduction in their food resource could increase space use, which might decrease flock attendance. Regardless of the mechanism, reduced attendance and subsequent changes in flock composition will influence the stability, cohesion and integrity of these complex multi-species interactions [66].

(b) Habitat and the consequences of changes in social structure

Flock cohesiveness within the network, as measured by weighted clustering coefficients, was positively correlated with mean vegetation height (figure 5b). Importantly, vegetation height is a good proxy for structural habitat complexity [67,68] as PFs and 100 ha fragments also tended to have greater vertical forest stratification than small fragments and SF. The positive relationship between vegetation height and clustering coefficients is best explained by two possible mechanisms. First, vegetation height could have directly influenced network structure if the number of interspecific associations within flocks is driven, in part, by structural components of the habitat. The documentation of strong vertical

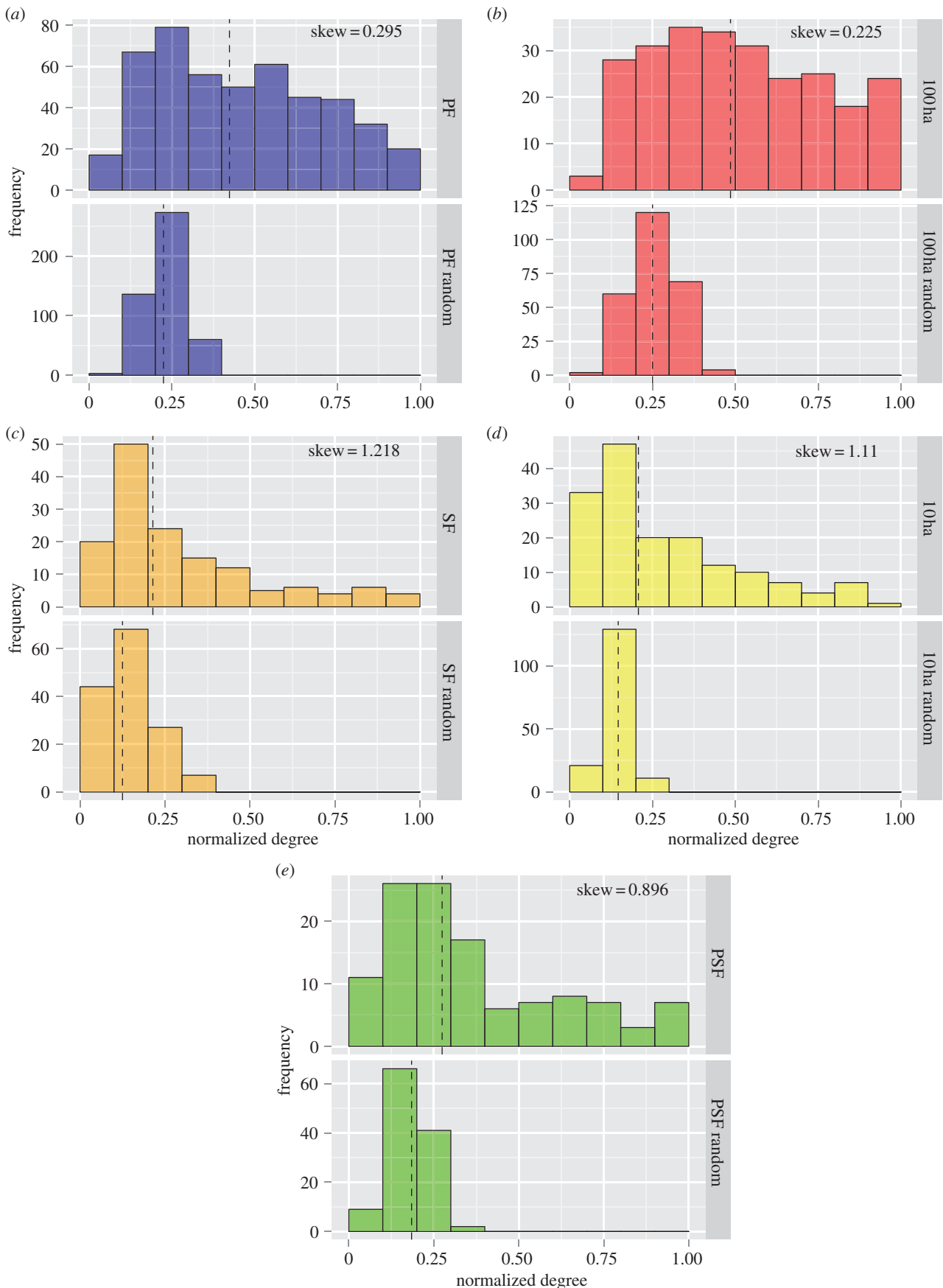


Figure 4. Cumulative degree distributions highlight differences in mixed-species flock network structure across a habitat gradient in the Brazilian Amazon. Pairs of histograms for observed and randomized networks show that degraded habitats are characterized by low medians and high skew while more intact habitats have higher medians and lower skew. Dashed lines represent the median normalized degree. (Online version in colour.)

stratification within Amazonian bird communities partially support this idea [69,70]. Second, vegetation height could indirectly affect network structure if predation pressure covaries

