

Commentary

Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges



Damien R. Farine*

Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, Oxford, U.K.

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Grouping is a very common outcome of selection that operates on individual animals. Largely considered to be driven by immediate benefits, such as avoiding predators, animal groups often consist of individuals that are phenotypically more similar than expected from the population distribution. This suggests that the distribution and fitness of phenotypes may be shaped by multiple levels of selection operating along different axes of behaviour. Thus, quantifying assortative mixing, or the measure of association between similar individuals in social networks, should be a key component of the biologist's toolbox. Yet, assortment is rarely tested in animal social networks. This may be driven by a lack of tools for robust estimation of assortment, given the reliance of current methods on binary networks. In this paper, I extend existing approaches that calculate the assortativity coefficient of both nominal classes and continuous traits to incorporate weighted associations. I have made these available through a new R package 'assortnet'. I use simulated networks to show that weighted assortment coefficients are more robust than those calculated on binary networks to added noise that could arise from random interactions or sampling errors. Finally, I demonstrate how these methods differ by applying them to two existing social networks estimated from wild populations, exploring assortment by species, sex and network degree. Given the parallel theoretical developments of the importance of local social structure on population processes, and increasing data on social networks being collected in free-living populations, understanding phenotypic assortment could yield significant insight into social evolution.

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Group living is frequently considered to be an adaptive strategy primarily driven by ecological factors (Krause & Ruxton, 2002). However, the fitness benefits accrued by individual participants may vary not just with group size, but also as a function of its phenotypic composition. For example, the predator confusion effect relies upon individuals being physically identical to other members of their group (Landeau & Terborgh, 1986); that is, they gain fitness benefits through being phenotypically assorted by size, shape and colour. Alternatively, individuals may reduce resource competition by associating with others that are specialized on different niches, which may lead to disassortment by species as seen in mixed-species foraging groups (Buskirk, 1976). In this way, repeated nonrandom interactions between individuals of similar or different phenotypes (or genotypes) can have profound evolutionary implications (West-Eberhard, 1979; Wolf, Brodie, & Moore, 1999).

Social network analysis is a quantitative approach that captures the emergent population-level properties of repeated interactions between individuals (Croft, James, & Krause, 2008; Krause, Croft, & James, 2007; Whitehead, 1997, 2008). Numerous reviews have suggested that this method will provide an accessible way of estimating the evolutionary consequences of social processes (Croft et al., 2008; Farine, Garroway, & Sheldon, 2012; Krause et al., 2007; Wey, Blumstein, Shen, & Jordan, 2008). Yet, one of the simplest and most consequential social network measures, assortative mixing (Newman, 2002a), has been relatively unexplored in animal behaviour, particularly outside of fishes (see Croft et al., 2012; Croft et al., 2009). This is surprising given that it is generally accepted that local social structure within populations can influence individual fitness (for example through indirect fitness, Hamilton, 1964).

Assortment can arise through either active or passive processes. Active assortment typically arises from attraction of individuals to others that are similar. For example fish will often form shoals of similarly sized fish of both single and multiple species (Hoare, Krause, Peuhkuri, & Godin, 2000; Hoare, Ruxton, Godin, & Krause, 2000; Krause, Butlin, Peuhkuri, & Pritchard,

* Correspondence: D. R. Farine, Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

2000), potentially to increase predator confusion (Krause & Ruxton, 2002). Active attraction of behavioural phenotypes, such as degree assortment (strong connections between similarly gregarious individuals), is thought to be critical in mediating processes in networks such as the spread of disease (Ashby & Gupta, 2013) or the evolution of cooperation (Pusch, Weber, & Porto, 2008). Active avoidance may also occur, resulting in disassortment between interacting individuals. This is likely to be common in systems in which different classes, such as males and females, preferentially associate together, as in Tasmanian devils, *Sarcophilus harrisii* (Hamede, Bashford, McCallum, & Jones, 2009). In contrast to active attraction, assortment can arise from passive processes such as differences in habitat use strategies. For example, in some taxa individuals at different life stages commonly occupy different niches, resulting in greater spatial overlap (therefore social association) between similar conspecifics (Holyoak, Casagrandi, Nathan, Revilla, & Spiegel, 2008).

A common method to measure assortment is the assortativity coefficient (Newman, 2002a, 2003). This provides an index to measure whether associations are typically between phenotypically similar or dissimilar individuals. Although Newman's assortativity coefficient has been used in a number of studies (Aplin et al., 2013; Green, Gregory, & Munro, 2009; Hamede et al., 2009; Leu, Bashford, Kappeler, & Bull, 2010; Lusseau & Newman, 2004; Lusseau et al., 2006; Manno, 2008; Mourier, Vercelloni, & Planes, 2012; Wiszniewski, Lusseau, & Moller, 2010; Wolf, Mawdsley, Trillmich, & James, 2007), its current restriction to binary networks may have hampered wider uptake in animal studies. This is potentially because association data in animal social networks are more frequently inferred (A was seen with B) than known (A directly interacted with B) as is more typical in human networks (Croft, Madden, Franks, & James, 2011; Franks, Ruxton, & James, 2010). As a result, this increases the relative influence of sampling error, or noise, in the data. Thus, binary network-based assortment measures could be underestimating assortment in animal studies. For example, imagine a network in which individuals found in stable groups of six always have the same five associates (they do not have an edge to themselves), and all have the same phenotype. If one sample randomly captures two groups together (through either observer error or otherwise), then each individual in these two groups will have five edges connected to associates of the same phenotype, and six connected to associates with a different phenotype. If both groups are sampled 50 times, then a weighted network will capture the fact that the proportion of edge weights to the nonsimilar phenotypes will be very low. In contrast, a binary network does not make this distinction. Consequently, rare chance events can have significantly greater influence on the perceived social structure in a binary network by being given the same weight as all other observed edges.

One approach that has been suggested for overcoming the limitations of binary networks, such as in the example described above, is to construct these after first thresholding (removing or setting to zero) edges above or below a certain value (James, Croft, & Krause, 2009; Lusseau, Whitehead, & Gero, 2008). In general, biologists typically repeatedly sample populations in order to infer the social network (Franks et al., 2010; Lusseau et al., 2008); hence thresholding is one way of maintaining some of the information contained in the edge weights that would otherwise be thrown away (Croft et al., 2011; Lusseau et al., 2008). The process of then converting networks to binary is generally by directly replacing nonzero edge values with one. For example, Newman's original assortativity coefficient is estimated based on the number of edges that occur between different classes or phenotypes. By counting

edges of each type (where each edge adds 1 to the count), this process is functionally equivalent to having all edge weights converted to equal one.

To assess the biological importance of a network measure, one needs to specify a relevant null model (Gotelli & Graves, 1996). Yet, it remains unclear what constitutes an appropriate method for building null models to assess the significance of the assortativity coefficient in an observed network. In most studies using Newman's assortativity coefficient, authors have reported the standard error calculated from jackknife simulations. However, Croft et al. (2011) highlighted the need for care to be taken when testing significance. They, and other authors (Bejder, Fletcher, & Brager, 1998; Whitehead, 1999; Whitehead, Bejder, & Ottensmeyer, 2005), suggested that null models for social networks should account for potential sampling biases and nonindependence in the data. In the case of assortment, this suggests that it may be inappropriate to assume that the null expectation is a coefficient index of 0 if the sampling method could have introduced some biases. Here there are two generally accepted alternatives that can be used. The first approach for resolving this is a node-based permutation, in which the association matrix is repeatedly randomized by shuffling the rows and columns while keeping the node labels fixed (for example in Aplin et al., 2013). The second method shuffles the data stream in order to control for individual gregariousness and group size distribution. Both these methods have been extensively described in the context of testing hypotheses for social networks (Bejder et al., 1998; Croft et al., 2011; Manly, 1997; Whitehead, 2008; Whitehead et al., 2005). However, they have rarely been compared using empirical data in the context of assortativity.

