



The potential impacts of the songbird trade on mixed-species flocking

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ABSTRACT

Mixed-species flocking is an important avian social system that supports a large number of species. Current reviews of threats to mixed flocks have only examined two types of anthropogenic pressures: different land use intensity and fragmentation. We highlight the bird trade as another major potential threat for many mixed-species flocking species in Southeast Asia. We examine the potential indirect impact of the bird trade by comparing social networks of flocking data collected over two periods nearly 20 years apart (1997 and 2016) from the same site in Sumatra, Indonesia. We find that the structure of the two networks was significantly correlated. However, of the 90 species observed, 49 had previously been identified as part of the bird trade. These species experienced a significantly greater decrease in network centrality over time compared to the non-traded species, resulting in a loss of structure in the mixed-species flocking network. Simulating further disturbances suggests that flocks may not be resilient to the complete loss of two or more traded species. Our results suggest that trapping is likely to be contributing to the degradation of flocks, and ultimately could lead to the widespread declines in those other species that also rely on mixed-species flocking.

1. Introduction

There is increasing awareness of the need to conserve ecological networks. Interactions between species, such as pollinator-plant networks (Burkle et al., 2013) and predator-prey food webs (Dunne et al., 2002), are widespread and form an essential part of ecosystem functioning. One very common, but often overlooked system of interactions are mixed-species groups. For example, mixed-species bird flocks ('mixed flocks' hereafter) have been reported in many parts of the world (Munn, 1985; Hutto, 1994; Develey and Peres, 2000; Lee et al., 2005; Sridhar and Shanker, 2014). They can represent a significant proportion of the avifauna (e.g. over 50% of species reported in Madagascar, Eguchi et al., 1993; in Australia, Bell, 1983; and in the Dominican Republic, Latta and Wunderle, 1996) and many species are obligate flock members. In mixed flocks, participants (two or more species) travel together in search of dispersed food (Buskirk, 1976; Bell, 1983), actively maintaining group cohesion with both conspecifics and heterospecifics (Farine et al., 2014). Doing so can bring important fitness benefits for participants (Dolby and Grubb, 1998), and the survival rates of obligate mixed flock members has been shown to be significantly higher than for species feeding alone or in pairs (Jullien and

Clobert, 2000). Thus, conserving mixed-species flocks is likely to be important for maintaining the presence and abundance of many species.

Mixed flock formation can be highly sensitive to environmental change (Mokross et al., 2014), and, in particular, the loss of key species can fundamentally alter the dynamics of mixed flock composition (e.g., Maldonado-Coelho and Marini, 2000). This could be because flocking can facilitate transfer of information about food resources among individuals (Aplin et al., 2012), with some species playing a keystone role in spreading information about new food resources (Suzuki, 2012; Farine et al., 2015). Flocking can also confer anti-predator benefits (e.g., Thiollay, 1999), with certain species providing significant vigilance benefits (Goodale and Kotagama, 2005; Martinez and Zenil, 2012; Martinez et al., 2016). Species in mixed flocks are typically thought to take on one of two different roles: nuclear species (the initiator of mixed flocks) and attendant species (Moynihan, 1962); and nuclear species have been shown to provide important benefits for attendant species that cannot be gained in their absence (Dolby and Grubb, 1998). However, in terms of ecosystem function, the loss of a common attendant species could be equally severe if these bring survival benefits to nuclear species via group augmentation or by providing foraging

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benefits (e.g. Satischandra et al., 2007). Thus, identifying species that are central in their communities, both nuclear or attendant, and identifying key threats they face is an important goal for conservation biologists (Goodale et al., 2017).

Human disturbances are a major source of threats for ecosystems worldwide. Two main anthropogenic disturbance impacts to mixed flocks have been studied: forest fragmentation and different land-use intensity (see review by Goodale et al., 2015). Across studies, evidence suggests that disturbed areas typically contain smaller flocks with reduced species richness (Goodale et al., 2015). A few recent studies have also suggested that community structure (i.e. the network of interactions among species) can also be affected (Mokross et al., 2014), with the changing composition of species in the landscape impacting how species interact with one-another (Mammides et al., 2015). This community-centric approach is important because it more directly links anthropogenic disturbances to functional change in the communities involved. Such an approach is likely to be particularly important for disturbances in which the impacts may be as severe as those caused by habitat disturbances, but where the cues much less noticeable. One such potential threat, that has yet to be examined in the context of conservation of avian communities, is bird trapping.

The wild bird trade is widespread in South-east Asia. Thousands of birds are sold to fulfill various purposes: as pets or household ornaments, for food, religious release, traditional medicine (Jepson and Ladle, 2009; Shepherd, 2012), or for bird singing competitions (where bird owners use species such as White-rumped Shama *Kittacincla malabarica* and compete for the best song; Eaton et al., 2015). Birds are sourced both locally and more widely. A recent assessment in the three largest bird markets in Jakarta shows that 98% of the total volume of birds traded (182 species) are native to Indonesia (Chng et al., 2015). However, the enormous demand for birds (the wildlife trade is worth an estimated US\$2.5 billion/year in East Asia and the Pacific, and perhaps up to USD\$1 billion/year in Indonesia alone; UNODC, 2013) has severely depleted animal populations in local forests. For example, many of the wild bird species that are sold in the markets of Jakarta (on Java) are becoming very rare and now being sourced from neighbouring Sumatra (Jepson and Ladle, 2009; Shepherd, 2012; Chng and Eaton, 2016). If the same species that are being trapped and traded are also species that are central in mixed flocks, for example drongos are among the most commonly traded species (Shepherd, 2012; Chng and Eaton, 2016) and often considered as being nuclear in mixed flocks (Satischandra et al., 2007), then the loss of these species could alter the entire structure of communities. Subsequently, this could have significant repercussions on the behaviour of remaining species in the community (Dolby and Grubb, 1999), with potential carry-over effects into foraging and reproductive success.