with habitat type. For example, predator communities have been shown to drive flocking propensity and may vary across degraded tropical forests [71,72].

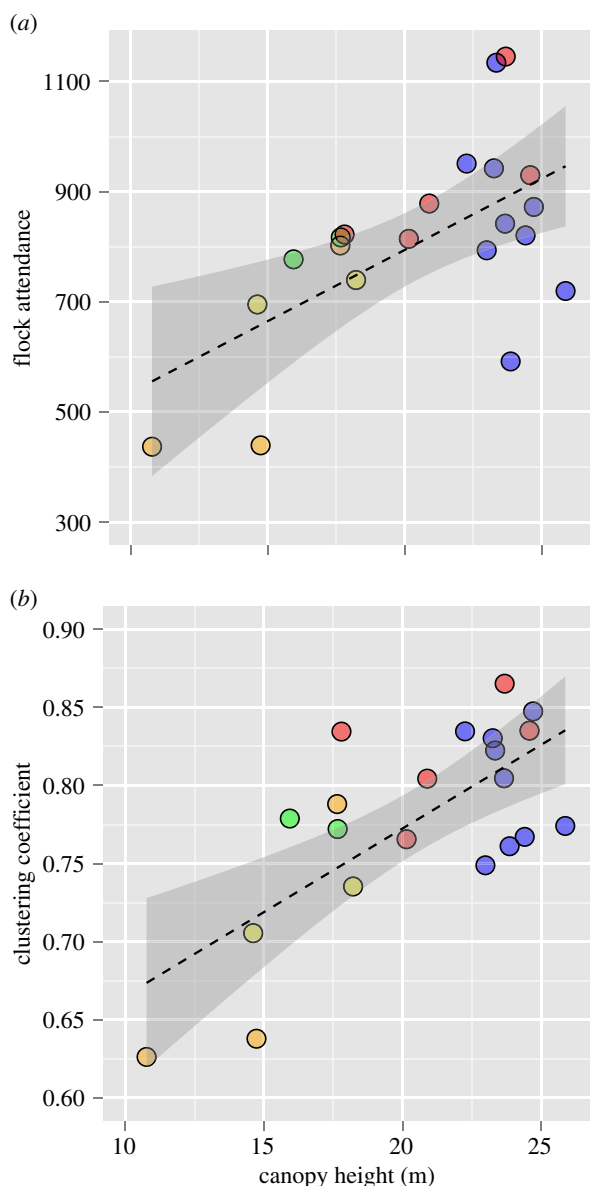


Figure 5. Mixed-species flock cohesiveness (clustering) and attendance show strong positive correlation with vegetation structure. (a) Relationship between flock global clustering coefficient and mean vegetation height. (b) Relationship between species attendance and mean vegetation height. The y-axis represents the cumulative amount of time all species in a given habitat participated in a flock. Flocks (points in the graph) are shaded for habitat type (medium grey, PF; light grey, 100 ha; white, 10 ha; dark grey, PSF; black, SF). Dashed line represents the β coefficient from the model and the grey shaded area is the 95% confidence interval. (Online version in colour.)

Changes in network properties may influence individual performance of species whose natural history revolves around joining flocks. For example, reduced flock attendance may reduce predation avoidance and foraging optimality [60,73]. Flocks in highly disturbed areas were unstable, not lasting more than a few weeks, where pairs of *Thamnomanes caesioides* were inconsistently present. By contrast, flocks in continuous forest are known for their long-term stability, even as individual participants disappear and are replaced [17,74]. Assuming that changes in flock network structure influence individual fitness, future work should focus on measures of fitness by gathering species-level data on foraging efficiency and space use, as well as community-level data on predator communities and resource distribution.

