Species importance in a heterospecific foraging association network

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There is a growing recognition of the need to integrate non-trophic interactions into ecological networks for a better understanding of whole-community organization. To achieve this, the first step is to build networks of individual non-trophic interactions. In this study, we analyzed a network of interdependencies among bird species that participated in heterospecific foraging associations (flocks) in an evergreen forest site in the Western Ghats, India. We found the flock network to contain a small core of highly important species that other species are strongly dependent on, a pattern seen in many other biological networks. Further, we found that structural importance of species in the network was strongly correlated to functional importance of species at the individual flock level. Finally, comparisons with flock networks from other Asian forests showed that the same taxonomic groups were important in general, suggesting that species importance was an intrinsic trait and not dependent on local ecological conditions. Hence, given a list of species in an area, it may be possible to predict which ones are likely to be important. Our study provides a framework for the investigation of other heterospecific foraging associations and associations among species in other non-trophic contexts.

Species in communities are enmeshed in a web of multiple interactions. For a clear picture of community organization, it is not enough just to focus on species identities, but also to understand the interaction web (Paine 1966, Ings et al. 2008). Incorporation of network analysis in ecology has helped this endeavor by offering a suite of metrics at the species, interaction and whole-community level (Estrada 2007). While the network approach has largely been restricted to trophic interactions such as food webs and plant-animal mutualisms (Ings et al. 2008; although mutualistic networks also include indirect non-trophic interactions, e.g. pollinators linked through a shared host-plant) and host-parasite interactions (Blick et al. 2012), emphasis has been placed on incorporating direct non-trophic interactions (Kéfi et al. 2012, Pocock et al. 2012) in order to gain a more complete picture of community organization. A first step towards this is building and understanding direct non-trophic interaction networks.

Direct non-trophic interactions are usually thought of only in terms of competition; recent work has however highlighted the prevalence of positive interactions in communities and the need to incorporate them into ecological theory (Bruno et al. 2003). Till date, only a few positive interactions, such as cleaner fish mutualisms (Sazima et al. 2010) and nurse plant-seedling facilitations (Verdú and Valiente-Banuet 2008), have been visualized and examined using the network approach. In this study, we extend it to a class of positive interactions that are fairly common in a foraging context, namely heterospecific foraging associations,

i.e. temporary social groups formed by individuals of different species (Morse 1977). Individuals joining such groups are known to benefit either through direct foraging facilitation, better protection from predators, or improved foraging as a consequence of reduced vigilance (Sridhar et al. 2009). Across multiple such groups in an area, populations of different species can be viewed as linked in an ecological network of interdependencies.

Heterospecific foraging associations have been documented from numerous taxa including invertebrates, fishes, birds and mammals (reviewed by Morse 1977). Here we examined the most prominent and speciose of these associations, mixed-species bird flocks (flocks hereafter) in terrestrial habitats. Flocks are known to form important subunits of terrestrial bird communities the world over (Goodale et al. 2010) with substantial proportions of total bird species, particularly insectivores, in each community participating in flocks (King and Rappole 2001). Flocks can range in size from just two heterospecific individuals to over a hundred individuals representing tens of species (Terborgh 1990). Different lines of evidence, such as obligate flock participation of species (Munn and Terborgh 1979, Jullien and Thiollay 1998) and links between flock participation and life-history traits (Jullien and Clobert 2000), suggest that flocks play a fairly important role in species' ecologies. Given this, it is likely that interdependencies among flock participant species could scale up to influence patterns at higher levels (Goodale et al. 2010) including other ecological networks of which these species form a part.