In this study, we investigate the potential indirect effects of bird trapping to have an impact on the formation and maintenance of mixed-species flocks. We conducted two surveys (1997 and 2016) in Lampung Province, in southwest Sumatra, Indonesia, where birds are actively being targeted for the bird trade (see Fig. 1 for example). We use social network analysis to investigate changes in the community structure over time. Social network analysis provides a powerful toolbox for quantifying structural properties of multi-species communities, thus moving beyond simple descriptors of flocking propensity. Specifically, it provides quantitative measures of the importance of each species (i.e. its centrality, determined by the extent of co-occurrences in flocks with other species) as well as modelling tools (i.e. null models similar to those used in community ecology, Gotelli and Graves, 1996; Miller et al., 2017) to evaluate whether mixed flock communities show non-random structural patterns. The latter question is particularly important for determining the presence of interspecific relationships that are important for the ongoing functioning of the system.

The aim of our study is to assess the changes in flocking structure in a protected area that has experienced ongoing illegal bird trapping. Specifically, we use mixed flock networks generated from our two

surveys to test (i) whether networks in the two years are more structured than expected under indiscriminate flocking (showing preferred associations between certain species), (ii) whether the propensities for species to flock together (and thus the resulting network structure) are correlated over the two survey periods spanning 19 years, (iii) whether traded species and non-traded species differ in their social network centrality, (iv) whether the centrality of traded and non-traded species changed over time, and (v) whether the mixed flock networks are resilient to the complete removal of traded species. Our study also represents the first major dataset on mixed flocks from Sumatra.

2. Study area

The Way Cangkuk Research Station (Lat. -5.658643 , Long. 104.407098 ; Fig. 2) is located inside the Bukit Barisan Selatan National Park (325,000 ha) and was established in 1997. The national park is the third largest protected area in Sumatra, and contains some of the last intact areas of lowland rainforest on this island (O'Brien and Kinnaird, 1996). Our study was conducted along a trail system covering an area of approximately 380-ha of intact lowland forest contained within the Way Cangkuk Research Station area. The study area, and the research station, are surrounded by a larger contiguous primary forest (the national park), while the national park is surrounded by matrix of intact forest, burned forest, areas disturbed by illegal logging, and agricultural lands. Illegal logging and encroachment for agricultural expansion are the main threats to the national park, but this is not a threat inside the research station itself (Gaveau et al., 2007). Two main anthropogenic disturbances occur in the Way Cangkuk Research Station: forest fires and bird trapping. Forest fires occurred twice: 165 ha were burned in 1997/1998 (Kinnaird and O'Brien, 1998) and in 2015, 7 ha of this previously damaged forest was burned a second time (William Marthy pers. obs.). However, we conducted all surveys in areas > 600 m (beyond the impact of fire in this community, Adeney et al., 2006) and buffered by a river from areas affected by fire, and thus do not believe it has a confounding effect. By contrast, trapping of birds for trade has persisted on Way Cangkuk Research Station, and in our specific study area, since the late 1990's (O'Brien and Kinnaird, 1996; Harris et al., 2017), and continues to occur despite the presence of the research station staff and increased patrolling efforts in the larger Bukit Barisan Selatan National Park (unpublished data based on interviews of research station and national parks staff). For example, between 2014 and early 2017, the research station staff recorded 13 incidents of bird trapping: in 10 instances the staff found evidence that bird trapping had occurred (i.e. dead birds, camps, poles for nets), and in three instances the staff met directly with the perpetrators (in two instances the perpetrators were arrested). As a consequence of trapping, two of targeted species, the White-rumped shama and the Grey-cheeked bulbul *Alophoixus bres* are now extremely rare, although a recent study by Harris et al. (2017) suggests that abundances of birds in the study area have remained relatively stable. Trappers active in the research station area typically use a lure (e.g. a male Blue-winged Leafbird *Chloropsis moluccensis*; Fig. 1) to attract and capture target birds in mist-nets or with bird-lime (an adhesive made from tree sap; Shepherd et al., 2004). During the capture process, other species can also be caught (i.e. as "bycatch"). Individuals of these species can be released, die or be killed (e.g. Fig. 1), or kept by trappers.

3. Data collection

3.1. Field observations

We conducted two surveys, the first between July and October 1997 for a total of 24 observation days, and the second between August and November 2016 for a total of 18 observation days. Observations were made by the same observer (WM) and along the same trail system, which had been cut and mapped through the forest in order to facilitate



Fig. 1. Confiscated Blue-winged Leafbird *Chloropsis moluccensis* that was used as bait to attract birds by the illegal bird trappers and examples of birds that died or were killed during the capturing process Photos were taken at the study site. Copyright: WCSIP/Fahrudin Surahmat.