Table 3. The relative changes in the presence/absence and attendance from PF to degraded forest for mixed-species flocks. (Species were recorded as absent when detected in PF but not degraded habitats and decreasing attendance when detected in both habitats but in a lower relative proportion. Magnitude of change describes the average differences in encounter rate between primary and degraded habitats.)

habitat type	% spp. absent	% spp. decreasing attendance	mean magnitude of change
10 ha	3.0	47.7	-3.79 ± 2.50
secondary forest	12.3	47.7	-5.75 ± 3.44
primary-secondary	3.3	56.7	-2.62 ± 4.37
100 ha	2.4	55.1	-1.94 ± 2.50

5. Conclusion

Forest clearing is one of the largest threats to biodiversity today [75]. In the Amazon, the impact of forest fragmentation on avian species is well documented [25,63,76], yet changes in behaviour, interspecific interactions and community dynamics are less well known. Identifying the mechanisms that disrupt ecological processes in human-modified habitats is an essential step in mitigating and conserving diverse tropical communities. Network analyses are a powerful tool for quantifying how trophic and non-trophic interactions and subsequent ecological networks change across landscape gradients, because they enable us to quantify the role that species play in community structure and function. Moreover, this approach is likely to be especially useful in the tropics because of the high diversity and subsequent complexity of interspecific interactions. Future research must move beyond simply tallying species lists and towards identifying mechanisms that alter species interactions and community function [12]. The results presented here advance our understanding of how non-trophic interspecific interactions and subsequent community structure change along a disturbance gradient. Ultimately, if behavioural interactions and the structure of non-trophic networks tend to be highly sensitive to environmental change, as shown here, a more nuanced approach may be needed when thinking about the resiliency of ecology networks.

