Niche-based processes and neutrality influence patterns of indirect interactions in mutualistic networks

Benno I. Simmons[1,2*], Andrew P. Beckerman[1], Katrine Hansen[3], Pietro K. Maruyama[4], Jeferson Vizentin-Bugoni[5] and Bo Dalsgaard[3]

[1] Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK

[2] Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn, UK

[3] Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

[4] Centro de Síntese Ecológica e Conservação, Departamento de Genética, Ecologia e Evolução, ICB, Universidade Federal de Minas Gerais – MG, Brazil

[5] Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, 1102 S. Goodwin Ave, Urbana, IL, 61801, USA

* **Corresponding author:** Benno I. Simmons. Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn, UK. Email: benno.simmons@gmail.com

Abstract

Indirect interactions are central to ecological and evolutionary dynamics in pollination communities, yet we have little understanding about the processes determining patterns of indirect interactions, such as those between pollinators through shared flowering plants. Instead, research has concentrated on the processes responsible for direct interactions and whole-network structures. This is partly due to a lack of appropriate tools for characterising indirect interaction structures, because traditional network metrics discard much of this information. The recent development of tools for counting motifs (subnetworks depicting interactions between a small number of species) in bipartite networks enable detailed analysis of indirect interaction patterns. Here we generate plant-hummingbird pollination networks based on three major assembly processes – neutral effects (species interacting in proportion to abundance), morphological matching and phenological overlap – and evaluate the motifs associated with each one. We find that different processes produce networks with significantly different patterns of indirect interactions. Neutral effects tend to produce densely-connected motifs, with short indirect interaction chains, and motifs where many specialists interact indirectly through a single generalist. Conversely, niche-based processes (morphology and phenology) produced motifs with a core of interacting generalists, supported by peripheral specialists. These results have important implications for understanding the mechanisms determining indirect interaction structures.

Keywords: motifs, hummingbird, pollination, plant-pollinator network

Introduction

Species in a community are often influenced by other species they do not interact with directly [1–3]. Such indirect interactions are a fundamental component of communities, governing ecological and evolutionary processes as much as, or more than, direct effects [1,4–6]. For example, in plant-pollinator communities, indirect interactions between plants can be mediated by shared pollinator species. These can be facilitative, where one plant attracts pollinators that also visit co-occurring plant species, or competitive, where one plant attracts pollinators away from another, through being more abundant or more attractive to the pollinator than the competing plant [7–9]. These indirect interactions can have important implications for community persistence and stability. For example, in communities dominated by apparent competition, the sharing of interaction partners is restricted, and thus perturbations are limited in how much they can propagate through the community [10]. Conversely, communities dominated by apparent facilitation favour connected, nested structures with enhanced species coexistence [10,11].

Despite the importance of indirect interactions for ecological and evolutionary dynamics, we have little understanding of the processes that lead to their formation and maintenance in mutualistic networks. Instead, research has focused on determining the ecological and evolutionary processes that give rise to whole-network patterns or individual direct interactions, leaving the determinants of local-scale patterns of indirect interactions relatively unexplored [12–15]. One possible reason for this is the lack of appropriate tools for characterising patterns of indirect interactions in sufficient detail. Instead, mutualistic networks are generally characterised using metrics that capture a particular facet of whole-network structure in a single number, such as levels of connectance, nestedness and modularity [16,17]. While these metrics are undoubtedly useful, they are not always appropriate for considering

indirect interactions in detail because compressing a network into a single number necessarily discards a substantial amount of information about indirect interactions [18].

To fill this methodological gap, motifs have recently been proposed as a way to capture indirect interactions in bipartite networks in much greater detail than traditional metrics [18,19]. Just as LEGO sets are complex structures made from many small, distinct parts [20], networks can be thought of as being composed of many small subnetworks, or 'building blocks', known as motifs. Motifs take the form of small groups of species interacting with each other in particular ways. As there is only a finite number of ways to arrange interactions between a given number of species, there is also only a finite number of motifs with a given number of nodes. In other words, all networks are made up of a limited number of different types of building block. Figure 1 shows all possible motifs up to five species.

By breaking down a network into its constituent motifs, it is possible to explicitly characterise indirect interaction structures between small groups of species, without losing any information about broader network structure. Specifically, motifs capture the topology of interaction chains, where changes in the abundance of one species influence the abundance of another species, through altering the abundance of one or more intermediary species [3,18]. For example, consider a motif where two plant species interact indirectly through a single pollinator species ('motif 3' in Figures 1 and 2). This could represent indirect facilitation, where an increase in the abundance of the first plant, increases the abundance of the shared pollinator which, in turn, increases the abundance of the second plant [21,22]. Alternatively, such a motif could represent exploitative competition for the pollinator or interference competition through heterospecific pollen deposition [8,18,21,23–26]. Larger and more complex motifs contain rich detail on indirect interaction structures. Motif 11, for example, contains 28 different indirect interaction chains, with up to 3 intermediary species (see Figure A5 in [12]). This high level of detail is the advantage of the motif approach, allowing information about indirect interactions to be captured with a level of precision that is not possible when using traditional network metrics. Importantly, this extra information translates into novel and important insights into empirical data. For example, a recent study quantified species roles using a popular specialisation metric, d', which measures the extent to which species' interactions diverge from what would be expected if available partners were visited randomly [27]. Using this metric, two key pollinator species were found to play similar roles in the community, both being super-generalists [27]. However, when their roles were quantified using motifs, details of their indirect interactions were uncovered, revealing that the species actually played significantly different roles in the community: one was found to interact indirectly with generalist pollinators, while the other interacted indirectly with more specialist pollinators via shared specialist plants [18].