In this paper, I have the following aims. (1) I first present a method to incorporate weighted network edges into the Newman (2003) assortativity coefficient. Although this approach was derived for continuous measures (Leung & Chau, 2007), I extend it by also deriving the weighted-edge coefficient for nominal node values. To my knowledge, this method has never been used in animal social networks, so I developed an R (R Development Core Team, 2013) package 'assortnet' in order to promote its wider use. (2) I then quantify the relative performance of the different approaches of calculating assortativity by assessing the robustness of using weighted, thresholded and binary networks to sampling error. Using simulations, I show that indices incorporating weighted edges are significantly more robust to sampling noise than those using binary edges. (3) Using networks from two recently published studies (Farine et al., 2012; Farine & Milburn, 2013), I then investigate assortment according to different phenotypic traits and demonstrate how weighted and binary measures differ. Given the potential for random interactions to have a strong influence on binary network structure, I predicted that a weighted assortment measure is likely to provide a more robust estimate of assortment when compared to a binary assortment measure applied to the same network. (4) Finally, I compare the three common approaches for testing significance in the assortment measure to determine whether there are incompatibilities between these approaches.

METHODS

Incorporating Edge Weight into Assortment Measures

Newman (2003) defined the assortativity coefficient for nominal classes of individuals as:

$$r_d = \frac{\sum_i e_{ii} - \sum_i a_i b_i}{1 - \sum_i a_i b_i} \quad (1)$$

where e represents a proportion of a particular type of edge in the overall network. e_{ii} is the count of the set of edges E_{ii} that occur within nodes of type i divided by the total number of edges M , such that $e_{ii} = M^{-1} \|E_{ii}\|$. The sum of e_{ii} over all values of i ($\sum_i e_{ii}$) gives the total proportion of all the network edges that are within-class (assorted). $a_i = \sum_j e_{ij}$ is then the proportion of all edges that start at i (finishing at all possible types of node j), and $b_j = \sum_i e_{ij}$ is the proportion of all edges that end at j (starting at all possible types of node i). These values range between 0 and 1 and represent the proportions of each type of starting and finishing edge in the network, such that $\sum_{ij} e_{ij} = 1$ and $\sum_{ij} e_{ji} = 1$. If the network is fully assorted, then $\sum_{ii} e_{ii} = 1$ and $\sum_{ii} a_i b_i = 0$. This equation generates an assortativity value of r_d that ranges from 1 (fully assorted) to $0 > r_d \geq -1$ where the maximum negative value of a fully disassorted network tends towards zero as the number of classes increases ($r_d = -1$ for two fully disassorted classes, -0.5 for three, -0.25 for four). The values for the different definitions of r that follow all have the same range. Although most applications of social networks in animals use undirected networks, here I present the assortativity coefficients for directed networks as these are the internal implementations in the assortnet package and are the most generalized form. In the case of undirected networks, the proportions of edges starting at i and arriving at j are reciprocal ($\sum_i e_{ij} = \sum_j e_{ji}$).

Calculating a weighted assortativity coefficient can be achieved by replacing the count of edges in Newman's discrete coefficient (shown as equation 1) with their weights as a proportion of the total weight of the graph. Here, each proportion of edges that occurs between nodes of class i ($e_{ii} = M^{-1} \|E_{ii}\|$) is replaced by a proportion of total edge weights that occurs between these ($e_{ii}^w = W^{-1} \sum_i V_{ii}$). Here, W is the sum of all weights in the network and $\sum_i V_{ii}$ is the sum of the edge weights for the set of edges V_{ii} that connect nodes of type i , which ranges from zero to one. If all edge weights are equal to 1, then $W = M$ and $\sum_i V_{ii} = \|E_{ii}\|$, which replicates Newman's binary coefficient. These measures form the weighted binary assortativity coefficient r_d^w by substituting edge weights into equation 1:

$$r_d^w = \frac{\sum_i e_{ii}^w - \sum_i a_i^w b_i^w}{1 - \sum_i a_i^w b_i^w} \quad (2)$$

where e_{ii}^w is the proportion of the total network edge weights that occurs within nodes of type i , $a_i^w = \sum_j e_{ij}^w$ is the proportion of the total edge weights that starts at nodes of type i , and $b_j^w = \sum_i e_{ij}^w$ is the proportion of the total edge weights that arrives at nodes of type j . In a fully assorted network, $\sum_i e_{ii}^w = 1$ and $\sum_i a_i^w b_i^w = 0$.

For continuous measures of phenotypes, such as size or network degree, Newman (2003) proposed using the Pearson correlation coefficient:

$$r_c = \frac{\sum_{xy} xy (e_{xy} - a_x b_y)}{\sigma_a \sigma_b} \quad (3)$$

where a_x and b_y are the fraction of edges that start and end at nodes with values x and y , and σ_a and σ_b are the standard deviations of a_x and b_y . Equation 3 can be rewritten in a form that is useful for calculating the assortativity coefficient in social networks (as given in Newman, 2003):

$$r_c = \frac{\sum_i (j_i k_i) - M^{-1} \sum_j j_i \sum_i k_i}{\sqrt{[\sum_i j_i^2 - M^{-1} (\sum_j j_i)^2] [\sum_i k_i^2 - M^{-1} (\sum_i k_i)^2]}} \quad (4)$$

where j_i and k_i are the phenotypic values (such as degree or size) for the incoming and outgoing nodes connected to each observed edge i in the network, and M is the total number of edges.

To derive a weighted version of the continuous assortativity coefficient, Leung and Chau (2007) proposed using the same process as I gave in the nominal coefficient above. For example, the average value of the phenotypes of individual n 's associates (given by $k_{ni} = 1/m_n \sum_{i \in \Gamma(n)} k_i$, where m_n is the degree of n) can be replaced by the weighted average of its neighbouring nodes (given by $k_{ni} = 1/w_n \sum_{i \in \Gamma(n)} \omega_{ni} k_i$, where ω_{ni} is the edge weight between the focal individual n and individual i , and w_n is the sum of weights of all edges $\Gamma(n)$ that are connected to n). Using this same process, the interaction between phenotypes in equation (4) can be scaled by the weight of the edge connecting them, giving:

$$r_c^w = \frac{\sum_i (\omega_{ji} k_i) - W^{-1} \sum_i (\omega_{ji}) \sum_i (\omega_i k_i)}{\sqrt{[\sum_i (\omega_{ji}^2) - W^{-1} \sum_i (\omega_{ji})^2] [\sum_i (\omega_i k_i^2) - W^{-1} \sum_i (\omega_i k_i)^2]}} \quad (5)$$

where j_i and k_i are the phenotypes of nodes that edge i leads into and out of, respectively, ω_i is the weight of edge i and W is the sum of all edge weights. Equation (5) is functionally equivalent to equation (15) given in Leung and Chau (2007) but in a more readable format. As with the nominal assortativity coefficient, assortment in a network in which all edges have a weight of $\omega_i = 1$ will give the same result as Newman's binary measure for continuous traits (and W is equal to the count of edges M).

I have implemented these methods in the R package assortnet which contains the functions assortnet.discrete and assortnet.continuous. Both take the same five arguments: (1) the network as an association matrix; (2) the phenotype values of each node; (3) a flag to define when weighted edges should be used or to make the network edges binary automatically (the latter giving the same results as the original definitions of the assortativity coefficients r_d and r_c); (4) a flag to calculate the standard error of the assortativity coefficient using a jackknife simulation (Efron & Tibshirani, 1994); and (5) a grouping size for the jackknife simulations. This grouping size parameter M removes n edges (as mutually exclusive groups such that each edge is contained in just one group) at once in order to speed up simulations for very large networks (Efron & Tibshirani, 1994). Ideally, M should not be less than one hundredth of the number of edges. This package is available from my website (<https://sites.google.com/site/drfarine/r-packages/assortnet>), and can interface directly with other network libraries in R.