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References

- May RM. 2006 Network structure and the biology of populations. *Trends Ecol. Evol.* **21**, 394–399. (doi:10.1016/j.tree.2006.03.013)
- Girvan M, Newman MEJ. 2002 Community structure in social and biological networks. *Proc. Natl Acad. Sci. USA* **99**, 7821–7826. (doi:10.1073/pnas.122653799)
- Proulx SR, Promislow DEL, Phillips PC. 2005 Network thinking in ecology and evolution. *Trends Ecol. Evol.* **20**, 345–353. (doi:10.1016/j.tree.2005.04.004)
- Bascompte J, Jordano P, Olesen JM. 2006 Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431–433. (doi:10.1126/science.1123412)
- Guimarães PR, Jordano P, Thompson JN. 2011 Evolution and coevolution in mutualistic networks. *Ecol. Lett.* **14**, 877–885. (doi:10.1111/j.1461-0248.2011.01649.x)
- Stouffer DB, Camacho J, Guimera R, Ng CA, Amaral LAN. 2005 Quantitative patterns in the structure of model and empirical food webs. *Ecology* **86**, 1301–1311. (doi:10.1890/04-0957)
- Ryder TB, McDonald DB, Blake JG, Parker PG, Loiselle BA. 2008 Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). *Proc. R. Soc. B* **275**, 1367–1374. (doi:10.1098/rspb.2008.0205)
- Ryder TB, Parker PG, Blake JG, Loiselle BA. 2009 It takes two to tango: reproductive skew and social correlates of male mating success in a lek-breeding bird. *Proc. R. Soc. B* **276**, 2377–2384. (doi:10.1098/rspb.2009.0208)
- Naug D. 2008 Structure of the social network and its influence on transmission dynamics in a honeybee colony. *Behav. Ecol. Sociobiol.* **62**, 1719–1725. (doi:10.1007/s00265-008-0600-x)
- Kaiser-Bunbury CN, Muff S, Memmott J, Muller CB, Cafisch A. 2010 The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.* **13**, 442–452. (doi:10.1111/j.1461-0248.2009.01437.x)
- Dunne JA, Williams RJ, Martinez ND. 2002 Food-web structure and network theory: the role of connectance and size. *Proc. Natl Acad. Sci. USA* **99**, 12 917–12 922. (doi:10.1073/pnas.192407699)
- Tylianakis JM, Tscharntke T, Lewis OT. 2007 Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* **445**, 202–205. (doi:10.1038/nature05429)
- Fortuna MKA, Bascompte J. 2012 Habitat loss and the disassembly of mutualistic networks. *Oikos* **122**, 938–942. (doi:10.1111/j.1600-0706.2012.00042.x)
- Wey T, Blumstein DT, Shen W, Jordan F. 2008 Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* **75**, 333–344. (doi:10.1016/j.anbehav.2007.06.020)
- Farine DR, Garroway CJ, Sheldon BC. 2012 Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Anim. Behav.* **84**, 1271–1277. (doi:10.1016/j.anbehav.2012.08.008)
- Munn C. 1985 Permanent canopy and understory flocks in Amazonia: species composition and population density. In *Ornithological monographs* (eds P Buckley, MS Foster, ES Morton, RS Ridgely, FG Buckley), pp. 683–712. Washington, DC: American Ornithologist's Union.
- Jullien M, Thiollay JM. 1998 Multi-species territoriality and dynamic of neotropical forest understory bird flocks. *J. Anim. Ecol.* **67**, 227–252. (doi:10.1046/j.1365-2656.1998.00171.x)
- Develey PF, Stouffer PC. 2001 Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conserv. Biol.* **15**, 1416–1422. (doi:10.1046/j.1523-1739.2001.00170.x)
- Powell GVN. 1985 Sociobiology and adaptive significance of interspecific foraging flocks in the neotropics. *Ornithol. Monogr.* **36**, 713–732. (doi:10.2307/40168313)
- Martinez AE, Zenil RT. 2012 Foraging guild influences dependence on heterospecific alarm calls in Amazonian bird flocks. *Behav. Ecol.* **23**, 544–550. (doi:10.1093/beheco/arr222)
- Martinez AE, Gomez JP. 2013 Are mixed-species bird flocks stable through two decades? *Am. Nat.* **181**, E53–E59. (doi:10.1086/669152)
- English PE. 1998 *Ecology of mixed-species understory flocks in Amazonian Ecuador*. Austin, TX: University of Texas.