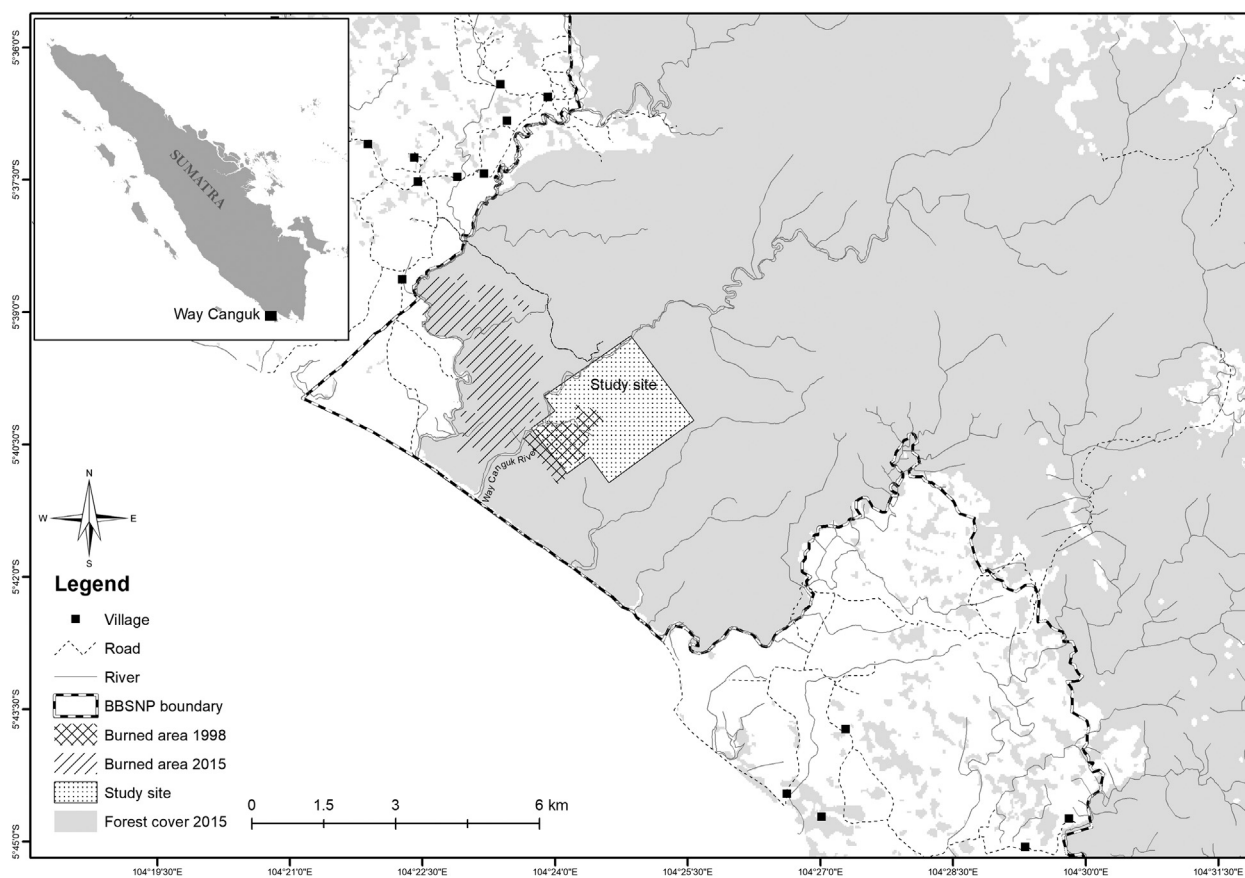


Fig. 2. Location of this study site in the Way Cangkuk Research Station within the Bukit Barisan Selatan National Park, Lampung-Sumatra, Indonesia.

observation of the avifauna. Both surveys were done during the non-breeding season for most species (van Marle and Voous, 1988), and the habitat (primary forest) remained the same across both surveys.

Mixed flocks were broadly defined as two or more bird species moving together in the same general direction (Buskirk, 1976; Hutto, 1994), and within the relative vicinity of each other – approximately 10–25 m of each other (Bell, 1983; Hutto, 1987). Each day, we walked through the study area from 07.00 to 17.00 h to search for flocks. For each flock we collected: time, location of flock in the study area, participating species, and the number of individuals. Flocks were followed for as long as possible (maximum 1 h) to record all species present. During observations, the observer briefly recounted species every 10 min to check for species that had been missed. Upon leaving a flock, the observer moved several hundred meters in a different direction to the flock trajectory before counting any new flocks, and aimed to cover a large area each day to avoid re-encountering the same flock twice. Both surveys used identical methodology. Our approaches are consistent with previous studies, e.g. mixed flocks observed in similar locations but on different days are considered as different (e.g. Sridhar et al., 2013). We did not apply filtering techniques to remove species with few observations as we used weighted network metrics (see below).

3.2. Trade status

Because raw data on the trapping effort for the bird trade are not available, we sourced data from market surveys to identify which species in our dataset are regularly traded. We used literature from markets in both Sumatra and Jakarta as many of the wild birds sold in the Javan markets are now sourced from Sumatra (Jepson and Ladle, 2009; Shepherd, 2012; Chng and Eaton, 2016) and there is clear evidence that the bird trade is a large market spanning the entire region (with birds being illegally shipped to neighbouring countries, <http://www.traffic.org/home>). As raw data on trapping takes were not available, we created a scoring system to estimate the likelihood for each species to be regularly traded. Species that have been directly identified as being harvested from the forests of Sumatra (using Shepherd et al., 2004; Shepherd, 2006; Harris et al., 2017) were given a score of 1. Because species traded in Java are now frequently sourced from Sumatra (Jepson and Ladle, 2009; Shepherd, 2012; Chng and Eaton, 2016), including from Bukit Barisan Selatan National Park, we added 0.5 to the score for species identified in bird markets in Java (using data from Jepson and Ladle, 2009; Chng et al., 2015). For species recorded in bird markets in multiple published surveys (our cited sources span approximately 10 years), we added 1 to the score (continuous impact). Hence, the highest score for a species was 2.5. While we were unable to account for intensity at which each species is traded, our system aims to increase the weighting of species that have been repeatedly reported in markets, known to be traded locally (observed in markets in Sumatra), and found to be traded in several regions (suggesting that they are commonly traded). We developed the scoring system based on our own observations (e.g. we have independently noted that species are traded across Indonesian islands), and validated the scores in consultation with park rangers and local conservation staff. For example, species with the highest trade scores are commonly known to be traded (e.g. Greater racket-tailed drongo *Dicrurus paradiseus* and Blue-winged leafbird, which were noted as among the most common in Sumatran markets by Shepherd, 2006 during our study period, both scored 2.5 using our framework), although we do not strictly interpret the trade scores in this way. However, because of potential limitations of our trade score in evaluating the trade pressure on a given species, we also discuss our results in terms of traded versus non-traded (i.e. binary) status and perform several analyses that support our findings independently of using the trade score (based mostly on Harris et al., 2017, a study conducted at the same study site).