Assessing Robustness

To compare the robustness of the binary, thresholded binary and weighted assortativity coefficients to random interactions, I created a simple simulation that cumulatively introduced random edges into networks of 10, 50 and 100 individuals (nodes). In each simulation, I created a base network that was fully assorted ($r = 1$) by allocating edges to individuals of the same class or with the same phenotype with values randomly drawn from a Poisson distribution with a mean of 0.3 (range 0–0.8). The mean is equivalent to two individuals each observed 10 times and each dyad associating on average 4.5 times if using the simple ratio index. It is worth noting here that the assortativity coefficient is not influenced by global network structure. At each simulation step, one dyad consisting of any two individuals was randomly selected and the edge value increased by a value between 0.01 and 0.1 drawn from a

uniform distribution. After each step, I recalculated the assortativity coefficient, setting the function flag to calculate either the weighted or binary assortativity index, and using a threshold of 0.2 (or twice the maximum random value) for the thresholded network. Because the same networks were used for calculating all three assortment measures, the results of these simulations are directly comparable.

Simulations were then repeated 100 times for each network size with two different nominal classes and 10 different values of a continuous phenotype. Simulations ran 200, 1200 and 4900 times for 10, 50, 100 nodes, respectively. This represents an additional 100%, 50% and 20% of the missing initial observations. For example 10 nodes of two types started with 20 edges present and 20 edges missing (between nonassociated types), each of which could have been observed 10 times. This process resulted in an addition of approximately 100%, 50% and 20% of the original weight being added to the network in total, but now distributed randomly across all edges. In the Appendix, I show that these results are consistent for both a greater number of nominal classes and a greater number of different phenotypic values.

Assortment in Animal Networks

I calculated both the weighted and binary assortativity coefficients for networks from two previously published studies in order to explore assortative mixing by degree, sex, species and foraging location in cooperatively breeding thornbills (*Acanthiza* spp., see Tables 1, 2) and tits (family Paridae, see Appendix Tables A1, A2). First, I repeated the species assortment calculation from Farine and Milburn (2013) using weighted edges, calculated assortment by foraging location (in this case strata or height from the ground) to test whether the methods could detect the spatial assortment by foraging preferences reported in the study, and tested for any sex assortment within the most common species (buff-rumped thornbill, *Acanthiza reguloides*). Second, I tested for species and sex level assortment in the mixed-species social network published by Farine et al. (2012) that is contained within the R package asnipe (Farine, 2013). Given that theory suggests that degree assortment is important for flow dynamics (Ashby & Gupta, 2013; Newman, 2003), I also calculated assortative mixing by degree in these two networks. Although I have no biological justification for introducing a threshold (see Discussion), I provide a comparison of the performance of thresholded networks with the binary and weighted assortativity coefficients in Appendix Table A3. Here, I thresholded the binary network at the

Table 1
Mixing matrix for binary assortment by species in thornbills and associates

	SCRO	STTB	BRTB	YRTB	SPWA	WTTC	WEHE	a_i
SCRO	0.001	—	—	—	—	—	—	0.044
STTB	0.009	0.046	—	—	—	—	—	0.182
BRTB	0.018	0.084	0.195	—	—	—	—	0.449
YRTB	0.011	0.025	0.100	0.05	—	—	—	0.212
SPWA	0.003	0.011	0.031	0.017	0.005	—	—	0.069
WTTC	0.001	0.003	0.008	0.004	0.000	0.000	—	0.017
WEHE	0.002	0.005	0.013	0.005	0.002	0.000	0.000	0.027
b_i	0.044	0.182	0.449	0.212	0.069	0.017	0.027	1.000

Mixing matrix for assortment in seven species from Farine and Milburn (2013) showing the distribution of edges between each species using the binary network. Values in cells represent the proportion of edges that correspond to edges between different types of nodes; a_i are the row sums, b_i the column sums (the table is symmetric but only half of the values are shown). SCRO: scarlet robin, *Petroica boodang*; STTB: striated thornbill, *Acanthiza lineata*; BRTB: buff-rumped thornbill, *Acanthiza reguloides*; YRTB: yellow-rumped thornbill, *Acanthiza chrysorrhoa*; SPWA: speckled warbler, *Pyrholaemus sagittatus*; WTTC: white-throated treecreeper, *Cornobates leucophaea*; WEHE: white-eared honeyeater, *Lichenostomus leucotis*.

Table 2
Mixing matrix for weighted assortment by species in thornbills and associates

	SCRO	STTB	BRTB	YRTB	SPWA	WTTC	WEHE	a_i^w
SCRO	0.005	—	—	—	—	—	—	0.058
STTB	0.006	0.058	—	—	—	—	—	0.157
BRTB	0.023	0.064	0.204	—	—	—	—	0.432
YRTB	0.018	0.015	0.093	0.097	—	—	—	0.250
SPWA	0.003	0.006	0.028	0.020	0.005	—	—	0.063
WTTC	0.001	0.002	0.008	0.004	0.000	0.000	—	0.016
WEHE	0.001	0.006	0.012	0.003	0.001	0.001	0.000	0.024
b_i^w	0.058	0.157	0.432	0.25	0.063	0.016	0.024	1.000

Mixing matrix for assortment in seven species from Farine and Milburn (2013) showing the distribution of edge weights (% of total weight) between each species using from the weighted network (species are per Table 1). The table is symmetric; therefore only half the values are shown.

mean nonzero edge weight (Croft et al., 2008) prior to recalculating the binary assortativity coefficient.

Significance Testing

I used two permutation methods for calculating the significance of the observed assortment value. Permutation tests create a posterior distribution against which a measure can be assessed by randomizing the original data. This process is important as the observations of interacting individuals are typically not independent from each other, therefore violating the assumptions in most parametric statistical tests (Bejder et al., 1998). The first method involves randomizing the relationships between the nodes and the phenotypic characteristic. I compared the observed assortment value with 1000 networks in which the phenotypic values of the nodes were randomized while maintaining the edge structure of the network. Significance using the node permutation method (P_n) was calculated as the proportion of randomized values that were larger than the observed values in the case of assortment and more negative than the observed values in the case of disassortment. The second permutation method randomizes the observations of individuals between groups in the original data stream. Each step in the randomization selects two individuals from different groups and swaps their observations, thereby keeping constant the number of observations for each individual and the distribution of group sizes (Manly, 1997). Following suggestions by several authors (Sundaresan, Fischhoff, & Dushoff, 2009; Whitehead, 1999, 2008; Whitehead et al., 2005), I restricted these swaps to pairs of individuals from groups that were observed in the same location on the same day. This is a conservative null model because any social behaviour implied by the choice of a given location on a given date is controlled for. Significance using the data stream method (P_d) was also calculated by comparing the observed value with the distribution of randomized association coefficients. In all cases, I also report the standard error of the assortativity coefficient calculated using the jackknife method as described by Newman (2003).

RESULTS

Simulating Noise in Assorted Networks

Weighted edges significantly reduced the impact of random associations on a perfectly assorted network when compared with either a binary or a thresholded binary network (Fig. 1, Appendix Figs A1–A3). In most cases, the assortativity coefficient using a binary network dropped below 0.5 very rapidly, even when few additional edges were added (for example Fig. A3a drops below 0.5

at approximately 0.15, which represents an increase in density from 0.6 to 0.8 in Fig. A4a). This suggests that a large amount of information and robustness is lost when edge weights are discarded (Croft et al., 2008). Thresholded binary networks generally provided an improvement on a nonthresholded network. However, these improvements are only valid under the assumption that there should be a strong dichotomy in the edge weights of within- and between-class nodes (that is, where the real network is in a state that is close to the left-hand side of the plots in Fig. 1). In contrast, the weighted network coefficient performed robustly even when noise was added to mixed networks showing some assortment (for example when the real network is somewhere in the middle of each plot).

Assortment in Mixed-species Flocks of Thornbills

Farine and Milburn (2013) observed 4098 co-occurrences between 63 colour-marked individuals. These individuals were made up of seven species participating in mixed-species flocks in Australia (see Table 1). Using these co-occurrences, they calculated the associations between individuals with the simple ratio index. This describes the proportion of times the individuals were seen together as a function of their combined number of observations (Whitehead, 2008).