- Beauchamp G. 2004 Reduced flocking by birds on islands with relaxed predation. *Proc. R. Soc. B* **271**, 1039–1042. (doi:10.1098/rspb.2004.2703)
- Butler RA, Laurance WF. 2008 New strategies for conserving tropical forests. *Trends Ecol. Evol.* **23**, 469–472. (doi:10.1016/j.tree.2008.05.006)
- Stouffer PC, Bierregaard RO. 1995 Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* **76**, 2429–2445. (doi:10.2307/2265818)
- Stouffer PC, Bierregaard RO. 2007 Recovery potential of understory bird communities in Amazonian rainforest fragments. *Rev. Bras. Ornitol.* **15**, 219–229.
- Barlow J *et al.* 2007 Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl Acad. Sci. USA* **104**, 18 555–18 560. (doi:10.1073/pnas.0703331104)
- Sodhi NS, Posa MRC, Lee TM, Warkentin IG. 2008 Effects of disturbance or loss of tropical rainforest on birds. *Auk* **125**, 511–519. (doi:10.1525/auk.2008.1708)
- Thiollay JM. 1997 Disturbance, selective logging and bird diversity: a neotropical forest study. *Biodivers. Conserv.* **6**, 1155–1173. (doi:10.1023/A:1018388202698)
- Maldonado-Coelho M, Marini MA. 2000 Effects of forest fragment size and successional stage on mixed-species bird flocks in southeastern Brazil. *Condor* **102**, 585–594. (doi:10.1650/0010-5422(2000)102[0585:eoffsa]2.0.co;2)
- Stotz DF. 1993 Geographic variation in species composition of mixed species flocks in lowland humid forests in Brazil. *Papeis Avulsos de Zoologia* **38**, 15.
- Lee TM, Soh MCK, Sodhi N, Koh LP, Lim SLH. 2005 Effects of habitat disturbance on mixed species bird flocks in a tropical sub-Montane rainforest. *Biol. Conserv.* **122**, 193–204. (doi:10.1016/j.biocon.2004.07.005)
- Sridhar H, Sankar K. 2008 Effects of habitat degradation on mixed-species bird flocks in Indian rain forests. *J. Trop. Ecol.* **24**, 135–147. (doi:10.1017/s0266467408004823)
- Lovejoy TE *et al.* 1986 Edge and other effects of isolations on Amazon forest fragments. In *Conservation biology: the science of scarcity and diversity* (ed. ME Soulé), p. 584. Sunderland, MA: Sinauer.
- Bierregaard RO *et al.* 2001 Principles of forest fragmentation and conservation in the Amazon. In *Lessons from Amazonia: the ecology and conservation of a fragmented forest* (eds RO Bierregaard, C Gascon, TE Lovejoy, R Mesquita), pp. 371–385. New Haven, CT: Yale University Press.
- Mesquita RCG, Ickes K, Ganade G, Williamson GB. 2001 Alternative successional pathways in the Amazon Basin. *J. Ecol.* **89**, 528–537. (doi:10.1046/j.1365-2745.2001.00583.x)
- Colwell RK. 2013 ESTIMATE: Statistical estimation of species richness and shared species from samples (9th edn). See <http://viceroy.eeb.uconn.edu/estimates/>.
- Chao A, Chazdon RL, Colwell RK, Shen TJ. 2006 Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* **62**, 361–371. (doi:10.1111/j.1541-0420.2005.00489.x)
- Beyer HL. 2012 Geospatial modelling environment. (0.7.2.0) edn. See <http://www.spatial ecology.com/gme/>.
- Croft D, James R, Krause J. 2008 *Exploring social animal networks*, p. 192. Princeton, NJ: Princeton University Press.
- Franks DW, Ruxton GD, James R. 2010 Sampling animal association networks with the gambit of the group. *Behav. Ecol. Sociobiol.* **64**, 493–503. (doi:10.1007/s00265-009-0865-8)
- Borgatti SP, Everett MG, Freeman LC. 2002 *Ucinet for windows: software for social network analysis*. (6.456 edn). Harvard, MA: Analytic Technologies.
- Opshal T. 2009 *Structure and evolution of weighted networks*. London, UK: University of London.
- Butts CT, Hunter D, Handcock MS. 2012 network: classes for relational data (1.7–1 edn). See <http://cran.r-project.org/web/packages/network/>.
- Albert R, Barabasi AL. 2002 Statistical mechanics of complex networks. *Rev. Mod. Phys.* **74**, 47–97. (doi:10.1103/RevModPhys.74.47)
- Halvorsen K. 2012 ElemStatLearn: data sets, functions and examples from the book: 'The elements of statistical learning, data mining, inference, and prediction' (2012.04–0 edn). See