In this study we focused on species importance in the flock network. Quantifying species importance allows us to identify hubs or 'keystone species' i.e. those that are likely to have disproportionately large effects on flock ecology and evolution and whose removal could have cascading effects on communities in question (Jordán and Scheuring 2002, Estrada 2007, Pocock et al. 2012). This approach also allows us to examine whether processes at the level of individuals scale up to influence properties at the community level (Bascompte and Stouffer 2009, Stouffer 2010). Numerous studies, across flock systems from different geographic regions, have clearly shown two kinds of species to be functionally important in flocks: those which are found in conspecific groups (intraspecifically gregarious species) and those which feed by catching insects in air with short flights from stationary positions (sallying species; Hutto 1994, Goodale and Kotagama 2005, Sridhar et al. 2009, Srinivasan et al. 2010). Individuals of such species are often the 'nucleus' or leaders of flocks, presumably because of the direct benefits that other species gain by associating with them (Hutto 1994, Sridhar et al. 2009). Quantifying species importance in the flock network allows us to examine the link between functional importance in individual flocks and emergent community importance. This is particularly important since studies have demonstrated that the local extinction of functionally important species can result in the cessation of mixed-species flock activity even when other flock participants are present. (Stouffer and Bierregaard 1995). Going beyond the specifics of particular study sites, it is also useful to examine the generality of species importance in communities i.e. whether species importance is linked to a specific ecological setting or is an intrinsic characteristic of a species (Stouffer et al. 2012)? The latter, if true, will mean that a species' importance in networks can be predicted by its taxonomic or phylogenetic classification.

In this study we examined an ecological network formed as a result of flock participation in an evergreen forest site in the central Western Ghats, India. Nodes in this network represent species and edges represent level of co-occurrence in flocks. Edges in ecological networks typically represent direct interactions but given that characterizing interactions between a pair of species in multi-species flocks is intractable, we used co-occurrence as a proxy for interaction or interdependencies in flocks (following Araújo et al. 2011). To our knowledge, our dataset is the best-resolved (in terms of flocks sampled) flock co-occurrence matrix available till date. We examined three main questions in this study:

1. How is positional importance distributed across species in the flock network?
2. Is positional importance of species in networks linked to functional importance at the flock level?
3. Is species importance linked to taxonomy, i.e. are importance values of bird species, genera and families similar between our study site and other Asian wet forest sites?

Our study found that flock networks contain a small core of highly important species and that positional importance in the network was strongly correlated to functional importance of species at the individual-flock level. Comparisons

with other Asian wet forest sites showed that importance values were strongly congruent at species, genus and family levels.

Material and methods

Empirical data set

We conducted fieldwork in an evergreen forest site in Anshi National park (15°00'97.8"N, 74°38'72.2"E) situated in the Western Ghats mountain range along the west coast of India (Fig. 1). We collected data between January and March in 2010 and 2011, which is the non-breeding season for most evergreen forest bird species. Data collection was carried out along twelve trails in a 26 km² focal study area around the Anshi nature camp and Anshi village (Fig. 1). The minimum distance between flock locations on different trails was 500 m. Each trail was surveyed four times in 2010 and three times in 2011. On each trail walk, carried out between 08:30–15:00 h, two observers searched for mixed-species bird flocks. Flocks were defined as roving associations of two or more species, staying together for at least five min. The five minute cutoff was used to minimize the possibility of including chance groupings of independently moving heterospecifics. However, to obtain reasonable 'snapshots' of flock composition and minimize the likelihood of species turnover, we restricted observation time to 15 min per flock. We designated a species as belonging to the flock if it was within 10 meters of at least one other heterospecific individual. While it is possible that heterospecifics gain benefits of association even at distances greater than 10 m, this cutoff is often used in flock studies in dense forest habitats (Hutto 1994) because of poor detectability beyond 10 m. We included all species seen at least once during flock observation as being part of the flock. Though species differed in their detectabilities, given the lengths of our observations (5–15 min) it is likely that a species, if present in the flock, would have been detected. Nevertheless, even if we missed recording species of poor detectability in some flocks, it is unlikely to systematically bias species associations, our main variable of interest. Our observations were restricted to roving associations of insectivores and did not include frugivorous flocks, which are likely to be the result of species independently aggregating at clumped resources (Greenberg 2000); our interest was only in flocks that are likely to have formed as a result of interactions between species. We recorded 247 flocks including 52 species in 2010 and 250 flocks including 49 species in 2011. Flocks included an average of 6.7 (± 0.25 SE) species and 24.4 (± 0.83 SE) individuals in 2010 and 4.9 (± 0.24 SE) species and 18.9 (± 0.77 SE) individuals in 2011. Though our sampling involved repeating the same trails, we decided to treat flocks seen at the same locations on different days as independent data points for the following reasons. First, our field observations indicated that flocks form and dissociate on a scale of minutes to hours and therefore, flocks from the same location on different days represent outcomes of independent flock formation events. Second, a cluster analysis of flocks based on composition, implemented