4. Data analysis

For each sampling period (1997 and 2016), we generated an undirected social network for each observation period. Each node in this network represents a species. The edges between nodes represent the probability that the two species are observed in the same mixed flock given that at least one was observed in the flock. We used the “gambit of the group” approach, meaning that all species within a particular mixed flock are considered to be connected (Whitehead and Dufault, 1999; Franks et al., 2010; Mokross et al., 2014). We then used the “get_network” function in the asnipe R package (Farine, 2013) to calculate the edge weights and create the network. The sum of the edge weights connected to a given node (species) is called its weighted degree. This measure of centrality that represents that node's structural importance in the community (Farine and Whitehead, 2015). All computations were conducted in R version 3.1.2. (R Core Team, 2014).

4.1. Are networks more structured than expected under indiscriminate flocking?

To determine if mixed flocks represent non-random co-occurrences, we compared each network to an expectation by chance constructed using a permutation test (see Farine, 2017). In this analysis, we created a null model using a pre-network randomisation where we swapped the observation of species among groups (Farine and Whitehead, 2015). That is, for each step in the permutation process, we selected two species from two flocks in which the species did not co-occur, swapped them (following the algorithm first described by Bejder et al., 1998), and recalculated the network (herein called a *randomised network*). We then compared the Coefficient of Variation (CV: the standard deviation of the edge weights divided by the mean of the edge weights) of the observed network (CV_{observed}) to the CV of 1500 randomised networks (CV_{random}). A CV_{observed} larger than 95% of the values of CV_{random} suggests that the observed network contains more preferred/avoided relationships than expected under a scenario in which species form the same size flocks, but associate with other species at random (Farine and Whitehead, 2015). P values were calculated by taking the number of times the value from the random networks were larger than the values from the observed network, divided by the number of permutations (Farine, 2017). Our permutation test is an important part of our analyses as it controls for the observed abundance of each species in each sample by keeping the total number of observations per species constant in both the observed and the randomised networks. Thus, any differences arising are only due to the patterns in mixed flock composition and not potential changes in abundance of each species participating in mixed flocks over the two time periods.

4.2. Are the 1997 and 2016 networks correlated?

To establish whether there were some baseline similarities across our two sampling periods, we used a Mantel test to determine whether the edge weights in the two networks (in the form of two N×N matrices containing the edge weights) were correlated (Farine, 2018). We compared the result with the same test applied to the permuted networks (described above). To illustrate the network structure over the two periods, we also created a graph of each network (Fig. 3; left 1997 and right 2016). For the purpose of plotting the networks, we used the same permutation procedure (described above) to identify edges (co-occurrence between two species) that were significantly stronger than expected by chance. That is, for each edge we determined whether the observed edge weight was > 95% of the weights in the randomised networks (following Whitehead, 1999), and removed non-significant edges. All analyses were conducted on the complete network.

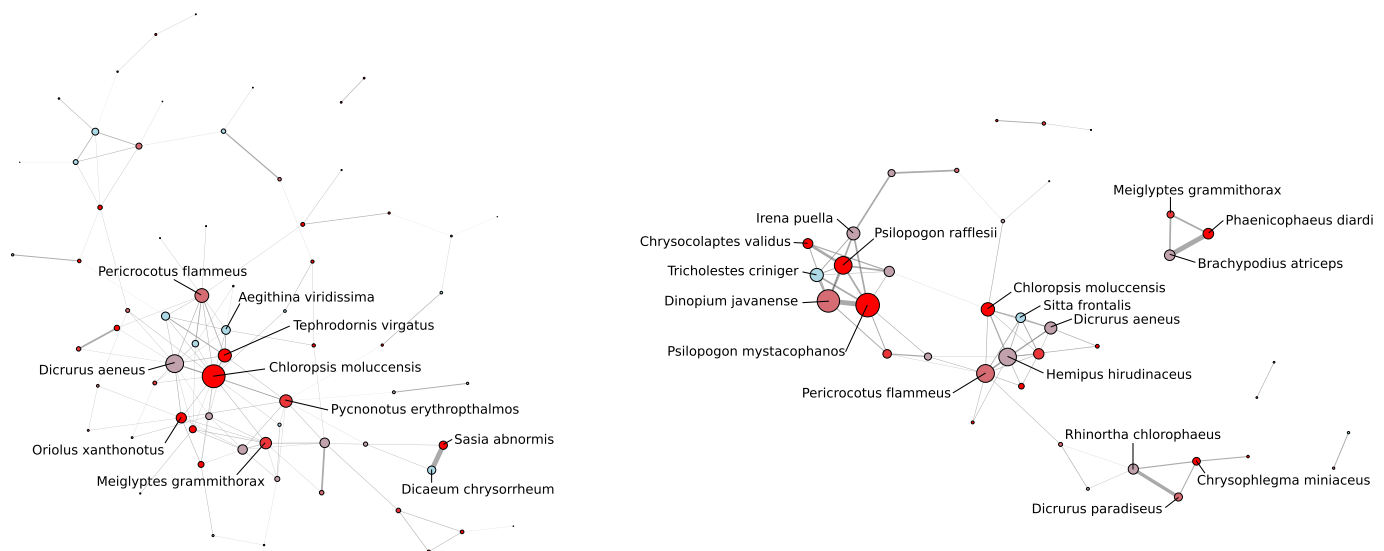


Fig. 3. Networks of significant relationships in each of the two periods, 1997 (left) and 2016 (right). In each network, nodes represent species and the edges represent the probability of observing both species in a flock given that one was observed. The size of the node represents the weighted degree for each species in the network comprising only non-random co-memberships in mixed flocks. The colour of the nodes represents the species' trade scores (brightest red = 2.5, lightest blue = 0, and grey = 1.5). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.3. Are traded species more central in the networks than non-traded species?

We tested whether traded species were more central in their network (for each year separately). Centrality was measured using the weighted degree, which refers to the structural importance based on position in the network (Farine and Whitehead, 2015). A greater propensity to participate in mixed flocks, or occur in more species-diverse flocks, results in a higher weighted degree. We fitted a linear model to evaluate the relationship between the species centrality values and their trade scores. Because networks data are inherently non-independent, the P value was again derived using our permutation test (described above), this time comparing the observed slope of the linear model to the 95% range of the slopes calculated using the randomised networks (Farine and Whitehead, 2015). As an alternative test, we compared the means for all traded species versus all non-traded species, calculating the P value by comparing the observed difference in means to the differences in means after 1000 permutations of the data.