As part of that study, the authors reported a nonsignificant value of assortment by species, suggesting random mixing ($r_d = 0.013 \pm 0.016$). However, examining the mixing matrix (Table 1) shows that approximately 20% of all edges occurred between buff-rumped thornbills, and the node-based and data stream permutations both suggested that assortment was greater than expected in randomized networks using the binary coefficient ($P_n < 0.001$, $P_d < 0.001$). The assortativity coefficient calculated using weighted edges more appropriately reflects this ($r_d^w = 0.122 \pm 0.018$), and both permutation tests using the weighted coefficient are highly significant ($P_n < 0.001$, $P_d < 0.001$). The mixing matrix by edge weight (Table 2) is significantly correlated with the mixing matrix from the binary method (mantel test: $Z = 0.065$, $P < 0.01$), which suggests that the weighted edge method was better at extracting the true value in this population.

I extended the results from Farine and Milburn (2013) to examine assortment by sex in the most common species from that study, the cooperatively breeding buff-rumped thornbill. Both the binary and weighted methods estimated a slight trend for disassortment by sex, where males and females associated more strongly than within the sexes ($r_d = -0.088 \pm 0.038$; $r_d^w = -0.082 \pm 0.049$). The tendency towards disassortment is perhaps not unexpected in cooperatively breeding groups if groups frequently consist of two males (M) and only one female (F). This is because triads have a unique property of having more between-class edges (two M–F edges) than within-class edges (one M–M edge). Both permutation tests were significant for the binary coefficient ($P_n = 0.012$, $P_d = 0.029$), whereas the weighted-edge coefficient suggested no significant disassortment ($P_n = 0.324$, $P_d = 0.084$).

One application of the assortativity coefficient is to determine whether individuals are assorted by geographical or habitat use overlap. Farine and Milburn (2013) noted the location in the habitat when recording co-occurrences, and found that there was significant nonrandomness in the location where associations took place. Thus, a useful test of the assortativity coefficient is whether it can detect spatial patterns of assortment without information about the location of interactions. I assigned a value ranging from 1 (low) to 3 (high) to each of the

three thornbill species based on their preferred foraging height when not associating in mixed-species flocks as reported in Figure 5 of Farine and Milburn (2013). I found strong support for assortment according to preferred foraging locations, both in the binary ($r_c = 0.113 \pm 0.016$; $P_n < 0.001$, $P_d < 0.001$) and the weighted-edge coefficient ($r_c^w = 0.296 \pm 0.018$; $P_n < 0.001$, $P_d < 0.001$). Thus, the assortativity coefficient successfully identified that individuals were more strongly connected to others with foraging preferences that were more similar than expected by chance. Furthermore, the weighted-edge measure was much larger and provided much stronger (threefold) support for this result.

Finally, I tested for assortment by degree in the mixed-species network of thornbills and associated species. Leung and Chau (2007) suggested that this important network property may be most prone to biases introduced by measuring binary rather than weighted assortativity, and I found strong disparity between the binary and weighted measures. The binary assortativity coefficient suggested that this network tended towards disassortment by degree ($r_c = -0.051 \pm 0.022$; $P_n = 0.610$, $P_d = 0.010$). In contrast, the weighted-edge coefficient found significant assortment ($r_c^w = 0.256 \pm 0.067$; $P_n = 0.007$, $P_d < 0.001$). Leung and Chau (2007) proposed that this difference could arise because of the highest probability of observing new edges between high-degree nodes and low-degree nodes, and the resulting difference in the influence of this edge in weighted (where it will have a small value) and binary networks.

Assortment in Mixed-species Flocks of Tits

Farine et al. (2012) described a social network consisting of four tit species (great tit, *Parus major*, blue tit, *Cyanistes caeruleus*, marsh tit, *Poecile palustris*, coal tit, *Periparus ater*) and Eurasian nuthatches, *Sitta europaea*. Individuals in this population were fitted with passive integrated transponder (PIT) tags, and associations inferred by their co-occurrences when detected at automated feeding stations. The authors detected 234 295 visits by 272 individuals over 4 weeks, and again used the simple ratio index to define the association matrix in this network.

Analysing the assortment by species in the tit network again found differences between the weighted and binary measures. The binary assortativity coefficient suggested a very mixed network ($r_d = -0.003 \pm 0.002$), and permutation tests suggested that this effect was either not different from random or significantly more disassorted than expected according to the node-based test ($P_n < 0.001$, $P_d = 0.657$). However, as with the thornbill network, the distribution of edges fell heavily within species (Appendix Table A1). Over 40% of all edges occurred within species, which is much higher than expected given the ratio of intraspecific to interspecific edge types. As a result, the weighted-edge assortativity coefficient (Appendix Table A2) showed weak but significant assortment by species ($r_d^w = 0.034 \pm 0.003$), supported by both permutation tests ($P_n < 0.001$, $P_d = 0.007$). This suggests that the weighted edge method was more robust in detecting these patterns.

All species in this study consisted of birds that breed in socially monogamous pairs, and unsurprisingly there was strong evidence for disassortment by sex within species (Table 3), although this appeared to be influenced by the ecology of each species. Blue and great tits form a large component of these mixed-species flocks and are considered to have a more fission–fusion type of social dynamics. These two species showed much weaker effects, with blue tits having no significant disassortment by sex. In contrast, the three species that maintain more stable pair bonds over winter