Figure 1. Map showing location of Anshi National Park, Western Ghats, India and sampling locations (filled circles) within the focal study area. Anshi village is indicated by an open square and Anshi nature camp by an open triangle.

in R (R Development Core Team) showed flocks from the same locations to be dispersed across the dendrogram and not clustered together (Supplementary material Appendix 1), i.e. location did not predict flock composition. Using data collected from field sampling, we constructed separate presence–absence matrices for 2010 and 2011. In each matrix, rows represented species, columns represented flocks, and ‘1’s and ‘0’s represented presence and absence of species in flocks respectively. Only species occurring in more than three flocks in a year were included in the network for that year because association patterns calculated from small sample sizes are unlikely to be reliable.

Apart from flock composition, we also recorded intra-specific group size and foraging behaviour of species in flocks, wherever possible. This was used to identify species which belonged to functionally important guilds (intra-specifically gregarious species and solitary sallying species; Hutto 1994, Goodale and Kotagama 2005, Sridhar et al. 2009, Srinivasan et al. 2010). For group size, we carried out complete counts of individuals of each species in a flock whenever possible; where full counts were not possible, we recorded intra-specific group sizes of species in appropriate class intervals. We carried out focal animal samples of randomly-selected flock participants to quantify the relative proportions of different foraging behaviours (glean, probe, peck, sally-glean, sally).

Association index

We weighted edges between species in network as follows. We used species pairwise co-occurrence values (number of

flocks in which both species are present) calculated from the presence–absence matrices as proxies for interaction strength. Based on these values, we characterized the link between each pair of species using an asymmetric association index thought to be appropriate for interactions based on joint co-occurrences in groups (following Araújo et al. 2011). This association index assumes that the effect of one species on another is proportional to the percentage of the latter’s flocks in which the former occurs. For example, if species A occurred in 50 flocks, species B occurred in 25 flocks and A and B co-occurred in 20 flocks, then;

$$\text{effect of A on B} = 20/25 = 0.8$$

$$\text{effect of B on A} = 20/50 = 0.4$$

Networks

Using data from each sampling year separately, we built two kinds of networks, based on different association cut-offs. In both networks, nodes represent individual species. First, we built a network using all pairs of species that were seen together in flocks at least once. We call this the ‘all associations’ network. The use of such networks has been criticized on the grounds that associations in them are likely to strongly reflect differences in abundances of individual species (Croft et al. 2008). However given that we are interested in species importance, whether in terms of active choice or passive sampling, the ‘all associations’ network is biologically relevant in our study. We also build a second network including only pairs of species that co-occurred

significantly more than expected by chance; links in this network are more likely to reflect active choice of species. We identified significant pairs as follows: first, we used a null model implemented through the program ECOSIM (Gotelli and Entsminger 2001) to randomize the flock presence-absence matrix of each year and create a set of random matrices. Our null model algorithm retained total occurrences of each species in flocks (row totals); benchmark tests have shown that null models which retain row totals are least susceptible to type 1 errors (Gotelli 2000); observed richness of flocks (column totals) were treated as probabilities (i.e. the probability of a species being placed in a particular flock in a random matrix was proportional to the observed species richness of that flock). While we used only one null model algorithm here, results using algorithms treating column totals as fixed or columns as

equiprobable were very similar (Sridhar et al. 2012). Using the observed data matrix and 5000 random matrices we identified significantly positively associated species pairs using software cooc (Sfenthourakis et al. 2006). A significantly positively associated pair was one whose observed co-occurrences lies in the higher tail (>95%) of the histogram of co-occurrences from the random matrices. We call this the 'significant associations' network. The edges between species, both in 'all associations' and 'significant associations' networks were weighted using the association index described in the previous section.