4.4. Has the centrality of traded and non-traded species changed over time?

To test whether traded and non-traded species changed in their centrality over the 19 years, we subtracted the weighted degree of each species in the 1997 network from their weighted degree in the 2016 network. We then fitted a linear model with change in degree as a function of trade score, using the same permutation approach described above to calculate significance (Farine and Whitehead, 2015). We also conducted a simpler analysis in which we compared the proportion of species that increased versus decreased their centrality (as a binary measure) against trade score (as a binary measure), calculating the P value by comparing the difference in the proportion of species that decreased in their centrality in the observed data versus the randomised networks.

4.5. Are mixed-species flocks resilient to the loss of central species?

We conducted a simulated removal experiment to determine how losing central traded species from the system would impact community structure. In many networks, the majority of the structure is determined by a few central nodes, and losing these nodes could reduce the

viability of the network. In this simulation, we sequentially removed species with the highest overall centrality values (i.e. summing the centrality values from the 1997 and the 2016 networks) and a trade score of 1 or more, starting with the species that was the most central. Removing a species involved removing it from both of the observed networks as well as all of the corresponding randomised networks. We then calculated the correlation between the 1997 and 2016 networks, having removed those species, using the same Mantel test procedure described above (including comparing the results of the Mantel test applied to the observed network with those using the randomised networks). We avoided calculating properties of the networks resulting from the node removals, as the biological relevance of metrics such as average centrality are unclear. Instead we focused on using this test to ask about how many species have contributed towards maintaining consistent structure (i.e. correlations) in the network across the 20 year period, and ultimately determine whether the mixed flock networks are robust to the loss of central species. By restricting our analysis to removing the same species from the paired networks and measuring the correlation between these, we also aim to minimize the limitations drawn by the fact that networks are likely to re-wire in response to changes in species' presence or abundance (assuming they would rewire in approximately the same way).

5. Results

In total, we observed 184 flocks in 1997 and 135 flocks in 2016. Flocks were comprised of 90 species in total (78 species in 1997 and 59 species in 2016; Table A1). Of the 90 species that were recorded participating in mixed flocks, one species has a Vulnerable status (Ruby-throated Bulbul *Pycnonotus dispar*) and 23 species are listed as Near-Threatened. The dominant foraging guild was insectivore (60 species). A further 25 species fed on insects but also include fruits and or nectar in their diet. Three species were frugivores, one was a predator of small vertebrates, and one was a terrestrial omnivore.

A total of 47 species were observed participating in mixed flocks in both sampling periods, with 31 species only recorded in 1997 and 12 species only recorded in 2016. The number of species detected in a single mixed flock ranged from 2 to 15 species in 1997 with a mean of 5.15 ± 2.8 SD, and 2 to 22 species in 2016 with a mean of 4.46 ± 2.77 SD. The total number of edges (species co-occurrence in

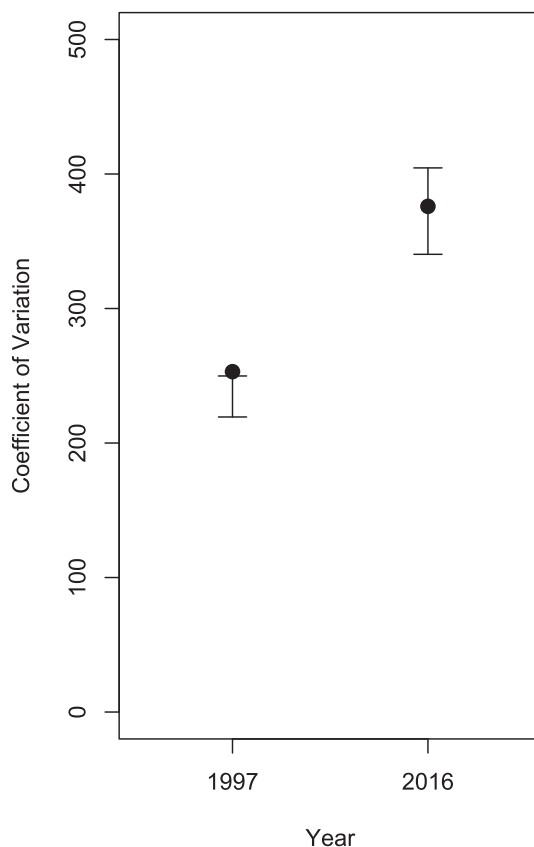


Fig. 4. Comparison of the observed network structure to the structure expected under indiscriminate flock membership. Points show the coefficient of variation values (black dots) from the 1997 and 2016 networks. Bars show the expected values (95% range of the Coefficient of Variation) based on a permutation test in which each species occurs the same number of times but are randomly allocated to flocks. While the 1997 network differs from random (the point is above the upper 95% quantile), the 2016 network does not.

mixed flocks) was 962 in the 1997 network and 572 in 2016. Using information from the published literature on bird trade, we identified 49 species that were part, or very likely to be part, of the bird trade in Sumatra. Of these, 44 were previously identified by Harris et al. (2017) from the same study site (see Table A2), and our study added an additional 5 species that were not observed in that study.

5.1. Are communities more structured than expected under indiscriminate flocking?

We constructed a separate social network for each of the two sampling periods (1997 and 2016). Summary statistics for these networks can be found in Table A3. We then tested whether the structure of these networks differed from networks formed by species flocking indiscriminately with others (but maintaining the same flock sizes). In the 1997 network, the comparison of the coefficient of variation (CV_{observed}) with the coefficient of variation from the randomisation process (CV_{random}) was significantly higher than random (CV_{observed} = 253, $P_{\text{rand}} = 0.003$; Fig. 4). By contrast, the 2016 network did not differ from chance (CV_{observed} = 376, $P_{\text{rand}} = 0.145$; Fig. 4), meaning that we cannot say that the species differentiate in their mixed flock attendance more than expected by chance (i.e. species participated in mixed flocks randomly with respect to species composition).