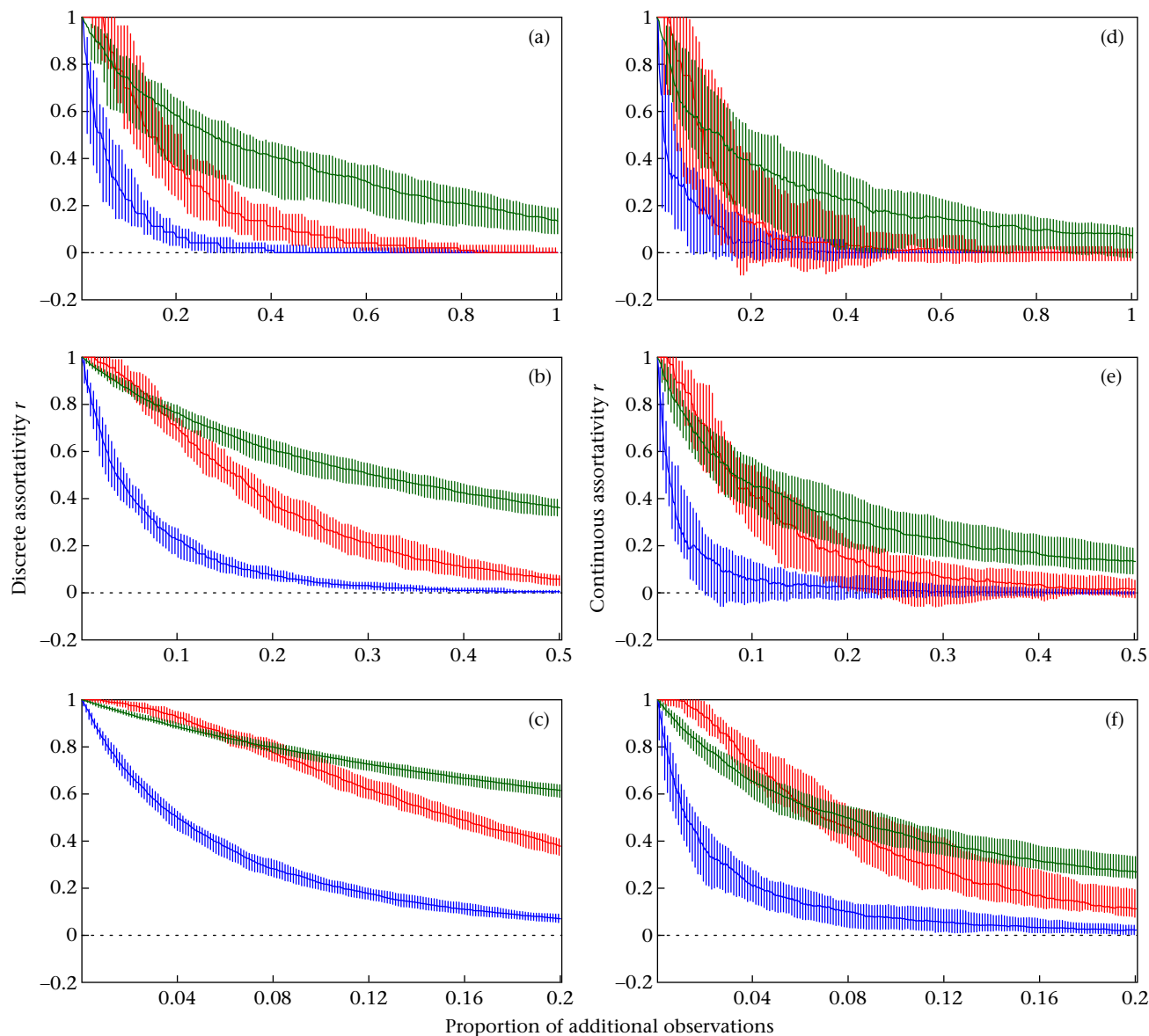


Figure 1. Effect of increasing random associations between (a–c) two discrete categories or classes of individuals, and (d–f) individuals with 10 different possible phenotypic values along a continuum. [Figures A1–A3](#) show the relationships above have very little spread when more classes are added. Each simulation had 10, 50 or 100 individuals, and was run 100 times. Simulations commutatively introduced 200, 1200 and 4900 interactions between random dyads that represented an additional 100%, 50% and 20% observations in the data. The assortativity coefficient was recalculated after each additional observation (starting at $r = 1$, or fully assorted). The network in each step was then analysed using binary (blue lines), thresholded binary (set at 0.2, red lines) or weighted (green lines) assortativity coefficients. The 95% confidence intervals from the simulations are shown by the vertical lines. The network is fully connected when the binary assortativity $r = 0$ (blue line), and the relationship between the number of added observations and network edge density (connectedness) is shown in [Fig. A4](#).

(coal tit; marsh tit; nuthatch), all had very strong mixing between sexes. In the case of coal tits and nuthatches, their edges were entirely constrained to dyads of different sexes.

Given the importance of resource discovery for winter survival ([Farine & Lang, 2013](#)), individuals in mixed-species flocks should maximize their associations with individuals with a high degree that would promote rapid diffusion of information ([Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Farine & Lang, 2013](#)). Highly connected or central nodes are thought to have a disproportionate effect on socially mediated transmission, at least in humans ([Lloyd & May, 2001; Newman, 2002b](#)), and previous work in this population has shown that central individuals had a higher probability of discovering novel foraging patches ([Aplin et al., 2012](#)). Here, both the binary ($r_c = 0.108 \pm 0.005$; $P_n < 0.001$, $P_d = 0.001$) and

weighted-edge ($r_c^w = 0.298 \pm 0.005$; $P_n < 0.001$, $P_d = 0.001$) coefficients suggest that tits show positive assortment by network degree. Although in this case the binary coefficient reported significant assortment (unlike in the thornbills), the weighted-edge coefficient was three times larger, suggesting that this pattern of association may be more difficult to detect using binary networks.

DISCUSSION

Incorporating weighted measures of dyadic associations resulted in much more robust estimates of assortment. This approach is equivalent to changing the assortativity coefficient from being a measure of the number of edges that occur between different phenotypes in the network to being a measure that describes the

proportion of interactions that occur between these phenotypes. As I demonstrated through the use of simulations, this has the effect of reducing the impact of sampling errors, random interactions or weak associations when estimating assortment.

In the analysis of phenotypic assortment in networks of wild birds, I have shown examples where a binary assortativity coefficient has failed to detect a pattern that was previously known to occur. By analysing the foraging height of different species in the network, Farine and Milburn (2013) found that species with closer foraging niches were more likely to be observed associating. This was confirmed using the weighted assortativity coefficient on the same network. However, the binary coefficient not only failed to detect the observed pattern but also suggested these species may be disassorted by niche. In this case, using binary assortment could have radically changed our biological interpretations of social structure. For example, Lusseau and Newman (2004) concluded that dolphin social networks differ from those in humans as they did not find assortative mixing by degree. This, in turn, can lead to very different conclusions about selective pressures operating on this population.

A difference in the results of binary and weighted coefficient results could suggest that active rather than passive mechanisms are driving assortment in these networks. If individuals are assorted according to niche differentiation (passive), then there may be fewer opportunities for random or casual associations between different phenotypes, and the binary and weighted assortativity coefficients should closely match. In contrast, active associations may lead to a greater potential for mixing, for example when two flocks temporarily forage nearby as with the thornbill example given above (Farine & Milburn, 2013). In these species, flocks would occasionally contain all three species when groups converged upon an area, and hence edges were formed between high-level foraging striated thornbills, *Acanthiza lineata*, and ground-foraging yellow-rumped thornbills, *Acanthiza chrysorrhoa*.

One recurring challenge for analysing animal social networks has been assessing the significance of observed trends (Croft et al., 2011). Typically, this arises from a lack of a defined null, which describes the expected pattern under a model of random association, for the population under study. The assortativity coefficient partially circumvents this problem as it provides a null model of random mixing ($r = 0$). However, the relationship between this null model and randomization has not been tested previously. In this paper, I reported both the data stream and node permutation approaches to estimating significances alongside the standard error. In almost every case, there was agreement between node permutations and data stream permutations. Permutation tests also agreed with the standard error: a standard error of approximately half the observed value concurred with marginal significance from permutation tests. The only exception occurred when the assortativity coefficient was close to 0, in which case the biological relevance of the randomizations should be interpreted with caution. Together, these findings, albeit from a limited range of scenarios,

suggest that any of the three methods are sufficient if they give strong support for rejecting the null hypothesis.

Although this paper describes a method for estimating the assortativity coefficient using weighted networks, two previous approaches have been used to circumvent the issues of binary networks in measuring assortment. The first compared the distribution of edges in the observed network after filtering out weak or strong edges with networks derived from permutations of the original data (Croft et al., 2012; Croft et al., 2005; Croft et al., 2009). If a greater proportion of edges of large weight between particular types of nodes were present in the observed compared to the random networks, then the network was considered to be assorted.

To assess the relative robustness of using a threshold, I calculated the assortativity coefficient after thresholding each network (Appendix Table A3). I found that although thresholding generally gave results intermediate between the other two methods, it may also be inconsistent with binary and weighted measures. For example, both binary and weighted networks reported strong assortment by degree in tits and nuthatches, whereas the threshold measure gave inconclusive results. This highlights one issue with thresholding in assortment, that the sum of weak edges may contribute to overall assortment. This could be important in studies that focus on phenotypic, rather than individual, interactions. By obscuring biologically relevant variation in network ties, thresholding can also cause substantial changes in the structure of the network (Butts, 2009). In the assortment example given by Croft et al. (2011), the authors found that thresholding a network could generate both type I and type II errors. Finally, given that different threshold values can generate different results (Butts, 2009; Langer, Pedroni, & Jäncke, 2013), one severe limitation of the method is that the value can easily be manipulated in order to obtain the most optimal P value (Langer et al., 2013).

An alternative method for measuring assortment in social networks uses Mantel tests to compare the independent similarity matrix (phenotypic characteristic) with the observed edge weights in the observed association matrix (Wey et al., 2008; Wiszniewski et al., 2010). Although this approach could potentially be combined with quadratic assignment procedures (QAP, Krackhardt, 1988), it has a more limiting framework on which to build null models as there is no established method for performing data stream randomizations with QAP. In contrast to these methods, the assortativity coefficient has been fully derived (from the Pearson correlation coefficient), and provides a measure that is comparable between systems. Importantly, the assortativity coefficient may be one of the few network measures to date that can be used in synthesis or comparative studies.