Network measures

We calculated species importance using two weighted node centrality measures:

Table 1. Species characteristics and positional importance in mixed-species bird flocks in Anshi national park, Western Ghats, India indicated by two different network measures (nWD_{out} and WI^3). Measures are calculated separately for data from two years (2010 and 2011) and for 'all associations' and 'significant associations' networks. Species are arranged in decreasing order of average across all standardized measures. Values were standardized by dividing by the maximum importance value for that index. Six species that consistently emerged as important in all calculated indices and which had substantially greater importances compared to remaining species are indicated in bold. Functional guild categories include intraspecifically gregarious (ig), solitary sallying (ss) and functionally unimportant (fu). In 'Resident or migrant' column, 'r' indicates resident species and 'm' indicates winter migrant.

Scientific name	Functional guild	Resident or migrant	code	2010				2011			
				all pairs		significant pairs		all pairs		significant pairs	
				nWD	WI^3	nWD	WI^3	nWD	WI^3	nWD	WI^3
<i>Phylloscopus occipitalis</i>	ig	m	35	76.89	3.37	25.87	4.12	65.10	2.89	19.41	1.95
<i>Alcippe poioicephala</i>	ig	r	03	69.60	3.00	18.58	2.46	72.60	3.14	29.19	2.73
<i>Dicrurus paradiseus</i>	ss	r	16	56.23	2.35	28.03	3.36	62.07	2.60	30.93	2.78
<i>Pericrocotus flammeus</i>	ig	r	27	53.29	2.22	20.65	2.25	57.13	2.33	25.85	2.44
<i>Hypothymis azurea</i>	ss	r	05	61.40	2.74	17.55	2.42	50.23	2.27	22.11	2.13
<i>Iole indica</i>	fu	r	36	69.91	2.99	12.48	1.95	51.80	2.28	21.30	B2.19
<i>Phylloscopus trochiloides</i>	fu	m	17	43.74	1.96	7.48	1.10	42.30	1.85	22.96	2.24
<i>Sitta frontalis</i>	fu	r	30	27.49	1.05	12.68	1.59	24.80	1.00	8.48	1.29
<i>Terpsiphone paradisi</i>	ss	r	01	34.23	1.50	7.16	1.03	23.20	1.05	11.26	1.01
<i>Dicrurus leucophaeus</i>	ss	m	02	29.86	1.20	8.48	1.25	28.33	1.19	6.11	1.20
<i>Cyornis pallipes</i>	fu	r	32	21.11	0.96	1.94	0.29	19.17	0.83	9.78	1.27
<i>Tephrodornis gularis</i>	ig	r	19	16.43	0.64	9.16	1.28	15.77	0.64	5.93	0.69
<i>Dicrurus aeneus</i>	ss	r	06	15.89	0.61	6.74	0.68	16.43	0.65	7.82	1.12
<i>Zosterops palpebrosus</i>	ig	r	24	33.37	1.49	1.19	0.25	27.80	1.21	0.00	0.00
<i>Megalaima viridis</i>	fu	r	34	20.31	0.84	5.94	0.94	8.67	0.39	5.26	0.62
<i>Rhopocichla atriceps</i>	ig	r	10	17.17	0.77	4.74	0.65	11.50	0.52	3.48	0.48
<i>Picumnus innominatus</i>	fu	r	28	16.40	0.71	2.19	0.35	12.73	0.56	4.44	0.45
<i>Pomatorhinus horsfieldii</i>	fu	r	26	18.29	0.80	4.26	0.77	9.80	0.52	1.19	0.21
<i>Coracina melanoptera</i>	fu	r	04	11.91	0.49	2.23	0.43	12.37	0.54	4.63	0.64
<i>Harpactes fasciatus</i>	fu	r	22	12.03	0.60	2.13	0.28	13.10	0.61	4.67	0.53
<i>Picus chlorophus</i>	fu	r	21	10.54	0.45	1.36	0.33	17.93	0.76	3.59	0.43
<i>Chloropsis aurifrons</i>	fu	r	14	15.74	0.60	6.03	0.86	7.07	0.33	0.00	0.00
<i>Hemipus picatus</i>	fu	r	07	11.11	0.45	4.39	0.52	7.23	0.30	3.04	0.34
<i>Oriolus oriolus</i>	fu	m	11	13.91	0.62	1.94	0.27	14.80	0.62	1.07	0.10
<i>Aegithina tiphia</i>	fu	r	09	14.60	0.59	3.65	0.60	5.53	0.27	0.00	0.00
<i>Hemicircus canente</i>	fu	r	18	6.43	0.29	2.32	0.27	8.40	0.36	2.15	0.23
<i>Phylloscopus magnirostris</i>	fu	m	20	8.23	0.39	0.39	0.07	7.10	0.32	1.48	0.34
<i>Dinopium javanense</i>	fu	r	08	4.89	0.21	0.68	0.14	9.70	0.42	1.44	0.16
<i>Eumyias thalassina</i>	fu	m	29	5.06	0.24	0.00	0.00	7.27	0.31	2.74	0.34
<i>Loriculus vernalis</i>	fu	r	31	10.37	0.41	3.32	0.47	0.00	0.00	0.00	0.00
<i>Zoothera citrina</i>	fu	m	23	7.43	0.34	1.61	0.31	3.37	0.16	1.04	0.05
<i>Dendronanthus indicus</i>	fu	m	13	2.11	0.09	0.81	0.64	0.00	0.00	0.00	0.00
<i>Dendrocitta leucogastra</i>	fu	r	33	4.23	0.21	0.32	0.06	1.60	0.09	0.22	0.04
<i>Irena puella</i>	fu	r	12	7.34	0.37	0.00	0.00	0.00	0.00	0.00	0.00
<i>Chrysocolaptes lucidus</i>	fu	r	15	7.11	0.33	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pycnonotus gularis</i>	fu	r	25	2.51	0.13	0.00	0.00	0.00	0.00	0.00	0.00