- <http://cran.r-project.org/web/packages/ElemStatLearn/>.
47. Opsahl T, Panzarasa P. 2009 Clustering in weighted networks. *Soc. Netw.* **31**, 155–163. (doi:10.1016/j.socnet.2009.02.002)
 48. Croft DP, Madden JR, Franks DW, James R. 2011 Hypothesis testing in animal social networks. *Trends Ecol. Evol.* **26**, 502–507. (doi:10.1016/j.tree.2011.05.012)
 49. McCullagh PN, Nelder JA. 1983 *Generalized linear models* p. 532, 2nd edn. London, UK: Chapman & Hall.
 50. Freeman LC. 1979 Centrality in social networks conceptual clarification. *Soc. Netw.* **1**, 215–239. (doi:10.1016/0378-8733(78)90021-7)
 51. Bates D, Maechler M, Bolker B. 2012 lme4: Linear mixed-effects models using Eigen and Eigen++ (0.999999–0 edn). See <http://cran.r-project.org/web/packages/lme4/index.html>.
 52. Skaug HFD, Nielsen A, Magnusson A, Bolker B. 2013 GlmmADMB package. (0.6.7.1 edn). See <http://glmmadmb.r-forge.r-project.org/>.
 53. Wickham H, Chang W. 2012 ggplot2: an implementation of the grammar of graphics. (0.9.3 edn). See <http://ggplot2.org/>.
 54. Vazquez DP, Melian CJ, Williams NM, Bluthgen N, Krasnov BR, Poulin R. 2007 Species abundance and asymmetric interaction strength in ecological networks. *Oikos* **116**, 1120–1127. (doi:10.1111/j.2007.0030-1299.15825.x)
 55. de Visser SN, Freyermann BP, Olff H. 2011 The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *J. Anim. Ecol.* **80**, 484–494. (doi:10.1111/j.1365-2656.2010.01787.x)
 56. O’Gorman EJ, Fitch JE, Crowe TP. 2012 Multiple anthropogenic stressors and the structural properties of food webs. *Ecology* **93**, 441–448. (doi:10.1890/11-0982.1)
 57. Beyer K, Gozlan RE, Copp GH. 2010 Social network properties within a fish assemblage invaded by non-native sunbleak *Leucaspius delineatus*. *Ecol. Model.* **221**, 2118–2122. (doi:10.1016/j.ecolmodel.2010.06.002)
 58. Laliberte E, Tylianakis JM. 2010 Deforestation homogenizes tropical parasitoid-host networks. *Ecology* **91**, 1740–1747. (doi:10.1890/09-1328.1)
 59. Albrecht M, Duelli P, Schmid B, Muller CB. 2007 Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *J. Anim. Ecol.* **76**, 1015–1025. (doi:10.1111/j.1365-2656.2007.01264.x)
 60. Thiollay JM. 1999 Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: an intertropical comparison. *J. Avian Biol.* **30**, 282–294. (doi:10.2307/3677354)
 61. Knowlton JL, Graham CH. 2011 Species interactions are disrupted by habitat degradation in the highly threatened Tumbesian region of Ecuador. *Ecol. Appl.* **21**, 2974–2986. (doi:10.1890/10-1886.1)
 62. Dolby AS, Grubb TC. 1999 Functional roles in mixed-species foraging flocks: a field manipulation. *Auk* **116**, 557–559. (doi:10.2307/4089392)
 63. Stouffer PC, Bierregaard RO, Strong C, Lovejoy TE. 2006 Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conserv. Biol.* **20**, 1212–1223. (doi:10.1111/j.1523-1739.2006.00427.x)
 64. Şekercioğlu CH, Ehrlich PR, Daily GC, Aygen D, Goehring D, Sandi RF. 2002 Disappearance of insectivorous birds from tropical forest fragments. *Proc. Natl Acad. Sci. USA* **99**, 263–267. (doi:10.1073/pnas.012616199)
 65. Stouffer PC. 2007 Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. *Auk* **124**, 291–306. (doi:10.1642/0004-8038(2007)124[291:DTSALS]2.0.CO;2)
 66. Maldonado-Coelho M, Marini MA. 2004 Mixed-species bird flocks from Brazilian Atlantic forest: the effects of forest fragmentation and seasonality on their size, richness and stability. *Biol. Conserv.* **116**, 19–26. (doi:10.1016/s0006-3207(03)00169-1)
 67. Goetz SJ, Steinberg D, Betts MG, Holmes RT, Doran PJ, Dubayah R, Hofton M. 2010 Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. *Ecology* **91**, 1569–1576. (doi:10.1890/09-1670.1)
 68. Whitfield TJS, Kress WJ, Erickson DL, Weiblen GD. 2012 Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea. *Ecography* **35**, 821–830. (doi:10.1111/j.1600-0587.2011.07181.x)
 69. Walther BA. 2002 Grounded ground birds and surfing canopy birds: variation of foraging stratum breadth observed in neotropical forest birds and tested with simulation models using boundary constraints. *Auk* **119**, 658–675.
 70. Comin FA. 2010 *Ecological restoration: a global challenge*, p. 381. New York, NY: Cambridge University Press.
 71. Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, Stork NE, Miller SE. 2009 The potential for species conservation in tropical secondary forests. *Conserv. Biol.* **23**, 1406–1417. (doi:10.1111/j.1523-1739.2009.01338.x)
 72. Thiollay JM. 1985 Composition of Falconiforms communities along successional gradients from primary rain forest to secondary habitats. In *Conservation studies of raptors* (ed. INR Chancellor), p. 181. Cambridge, UK: International Council for Bird Preservation.
 73. Couzin ID, Krause J, James R, Ruxton GD, Franks NR. 2002 Collective memory and spatial sorting in animal groups. *J. Theor. Biol.* **218**, 1–11. (doi:10.1006/jytbi.2006.3065)
 74. Jullien M, Clobert J. 2000 The survival value of flocking in neotropical birds: reality or fiction? *Ecology* **81**, 3416–3430. (doi:10.1890/0012-9658(2000)081[3416:Tsvofj]2.0.co;2)
 75. Pimm SL, Raven P. 2000 Biodiversity: extinction by numbers. *Nature* **403**, 843–845. (doi:10.1038/35002708)
 76. Stouffer PC, Strong C, Naka LN. 2009 Twenty years of understory bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. *Divers. Distrib.* **15**, 88–97. (doi:10.1111/j.1472-4642.2008.00497.x)