In this paper, I have shown that measuring the assortativity coefficient in social networks is a powerful approach for describing the social structure of populations, but are there any contexts in which a binary measure might be preferred over a weighted one? Croft et al. (2011) suggested that weighted networks are the gold standard for analysis, and the results from this study suggest that the weighted assortativity coefficient is the most robust. However, many questions are focused on events that might occur from single contacts, particular those related to transmission and other association-based processes. In these cases, it may be important to consider what social process(es) the network is describing and how these relate to the question. In general, social networks represent the probabilities of dyadic associations, that is, what is the chance of a dyad being observed co-occurring? Furthermore, animal networks are rarely continuously sampled in time. This can lead to some uncertainty that dyads with no edge are true zeros (Croft et al., 2011) or that weak edges are unimportant (Butts, 2009), thereby limiting the usefulness of binary and thresholded networks, respectively. Thus, the weighted assortativity coefficient will

Table 3
Binary and weighted assortment by sex in tits and nuthatches

	r_d	SE	P_n	P_d	r_d^w	SE	P_n	P_d
Blue tit	-0.039	0.010	0.047	0.001	-0.033	0.014	0.298	0.245
Great tit	-0.013	0.010	0.550	0.254	-0.053	0.014	0.041	0.010
Coal tit	-1.000	0.707	0.000	0.000	-1.000	0.707	0.000	0.000
Marsh tit	-0.194	0.047	0.070	0.014	-0.489	0.053	0.001	0.045
Nuthatch	-1.000	0.707	0.000	0.000	-1.000	0.707	0.000	1.000

Binary (r_d) and weighted (r_d^w) assortativity coefficients within sex within species of species in Farine et al. (2012). Standard error (SE) and significance from node (P_n) and data stream (P_d) are given for each coefficient. Values in bold indicate significance.

usually be more appropriate unless the network has low uncertainty. However, as I have shown above, using a combination of the two measures may be an informative way to isolate different mechanisms that could lead to assortment.

In conclusion, I have provided a new tool for calculating assortativity in social networks using weighted edges that has been implemented in an R package. I have also shown that this method is significantly more robust than the existing approaches using binary networks. Broader exploration of assortative mixing in social networks may be a useful approach for quantifying interactions between phenotypes. This may in turn provide an important component for estimating the strength and direction of selection arising from the social environment.

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Appendix

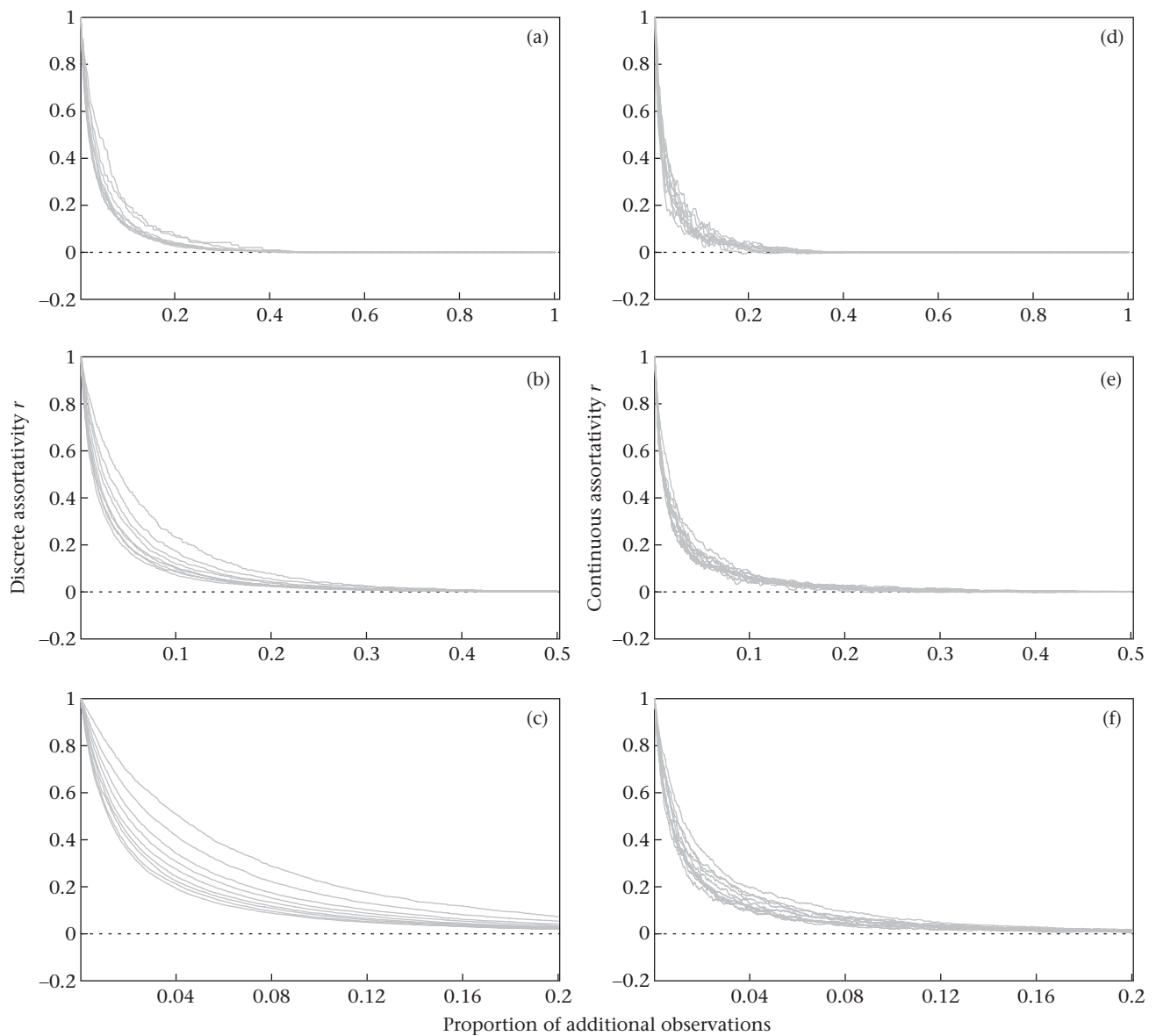


Figure A1. The effect of increasing random associations between (a–c) two and 10 different nominal classes, and between (d–f) 10 and 30 different continuous phenotypic values, when using the binary assortativity coefficient. The methods are identical to the blue line in Fig. 1 (representing two nominal classes and 10 continuous values). The values for Fig. 1 are the topmost line, with increasing number of classes/values shifting the line downwards.