Weighted degree – a local view

For characterizing the immediate, local neighbourhood of species in the flock network, we calculated their normalized weighted out-degree (nwD_{out}):

$$nwD_{out} = (100 \times wD) / ((N - 1) \times wD_{max})$$

where wD is the weighted out-degree (the sum of weights on links going out from a node), N is the number of nodes in the network and wD_{max} is the largest weighted out-degree in the network (Wassermann and Faust 1994).

Weighted importance – a mesoscale view

The topological importance (TI) measure was developed for the explicit study of indirect effects up to a given length (Jordán et al. 2003). The simplest case of calculating the effect of node j on node i ($a_{n,ij}$) is when $n = 1$ (i.e. the effect is direct):

$$a_{1,ij} = 1/D_i$$

where D_i is the degree of node i . We assumed that indirect effects are multiplicative ($a_{2,kj} = a_{1,ij} \times a_{1,ki}$) and additive ($a_{2,kj} = a_{1,ij} \times a_{1,ki} + a_{1,mj} \times a_{1,km}$). In weighted networks, the same calculation can be based on wD and the WI importance of network nodes is given by

$$WI_i^n = \frac{\sum_{m=1}^n \sigma_{m,i}}{n} = \frac{\sum_{m=1}^n \sum_{j=1}^N a_{m,ji}}{n}$$

where the α values are the individual $i-j$ effects in the weighted network (for a detailed explanation, see Jordán et al. 2003). This index provides a general, topological measure for the positional importance of nodes in weighted networks (Jordán et al. 2003).

Species importance

We compared species importance values across different measures (weighted degree vs weighted importance), association cutoffs (all associations vs significant associations) and years (2010 vs 2011) using Spearman's rank correlations and found strong correlations in all cases (Supplementary material Appendix 2). To examine the relationship between functional importance in flocks and positional importance in networks, we compared importance values of species known to be functionally important in flocks (intraspecifically gregarious species and solitary sallying species; Hutto 1994, Goodale and Kotagama 2005, Sridhar et al. 2009, Srinivasan et al. 2010) and other species in the network. We categorized all species with modal intra-specific group size greater than three as intraspecifically gregarious. Sallying species were those for whom sallying i.e. catching insects in the air, was the most common foraging method ($>80\%$ of foraging maneuvers); five species in our dataset foraged primarily by sallying, while for all other species sallying accounted for less than 2% of foraging maneuvers. We found no overlap in functional guilds in our dataset, i.e. none of the species were both intraspecifically gregarious and foraged primarily by sallying. Species which did not possess either of the