5.2. Are the 1997 and 2016 networks correlated?

Assuming that no anthropogenic disturbances occurred in the study site, we predicted that the 1997 and 2016 networks should be correlated. Despite the fact that the 2016 network did not differ from indiscriminate flocking (see above), the correlation in the edge weights between the two networks was greater than expected by chance (Mantel $r = 0.14$, $P_{\text{rand}} = 0.007$). This reflects some general stability in terms of flock membership. However, the correlation was relatively low and we observed some major shifts. From five species with the highest weighted degree values in 1997, only two species were in the top five species in 2016: the Blue-winged Leafbird and the Bronzed Drongo *Dicrurus aeneus* (Appendix S1). In 2016, the Asian Fairy-bluebird was the most central (weighted degree = 5.49), despite being peripheral in the 1997 network (weighted degree = 0.82).

5.3. Are traded species more central in the networks than non-traded species?

From the total of 90 species observed in mixed flocks (combined from the two samples), slightly more than half (54.4%) were identified as traded species (i.e. trade score > 0). In both networks, we found that the traded species had significantly higher centrality values (weighted degree) than the non-traded species ($\beta \pm \text{SE} = 0.126 \pm 0.153$, $P_{\text{rand}} = 0.019$ for the 1997 network, and $\beta \pm \text{SE} = 0.356 \pm 0.173$, $P_{\text{rand}} = 0.002$ for the 2016 network; Fig. 5). For example, the most central species in both years (1997: Blue-winged Leafbird, weighted degree = 5.40; 2016: Asian Fairy Bluebird *Irena puella*, weighted degree = 5.49) were traded species. The most central non-traded species were Rafflesia Malkoha *Rhinortha chlorophaeus* (1997, weighted degree = 4.76) and Black-winged Flycatcher-shrike *Hemipus hirsundinaceus* (2016, weighted degree = 4.20). These results were confirmed when using a binary score for trade status: in 1997 the mean degree for traded species was 1.88 versus 1.58 for untraded species ($P_{\text{rand}} = 0.008$), while in 2016 the mean for traded species was 1.83 versus 1.17 for untraded species ($P_{\text{rand}} = 0.004$). This latter analysis also reveals that the steeper relationship between trade score and centrality in 2016 ($\beta = 0.356$) versus 1997 ($\beta = 0.126$) is driven by a lower centrality in non-traded species in the latter year, rather than an absolute increase in centrality in traded species (see also Fig. 5).

5.4. Has the centrality of traded and non-traded species changed over time?

By subtracting the weighted degree for each species in 2016 from their weighted degree in 1997, we calculated the change in centrality over time. We found that species with higher trade scores had a significantly larger reduction in their weighted degree than non-traded species, and this reduction was larger than expected when compared to the randomised networks ($\beta \pm \text{SE} = -0.231 \pm 0.196$, $P_{\text{rand}} = 0.035$; Fig. 6). Although this effect is relatively small, it does suggest that the species with the highest trade score have an approximately 36% reduction in degree relative to the non-traded species. From 49 traded species, we found a reduction in centrality in 20 species (41%), whereas only 12 species out of 41 non-trade species (29%) decreased in centrality, which was a larger difference than expected when compared to the randomised networks ($P_{\text{rand}} = 0.020$).

5.5. Are mixed-species flocks resilient to the loss of central species?

We simulated the sequential removal of 10 traded species (from all networks) with the highest combined centrality values to test how resilient this correlation was to the further loss of central species. The simulation revealed a decrease in correlation between the network in 1997 and 2016 (black points in Fig. 7). After removal of the most central traded species (Blue-winged Leafbird), the network correlation was still different from random (i.e. the network still contained more

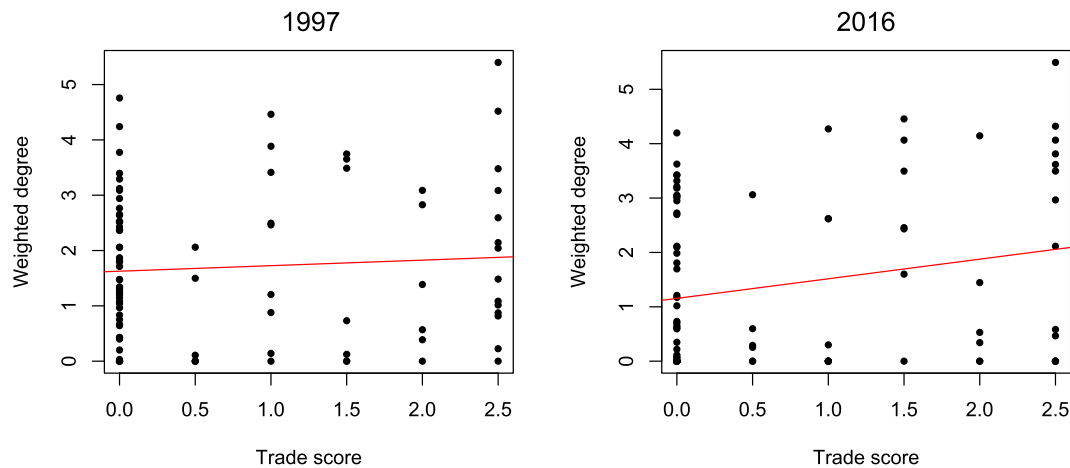


Fig. 5. In both years, there was a significant relationship between trade score and centrality in the network. Plots show the relationship between the observed trade score and the centrality value (weighted degree) for each species in mixed flock networks in 1997 (left) and 2016 (right). We calculated P values by comparing the observed coefficient value (red line) with a distribution of 1500 coefficient values drawn from a permutation test (see text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