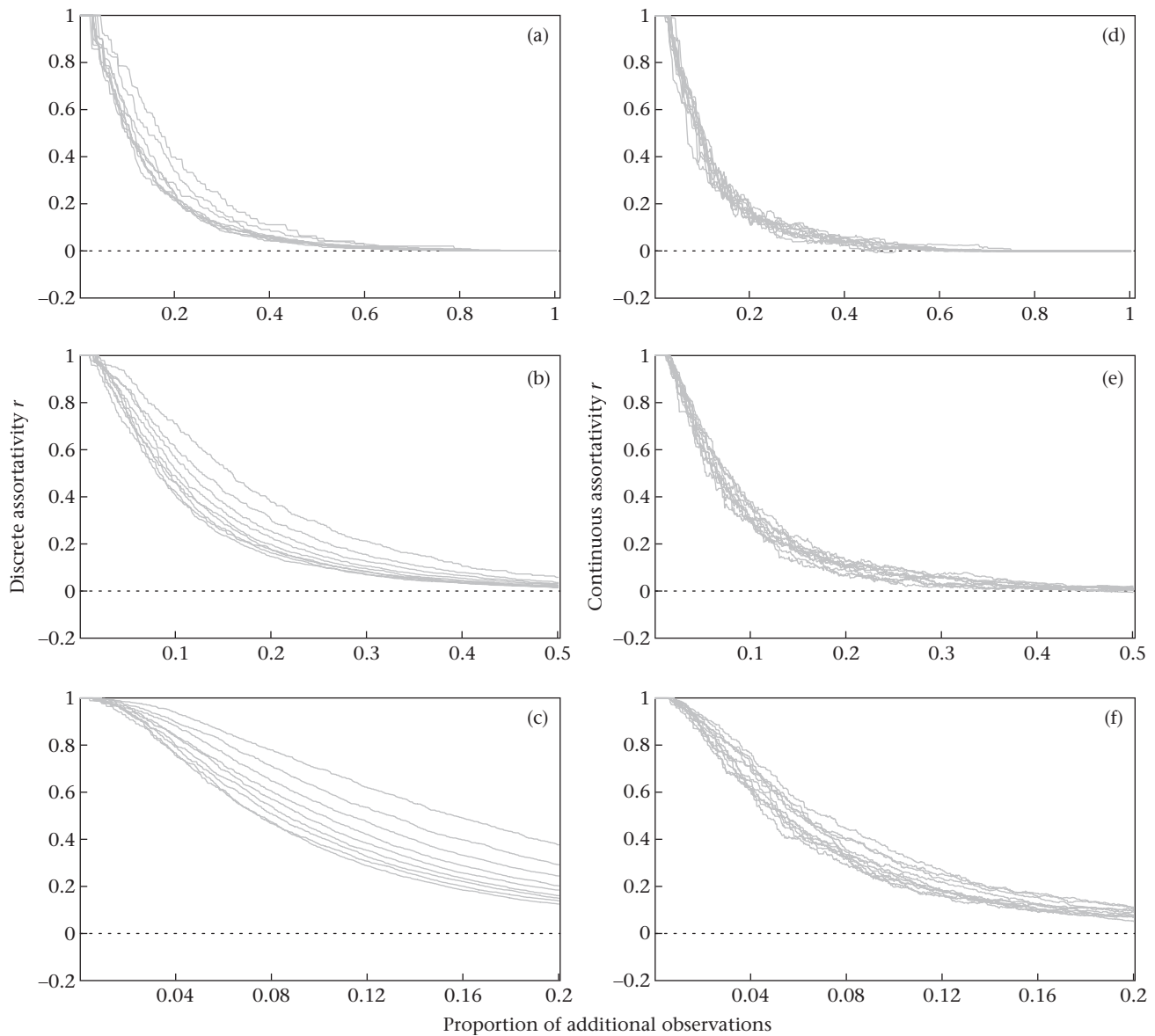


Figure A2. The effect of increasing random associations between (a–c) two and 10 different nominal classes, and between (d–f) 10 and 30 different continuous phenotypic values, when using the thresholded binary assortativity coefficient. The methods are identical to the red line in Fig. 1 (representing two nominal classes and 10 continuous values). The values for Fig. 1 are the topmost line, with increasing number of classes/values shifting the line downwards.

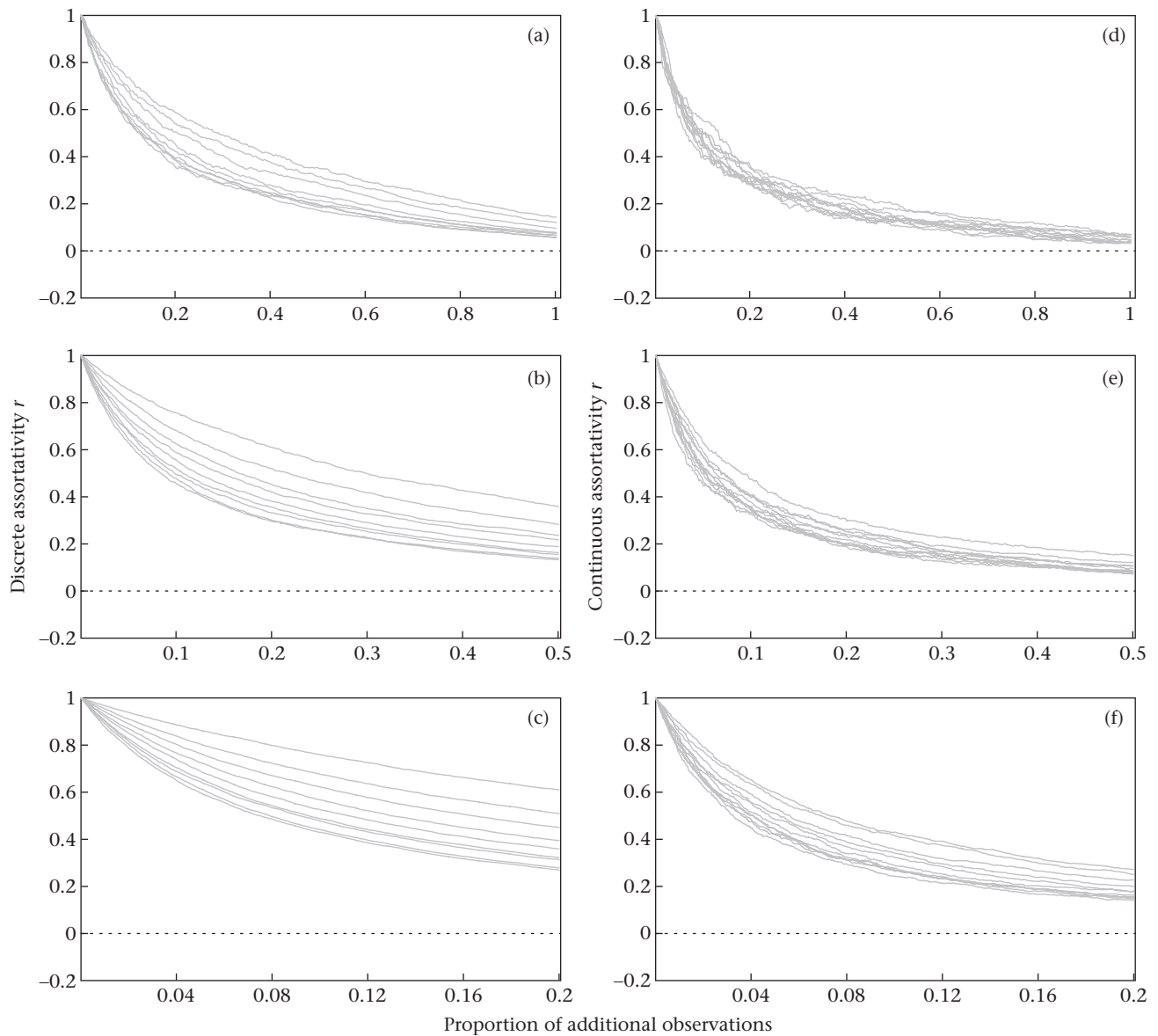


Figure A3. The effect of increasing random associations between (a–c) two and ten different nominal classes, and between (d–f) ten and thirty different continuous phenotypic values, when using the weighted assortativity coefficient. The methods are identical to the green line in Fig. 1 (representing two nominal classes and ten continuous values). The values for Fig. 1 are the topmost line, with increasing number of classes/values shifting the line downwards.