traits associated with functional importance, i.e. had modal group sizes less than three and rarely foraged by sallying ($<2\%$ of foraging maneuvers), we lumped together as functionally unimportant species. Given the non-normality of the data, we compared importance values of the three species categories using a randomized ANOVA implemented through the program ECOSIM (Gotelli and Entsminger 2001). In a randomized ANOVA, the test statistic from the observed groups is compared to statistics obtained from groups created by random shuffling of the same data (1000 iterations). To examine the generality of species importance we also built networks using data from flocks in four other Asian sites (Supplementary material Appendix 3 Table A3), obtained from the authors of those studies. We wrote to authors of these studies and requested them to share unpublished flock co-occurrence matrices. The sites included Manamboli in southern Western Ghats, India ($10^{\circ}12'N$, $76^{\circ}49'E$; Sridhar and Sankar 2008), Namdapha in eastern Himalayas, India ($27^{\circ}23'N$, $96^{\circ}15'E$; Srinivasan et al. 2010), Sinharaja in Sri Lanka ($6^{\circ}26'N$, $80^{\circ}21'E$; Kotagama and Goodale 2004) and Khao Yai in Thailand ($14^{\circ}26'N$, $101^{\circ}22'E$; Nimnuan et al. 2004). All the comparison sites were primarily composed of evergreen forest and are therefore likely to be structurally similar to our study site. We could not build

Figure 2. Networks in (a) 2010 and (b) 2011, of species co-occurrences in mixed-species bird flocks in an evergreen forest in central Western Ghats, India. Links are shown between species associating more than expected by chance. Nodes sizes indicate their nwD_{out} values; the sizes were almost identical for WI^3 measures. The six most important species in the 2010 network and seven most important species in the 2011 network are shown in black. Key to the species codes are provided in Table 1.

'significant association' networks for the comparison sites because of the small sizes of the datasets and therefore our comparisons are based only on 'all association' networks. We compared importance values of species in our study site with average importance values of same species across the comparison sites using Spearman's rank correlations. Given that only a small proportion of species were common to all sites, we also examined relationships at genus and family levels.

Results

Identifying important species

We consistently found a small core of highly important nodes in our networks (Table 1, Fig. 2, 3). This subset always included the following six species: western crowned warbler *Phylloscopus occipitalis*, greater racket-tailed drongo *Dicrurus paradiseus*, brown-cheeked fulvetta *Alcippe poiocephala*, black-naped monarch *Hypothymis azurea*, yellow-browed bulbul *Iole indica* and scarlet minivet *Pericrocotus flammeus*. Greenish warbler *Phylloscopus trochiloides* belonged to this subset in 2010, but not in 2011 (Table 1, Fig. 2, 3).

Guild-level comparison

In all eight sets of importance values (two network measures $\times$ two association cutoffs $\times$ two years), we found that functionally important groups of species (intraspecifically gregarious species and solitary sallying species) had significantly higher importance values compared to functionally unimportant species (solitary plant-substrate foragers;

randomized ANOVA, $p < 0.005$ in all cases; Fig. 4). Further, pair-wise tests revealed that the two functionally important groups did not differ in importance values (randomized ANOVA, $p > 0.65$ in all cases) but they both, independently, had significantly higher importance values compared to the functionally unimportant species (randomized ANOVA, $p < 0.0169$ (Dunn-Sidak p corrected for multiple comparisons) in all cases).

Comparisons with other Asian sites

We found significant correlation of importance values between our study site and other sites in the Asian region at the species (WI^3 : $\rho = 0.57$, $p = 0.002$; nWD_{out} : $\rho = 0.56$, $p = 0.0024$; Fig. 5a), generic (WI^3 : $\rho = 0.67$, $p = 0.0006$; nWD_{out} : $\rho = 0.61$, $p = 0.0012$; Fig. 5b) and family (WI^3 : $\rho = 0.73$, $p = 0.002$; nWD_{out} : $\rho = 0.67$, $p = 0.0046$; Fig. 5c) levels.