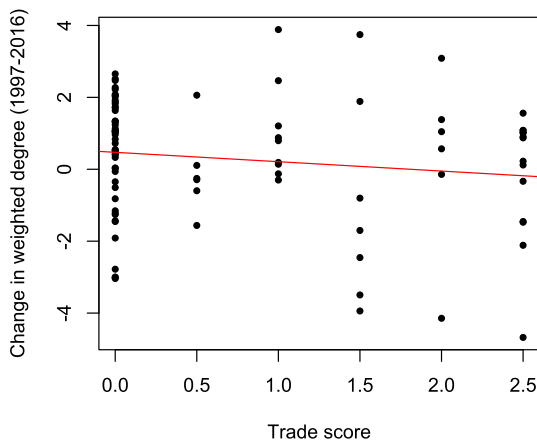


Fig. 6. Species with a high trade score had a significantly greater decrease in network centrality between 1997 and 2016. Plot shows the relationship between the observed change in centrality value for each species in mixed flocks and their trade score. We calculated the P value by comparing the observed coefficient value (red line) with a distribution of 1500 coefficients drawn from a permutation test (see text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

consistent preferred/avoided relationships across the two samples than expected by chance). However, the correlation across the two networks became inseparable from random after removal of the second species onwards. This suggests that the further loss of just two traded species,

on top of the existing changes already experienced in the system, could be sufficient to completely break down the structure of mixed-species flocking that was observed in the system prior to the onset of the bird trade in the study area.

6. Discussion

Mixed flocks represent an important social system in bird communities (Buskirk, 1976; Munn, 1985). To date, two main anthropogenic disturbances— forest fragmentation and land-use intensity – have been identified as causing negative effects on mixed flocking community structure (e.g., on species richness; Goodale et al., 2015). In this study, we demonstrate an additional potential effect—trapping for the bird trade—on structure in an avian community. Using data collected from the same forest subject to bird trapping almost 20 years apart, we found that mixed-species flocks observed in 2016 did not show evidence for containing preferred associations between species, unlike flocks observed in 1997. Flock sizes typically contained fewer species (but the same number of individuals per species), meaning that the resulting networks were less densely connected and with a lower mean degree, despite maintaining similar characteristics such as local clustering (see Table A2). Together, our findings suggest that the overall system has been disturbed. We then show evidence that changes in the network centrality of species was linked with their status in the bird trade. Finally, using simulations, we also showed that the current system may not be resilient to the complete loss of two or more of the currently traded species. Our results suggest that trapping is likely to be contributing to the degradation of mixed-species flocking patterns,

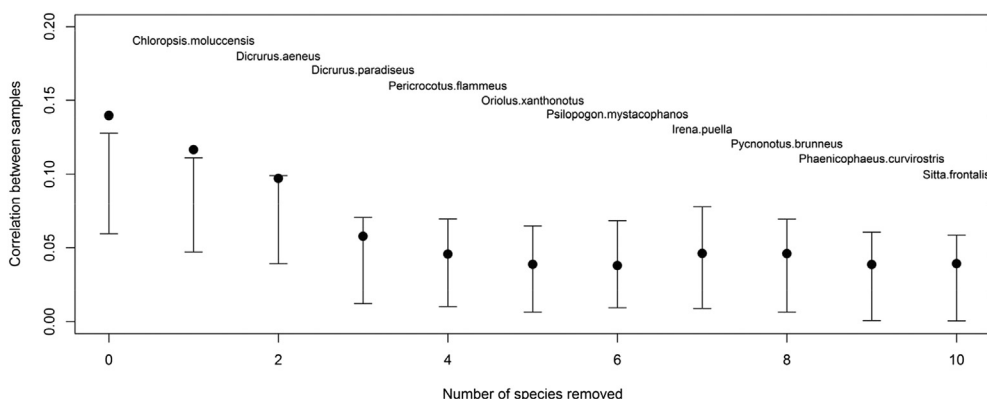


Fig. 7. The structure of the 2016 mixed-species flocking network is not resilient to the loss of more than one central traded species. Plot shows the correlation between the 1997 and 2016 networks (black dots) in the original network ($x = 0$), and after the simulated removal of up to 10 species with the highest degree that are part of the songbird trade. The bars represent the 95% range of the expected correlations based on the permutation test. Correlations where the black points overlap with the bars are not significantly different from random.

affecting both traded and non-traded species, and therefore could lead to widespread declines in the broader community structure of species that rely on mixed flocks for survival.

More than half of the species that participated in mixed flocks were traded. In both 1997 and 2016, these traded species had significantly higher centrality values than non-traded species. This finding suggests that, by being regular participants in flocks, traded species are likely to be important contributors to the maintenance of mixed flocks in this community. The fact that traded species were central in both periods is perhaps testament to having received some protection at the study site. However, despite this protection trapping remained active and we found that traded species had a significantly greater decrease in centrality over the two time periods than did non-traded species. While this could seemingly have arisen because the traded species have become less common, all of our analysis were based on permutation tests that only swap the identities of species observed in mixed flock (rather than generating flocks at random), thus maintaining constant the number of observations per species (i.e. the abundance in mixed flocks) in our statistical testing. Thus, if a pattern differs from chance, it differs from the distribution of the null hypothesis that is drawn using exactly the same number of observations, and therefore represents a significant change independent of changes in how often each species was observed. The hypothesis that changes occurred due to declines in abundance therefore seems unlikely. Rather it appears that the bird trade has driven a change in behaviour of several, or many, species.