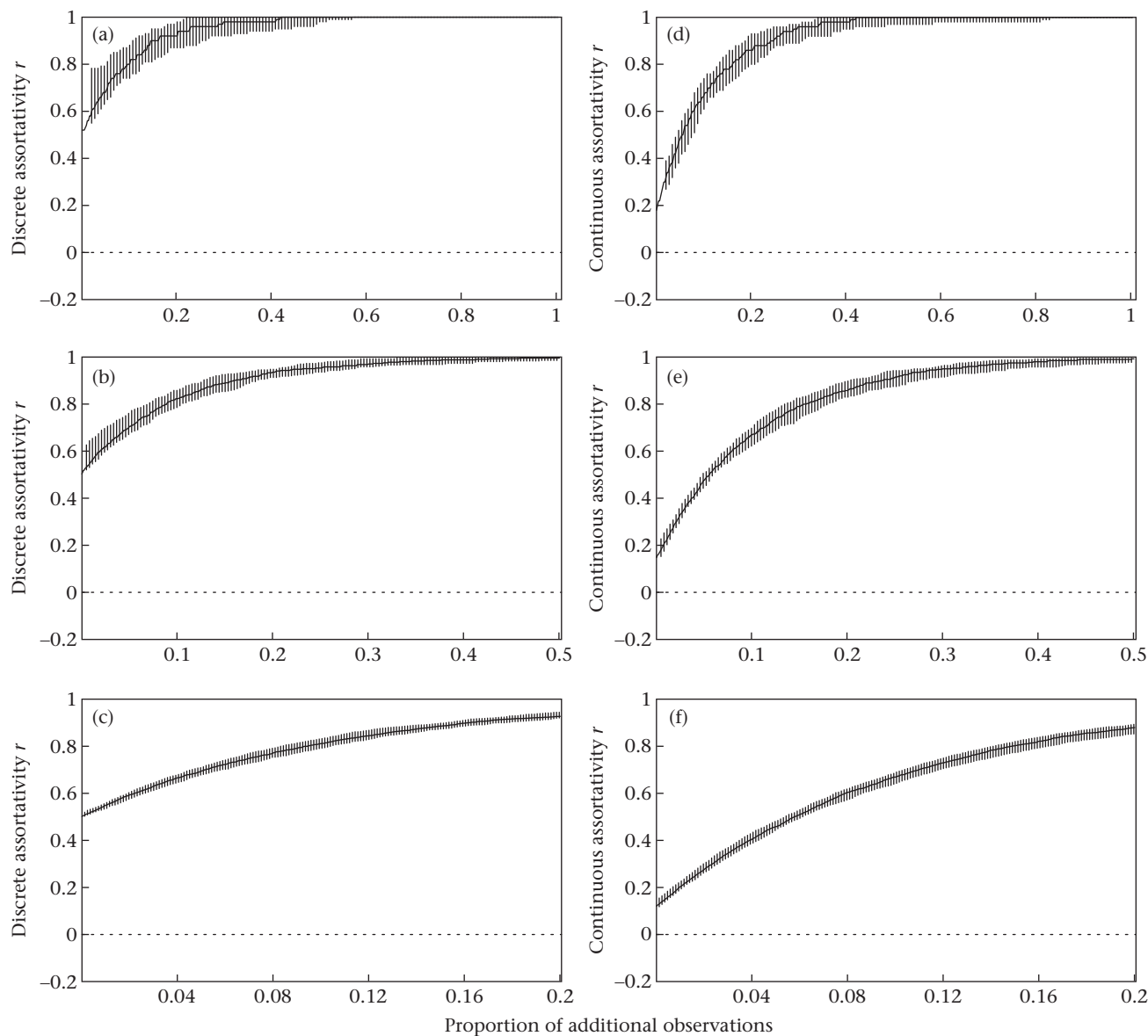


Figure A4. The relationship between added observations and network density (existing number of edges divided by potential number of edges) for (a–c) discrete simulations of 10, 50 and 100 individuals, and (d–f) continuous trait value simulations for 10, 50 and 100 individuals. Each panel provides background information on the simulation process used in the matching panels from Figs 1 and A1–A3, such that panel (a) in this figure provides the network density relationship for panel (a) in Figs 1 and A1–A3. Width of the response in each panel shows the 95% spread from the 100 simulations in each associated panel in Figs 1 and A1–A3.

Table A1
Mixing matrix for binary assortment by species in tits and nuthatches

	BLUTI	MARTI	GRETI	COATI	NUTHA	a_i
BLUTI	0.214	—	—	—	—	0.465
MARTI	0.032	0.005	—	—	—	0.069
GRETI	0.197	0.027	0.175	—	—	0.418
COATI	0.016	0.003	0.013	0.001	—	0.034
NUTHA	0.006	0.001	0.006	0.001	0.001	0.013
b_i	0.465	0.069	0.418	0.034	0.013	1.000

Mixing matrix for assortment in five species from Farine et al. (2012) showing the distribution of edges between each species using the binary network. Values in cells represent the proportion of edges that correspond to edges between different types of nodes; a_i are the row sums, b_i the column sums (the table is symmetric but only half of the values are shown). BLUTI: blue tit, *Cyanistes caeruleus*; MARTI: marsh tit, *Poecile palustris*; GRETI: great tit, *Parus major*; COATI: coal tit, *Periparus ater*; and NUTHA: Eurasian nuthatch, *Sitta europaea*.

Table A2
Mixing matrix for weighted assortment by species in tits and nuthatches

	BLUTI	MARTI	GRETI	COATI	NUTHA	a_i
BLUTI	0.208	—	—	—	—	0.451
MARTI	0.033	0.010	—	—	—	0.075
GRETI	0.183	0.025	0.180	—	—	0.410
COATI	0.019	0.005	0.015	0.003	—	0.047
NUTHA	0.009	0.002	0.007	0.001	0.001	0.019
b_i	0.451	0.075	0.410	0.047	0.019	1.000

Mixing matrix for assortment in five species from Farine et al. (2012) showing the distribution of edges between each species using the weighted network. Table structure and species abbreviations are as per Table A1.

Table A3

Comparison of binary, weighted and thresholded binary assortativity coefficient results for the analyses on the thornbill and tit studies

Phenotype	Binary	Weighted	Thresholded	P_n	P_d
Thornbills					
Species	$R_d = 0.013 \pm 0.016$	$R_d^w = 0.122 \pm 0.018$	$R_T = 0.072 \pm 0.117$	<0.001	<0.001
Sex	$R_d = -0.088 \pm 0.038$	$R_d^w = 0.082 \pm 0.049$	$R_T = -0.019 \pm 0.037$	0.587	0.690
Stratum	$R_c = 0.113 \pm 0.016$	$R_c^w = 0.296 \pm 0.018$	$R_T = 0.262 \pm 0.020$	<0.001	<0.001
Degree	$R_c = -0.051 \pm 0.016$	$R_c^w = 0.256 \pm 0.018$	$R_T = 0.286 \pm 0.020$	<0.001	0.088
Tits and nuthatches					
Species	$R_d = -0.003 \pm 0.002$	$R_d^w = 0.034 \pm 0.003$	$R_T = 0.008 \pm 0.002$	<0.001	0.090
Sex: blue tit	$R_d = -0.039 \pm 0.010$	$R_d^w = 0.033 \pm 0.014$	$R_T = 0.027 \pm 0.010$	0.045	0.313
Sex: great tit	$R_d = -0.013 \pm 0.010$	$R_d^w = 0.053 \pm 0.014$	$R_T = 0.027 \pm 0.010$	0.543	0.599
Sex: coal tit	$R_d = -1.000 \pm 0.707$	$R_d^w = -1.000 \pm 0.707$	$R_T = -1.000 \pm 0.707$	<0.001	<0.001
Sex: marsh tit	$R_d = -0.194 \pm 0.047$	$R_d^w = -0.489 \pm 0.053$	$R_T = -0.378 \pm 0.050$	0.101	<0.001
Sex: nuthatch	$R_d = -1.000 \pm 0.707$	$R_d^w = -1.000 \pm 0.707$	$R_T = -1.000 \pm 0.707$	<0.001	<0.001
Degree	$R_c = 0.108 \pm 0.005$	$R_c^w = 0.296 \pm 0.005$	$R_T = 0.302 \pm 0.004$	<0.001	0.115

Results from assortativity coefficients applied to the thresholded binary networks (r_T) compared to binary (r_d) and weighted (r_d^w) assortativity measures for different phenotypic traits in thornbills and tit networks. Bold values indicate significant effects (P values of binary and weighted methods are shown in the text), and significance estimated from node (P_n) and data stream (P_d) randomizations are given for the thresholded network measures. Networks were thresholded at the median nonzero edge weight (0.09 in the thornbill network, 0.05 in the tit network) before being converted into binary format.