Discussion

Our study provides a first description of species importance in a heterospecific foraging association network. The main features of the network revealed by our study are: 1) a small invariant core of important species; 2) link between importance in network and functional importance at the individual flock level. Additionally, comparisons with flock networks from other Asian sites showed that particular taxonomic groups are important wherever they occur. This suggests that importance is a trait intrinsic to species, independent of ecological context (see also Stouffer et al. 2012).

Figure 3. Rank-importance graph of species in mixed-species bird flocks in Anshi National park based on average of standardized values across different network measures and association cutoffs for each year. Species forming the core of networks in both years are indicated. These include *Phylloscopus occipitalis* (Rank 1 in 2010; 4 in 2011), *Dicrurus paradiseus* (2 in 2010; 2 in 2011), *Alcippe poiocephala* (3 in 2010; 1 in 2011); *Hypothymis azurea* (4 in 2010; 6 in 2011); *Iole indica* (5 in 2010; 5 in 2011) and *Pericrocotus flammeus* (6 in 2010; 3 in 2011). *Phylloscopus trochiloides* (7 in 2010; 7 in 2011) falls into the cluster of important species in 2011, but not in 2010.

Core of important species

Across network metrics, association cutoffs and sampling years we consistently found a small core of important species in the flock network, a pattern confirming earlier non-network based descriptions of the flock system (Greenberg 2000; Table 1, Fig. 2, 3). Moreover, the identity of this core was largely invariant. In other words, the same species were important both in terms of direct and indirect effects, considering all associations or only significant associations, and in different years. Studies have indicated that a small core of important species, if present in a network, can strongly influence its ecology and evolution (Jain and Krishna 2002, Bascompte and Jordano 2007, Sazima et al. 2010). This is all the more likely in the case of core species of our network because of their importance from multiple considerations (Sazima et al. 2010). In the context of flocks, an aspect of species ecology that is particularly important is

the ability to recognize heterospecific vocalizations. Species are known to eavesdrop on heterospecific alarm calls in flocks (Goodale and Kotagama 2005) and use vocal cues to find other species (Saracco et al. 2004). The network structure we described suggests that flock participants are likely to benefit most by learning to recognize the alarm calls and other vocal cues of the central core of species.

Functional vs positional importance

Given the existence of a small core of key species, understanding the factors underlying their importance is crucial. Our study revealed a strong link between functional importance of species at the flock level and positional importance in the network (Fig. 4). Numerous studies have found two kinds of species to be functionally important in flocks (Hutto 1994, Srinivasan et al. 2010). Intra-specifically gregarious species are known to lead flocks

Figure 4. Comparison of average ($\pm$ 95% CI) WI^3 values of functionally important (intraspecifically gregarious and solitary sallying) and unimportant species in mixed-species bird flocks in Anshi national park. Groups labeled with different alphabets were significantly different in WI^3 values. Comparisons are shown separately for ‘significant associations’ networks in 2010 (a) and 2011 (b). Graphs for nwD_{out} values or those based on using ‘all association’ networks were almost identical to those based on WI^3 values in ‘significant associations’ networks and are therefore not shown. Numbers in parentheses in x-axis title indicate number of species.

more often than non-gregarious species presumably because of the anti-predatory and direct feeding benefits they provide (Sridhar et al. 2009, Srinivasan et al. 2010). Even in our study site, we found that intraspecifically gregarious species were leaders of flocks more than expected by chance (unpublished data). Sallying species do not provide direct foraging benefits to flock associates but potentially warn them of the presence of predators, i.e. they function as sentinels (Goodale and Kotagama 2005). Our study found that intraspecifically gregarious species and solitary sallying species tended to have significantly higher importance values in networks compared with other species, but did not differ in importance from each other. In fact, five of the six species that formed the core of our flock network were either intraspecifically gregarious (*Alcippe poioicephala*,

Phylloscopus trochiloides and *Pericrocotus flammeus*) or solitary sallyers (*Dicrurus paradiseus* and *Hypothymis azurea*).