The changes in species' flocking behaviour could be because being targeted by bird traders changes their behaviour, or their perceived value by other species. For example, associating with Blue-winged Leafbirds may now be less beneficial or more risky than it was 20 years ago. While this process remains speculative, changes in behaviour in relation to risk has been noted in a number of relevant studies. For example, Hua et al. (2013) conducted playbacks of predators in habitat patches and found that while some species reduced in abundance (suggesting they left those patches), others instead became more cryptic (i.e. they reduced in their observability). A more directly relevant example is the White-rumped Shama, a species that is valued for its song and easily trapped (including in Sumatra) because of its combative response to playback (Eaton et al., 2015). During surveys conducted in Way Kambas National Park, Lampung (Sumatra), birds were noted as being silent when discovered, and only sang very quietly in response to playback (Eaton et al., 2015). This change in behaviour may have evolved because combative individuals are more easily caught, and thus trapping has generated strong selection against responding to vocalisations. Vocalisations have been widely reported as being important for the formation and maintenance of mixed flocks (Goodale and Kotagama, 2006; Pagani-Núñez et al., 2018). Selecting for reduced vocalizing could change the attractiveness of the species. Thus, the pursuit of highly prized species in the bird trade could affect communities not just directly as a result of removal of birds and mortality during bycatch, but also if the effect of being caught drives behavioural changes in species (both targeted and non-targeted) within the community.

We also conducted simulations to investigate the effect of complete removal of traded species, and found that the overall community is potentially not very resilient to the loss of important species (i.e. those species that interact with many species and were observed to be central). Although this is the worst case scenario (i.e. extinction of species from the forest) and a relatively simplistic simulation (i.e. it does not account for re-structuring of the network in case of a loss of a species), it at least indicates the urgency to protect traded species that are important contributors to mixed flocks. In an effort to initiate conservation efforts, the first Songbird crisis summit was held in 2015 in response to the songbird trade in the Greater Sunda region, and tried to identify the most threatened songbirds and propose actions to save them from extinction (Lee et al., 2016). The second meeting was held at the beginning of 2017. They identified 28 priority species, in which

three species have been identified as forming mixed flocks: White-rumped Shama, Grey-cheeked Bulbul, and Asian Fairy Bluebird. The latter is particularly important as we found that it had replaced other species as the most central in the 2016 mixed flock network. Thus, the protection of species will need to be dynamic if the behaviour of the traders and of the species are both responding to the changing dynamics in these songbird communities.

The capture of species in flocks arising from the wildlife trade could have additional broader impacts. From the 90 species recorded participating in mixed flocks, 21 species include fruits as part of their diet where 17 species were categorized as traded species (had been recorded in the bird market). Considering their potential roles in seed dispersal and the potential impact of bird trade to their population, the bird trade might also affect seed dispersal within these systems. Several flock-attending species, such as Red-throated Barbet *Psilopogon mystacophanos*, Spectacled Bulbul *Pycnonotus erythrophthalmos*, and Yellow-bellied Bulbul *Alophoixus phaeocephalus*, incorporate a large amount of fruit in their diet. Declines in these species could potentially limit their effectiveness at dispersing some fruits, as has been shown in other studies (e.g. McConkey and O'Farrill, 2016). However, whether any fruiting species rely heavily on species that form mixed flocks for seed dispersal in our study area is unknown, and warrants further investigation.

Social network analysis is a powerful tool for wildlife conservation (Snijders et al., 2017). Although the impact of anthropogenic disturbances (fragmentation or different land-use intensity) on mixed-species flocking has been widely documented (e.g., Stouffer and Bierregaard, 1995; Maldonado-Coelho and Marini, 2000; Sridhar and Sankar, 2008; Goodale et al., 2015), only one previous study used network analysis; examining the impact of forest fragmentation on mixed flock characteristics (Mokross et al., 2014). In that study, the associations among species, as shown by weighted degree, declined with increasing level of forest fragmentation and secondary forest (Mokross et al., 2014). This means that there was a reduction in mixed flock attendance with increasing habitat disturbance (Mokross et al., 2014). This result was also not attributed to a reduction in species abundance: despite several species having lower abundance, they still persisted in the degraded habitats (Stouffer and Bierregaard, 1995; Mokross et al., 2014). Social network analysis allowed us to find almost identical evidence of changes in mixed flock composition, with reduced richness and reduced weighted degree in 2016 compared to 1997. However, unlike in the previous study that focused on habitat effects, our changes arose from trapping from the bird trade.

It is becoming increasingly clear that mixed-species flocking plays an important part in the social system of many bird species. By using network analysis we evaluated the potential impact of bird trapping to mixed flocks in Sumatra. We note that the bird trade is notoriously difficult and dangerous to study. We made use of the best available and most local data we could find, and these data match the sentiment based on our, and others', experience of the study area. Traded species are important component of mixed flocks in our study area. By comparing data on mixed flocks from surveys almost 20 years apart, we have shown a degradation of the structure of mixed species flocks over time (measured independently of the trade score), and significant reductions in the centrality of traded species in mixed flock networks (both in terms of their score and a simple traded versus non-traded status, and using a permutation test that controlled for potential changes in abundance over the two sampling periods). Although the mechanisms leading to reduced attendance of species in mixed flocks are still not clear, our data suggests that bird trapping could have impacts beyond reductions in abundance alone. It is well established that the absence of nuclear species can significantly impact the behaviour of remaining species (Dolby and Grubb, 1998; Dolby and Grub, 2000). We add the suggestion that the perceived value of traded species to other attendant species in their flocks might also be reduced as a result of changes in behaviour or due to the higher risk of being caught as by-catch, even if they are not completely absent. Thus, both direct and

indirect effects of the bird trade on other flock participants may occur, and require urgent investigation. Further, protection and enforcement will need to be strengthened to protect not only species that have been identified as being in decline, but also to protect species that play an important role in the broader avian community (i.e. those that are central in mixed flocks, contributing either functionally or as attendant species contributing towards group augmentation).

Data accessibility

Raw data and R scripts can be downloaded from: <https://dx.doi.org/10.17617/3.1a>

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Appendix A. Supplementary tables

Additional supporting tables including: Table A1: a table of bird species observed in mixed flocks with their trade scores and respective weighted degree values in 1997 and 2016 (Appendix S1), Table A2: table of species identified as traded by Harris et al. (2017), a study conducted at the same study site as us, and Table A3: a table containing summary statistics of the survey data and the resulting networks. The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author. Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.04.015>.

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