It is important to note however, that there was a fair amount of variation in positional importance even within functional groups (range of average standardized importance values = 0.98–0.15). Also, the core in our network included one species which is not known to be functionally important at the individual-flock level (*Iole indica*). These two observations suggest that there are traits apart from functionality which also influence positional importance in networks. Studies have indicated that abundance could play an important role in influencing importance in networks (Lewinsohn et al. 2006). While we did not systematically quantify species abundance, our field observations indicate that the core species in our networks are among the

Figure 5. Relationships between species importance values (WI^3) in all association networks in Anshi and average important values in other evergreen forests in the Asian region measured at the species (a), genus (b) and family (c) level. The sites included Manamboli in southern Western Ghats, India (10°12'N, 76°49'E), Namdapha in eastern Himalayas, India (27°23'N, 96°15'E), Sinharaja in Sri Lanka (6°26'N, 80°21'E) and Khao Yai in Thailand (14°26'N, 101°22'E). Importance values for Anshi are averaged across 2010 and 2011. All correlations are significant (Spearman's rank correlation, $p < 0.05$). The relationships were almost identical using nWD_{out} values and are therefore not shown.

more common species in our study site and in other sites in the Western Ghats (Ranganathan et al. 2008). In fact, our field observations suggest that the one species in the core of our networks which is not known to be functionally important at the individual-flock level (*Iole indica*) is probably the most abundant species in our study area. Therefore it is very likely that relative abundances of species play a role in determining importance in flock networks in our study site. It is also likely that functional importance itself varies along a continuum. For example, even among intra-specifically gregarious species, flock leadership is known to be linked to traits such as average group size (Srinivasan et al. 2010), cooperative breeding (Sridhar et al. 2009) and foraging generalization (Contreras and Sieving 2011). Positional importance in flock networks is therefore likely to be determined by a complex interplay of a variety of species traits; a useful future direction of research will be to examine the relationship between positional importance of species and these different traits in a multivariate framework.

Generality of species importance

Our findings also provide evidence for the generality of species importance in networks. Importance values of species, genera and families were similar between our study site and other sites in the Asian region (Fig. 5). This indicates that certain taxonomic groups are important in flocks, irrespective of the details of the ecological communities in which they occur (see also Stouffer et al. 2012). This generality could be related to the link between functional and positional importance described earlier. Studies have indicated the universality of species traits associated with functional importance in flocks (Sridhar et al. 2009, Goodale and Beauchamp 2010). Given this, generality of taxonomic importance might reflect the fact that functionally important species are more likely to come from the same taxonomic groups as a result of phylogenetic conservatism, i.e. the more closely-related species are, the more likely they are to share the same habits (Losos 2008). For example, known functionally important taxa such as *Alcippe poiocephala*, *Dicrurus paradiseus* and *Pericrocotus flammeus* (Sridhar and Sankar 2008, Srinivasan et al. 2010) tended to be important in whichever Asian flock networks they occurred (Supplementary material Appendix 3 Table A3); in networks in which they do not occur, species closely-related to them were among the most important. Hence, given a list of species from an area, it is possible not only to predict potential functional importance at the individual flock level, but also potential positional importance in the emergent network. Whether the potential is realized will also be determined by other factors, such as species abundance, that are known to influence importance in networks (Lewinsohn et al. 2006) and are more likely to be influenced by local ecological factors (Bascompte and Jordano 2007).

Implications for community ecology and conservation

The most important outcome of our study is the identification of a small core of functionally important species in the flock network. Given that flock participants are generally from the same guild, these core species potentially represent

one of the few examples of intraguild 'keystones' (sensu Jordán and Scheuring 2002). Studies examining the ways in which these 'keystones' influence the ecologies of other participants will help shed light on the dynamics of flock networks. It is also important to note that none of these species currently receive any conservation attention; for example, all of them are classified as 'least concern' by IUCN (<www.iucnredlist.org/>). This is not surprising given that conservation prioritization schemes largely target rare and endangered species, and the core species in our network are neither. However, there have been recent attempts to also focus conservation attention on functionally and ecologically important species (Martín-López et al. 2011). In this context, our study not only identifies such species in our study site but also demonstrates that importance in flock networks can potentially be predicted from taxonomic or phylogenetic classification.

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Supplementary material (available online as Appendix oik-00101 at <www.oikosoffice.lu.se/appendix>). Appendix 1–3.