Here we aim to understand the determinants of different indirect interaction structures by comparing the motifs produced by three distinct assembly processes: morphological matching and phenological overlap (collectively known as niche-based processes), and neutral effects (assembly based on species interacting randomly in proportion to their abundance). By understanding the motif distributions that result from these different processes, we shed light on how different processes produce different patterns of indirect interactions, while also providing ecological interpretations of motifs that could guide future analyses.

Methods

We created simulated networks under our three processes from a dataset of 24 plant-hummingbird pollination networks from [28,29], which contained corresponding information on plant and hummingbird abundance, morphology (hummingbird bill length and floral corolla depth) and phenology. Communities sampled span from Mexico in the North to South Brazil. Full details of the data are given in [28].

For each of these sets of abundance, morphology and phenology data, we generated matrices giving the probabilities of species interactions under three different assembly processes, following Vázquez *et al.* (2009): neutral effects, morphological matching and phenological overlap. Neutrality was simulated using an abundance matrix, **A**. Elements of **A** were the product of each species' relative abundance. Thus, element a_{ij} represents the interaction probability between plant species i and hummingbird species j and is equal to the product of the relative abundances of i and j. This matrix therefore represents neutrality: the likelihood of interactions occurring by chance alone, as determined by species abundance.

We create two morphological match matrices, corresponding to two different methods in the literature. In the first matrix, $\mathbf{M_F}$, hummingbird bill lengths were first multiplied by 4/3 to account for the extension of the tongue beyond the length of the bill [30]. Matrix elements were then set to 1 if the bill length (plus the extension of the tongue) equalled or exceeded the floral corolla depth, and 0 otherwise [30]. This follows the 'forbidden link' concept where species are only able to interact if there is a morphological match (i.e. if the hummingbird can reach the nectar in the floral corolla). Matrix elements were then divided by the sum of the matrix to convert the elements to probabilities [30]. In the second matrix, $\mathbf{M_D}$, probabilities were inversely proportional to the difference between floral corolla depth and hummingbird bill length [31]. This approach relaxes the assumption that a hummingbird is equally likely to interact with all flowers that have a floral corolla equal to or shorter than its bill, and makes morphological match a continuous, rather than binary, quantity. If the difference between floral corolla depth and hummingbird bill length was 0, the difference was set to the minimum non-zero difference between corolla depth and bill length in the web to prevent errors when dividing by zero values.

Elements of the phenological overlap matrix, **P**, were calculated using matrix multiplication [12]. Plant and hummingbird phenology data, $\mathbf{O_P}$ and $\mathbf{O_H}$ respectively, had species as rows and dates as columns, with cells set to 1 for presence and 0 for absence of hummingbirds/flowers. Phenological overlap was then quantified as $\mathbf{P} = \mathbf{O_P}\ \mathbf{O_H}'$, where $'$ indicates the matrix was transposed [12].

For each assembly process, and for each dataset, we generated 1000 binary interaction matrices from the probability matrix using the 'mgen' function in the 'bipartite' R package [32]. In total there were 96,000 binary matrices (1000 generated matrices × four assembly processes × 24 sets of abundance, morphology and phenology data). Generated matrices had the same connectance as their corresponding empirical matrices.

The mean frequency of all motifs up to five nodes (see motif topology in Figures 1 and 2) was then calculated for each network and assembly process using the 'bmotif' R package [19]. To control for variation in network size, motif frequencies were normalised as a proportion of the total number of motifs within each motif size class (the number of nodes a motif contains) [33]. This was done to control for the fact that smaller motifs can be nested within larger

motifs. As there is only one two-node motif (a single link between two nodes), and thus only one motif in the two-node size class, this was excluded from analyses because its normalised frequency would always equal one. Six-node, and larger, motifs were excluded because commonly-studied indirect interactions, like apparent competition, are present in smaller motifs and five node motifs already contain varied and long interaction chains with up to three intermediary species between two indirectly interacting partners. Limiting to five node motifs was also beneficial for visualisation, interpretation and computational reasons.

We used an ANOVA framework to assess statistical differences between the frequencies of motifs in networks generated using different assembly processes. First, a MANOVA was used with frequencies of all 16 motifs as dependent variables and assembly process as the independent variable to determine whether there was an overall effect of assembly process on motif frequency distribution. Then, to identify how assembly processes affect specific dependent variables, we conducted univariate ANOVAs for each motif. For this, pairwise comparisons between assembly processes were calculated using the 'multcomp' R package [34]. Adjusted p-values were used to account for multiple comparisons, using the 'single-step' method in 'multcomp'.

Results

Different assembly processes produced significantly different motif distributions (MANOVA: df = 4, F = 2530.5, $p < 0.001$): neutral processes (abundance) were associated with more occurrences of motifs 6, 8, 11, 12, 16 and 17, while niche-based processes (morphological match and phenological overlap) were associated with more occurrences of motifs 5, 10 and 14 (see motif topologies and normalised frequencies in Figures 1 and 2). Furthermore, some differences were observed between morphological matching and phenological overlap matrices: phenological overlap matrices had significantly higher frequencies of motif 9 than morphological matching, but significantly lower frequencies of motif 14 (Figures 1 and 2).

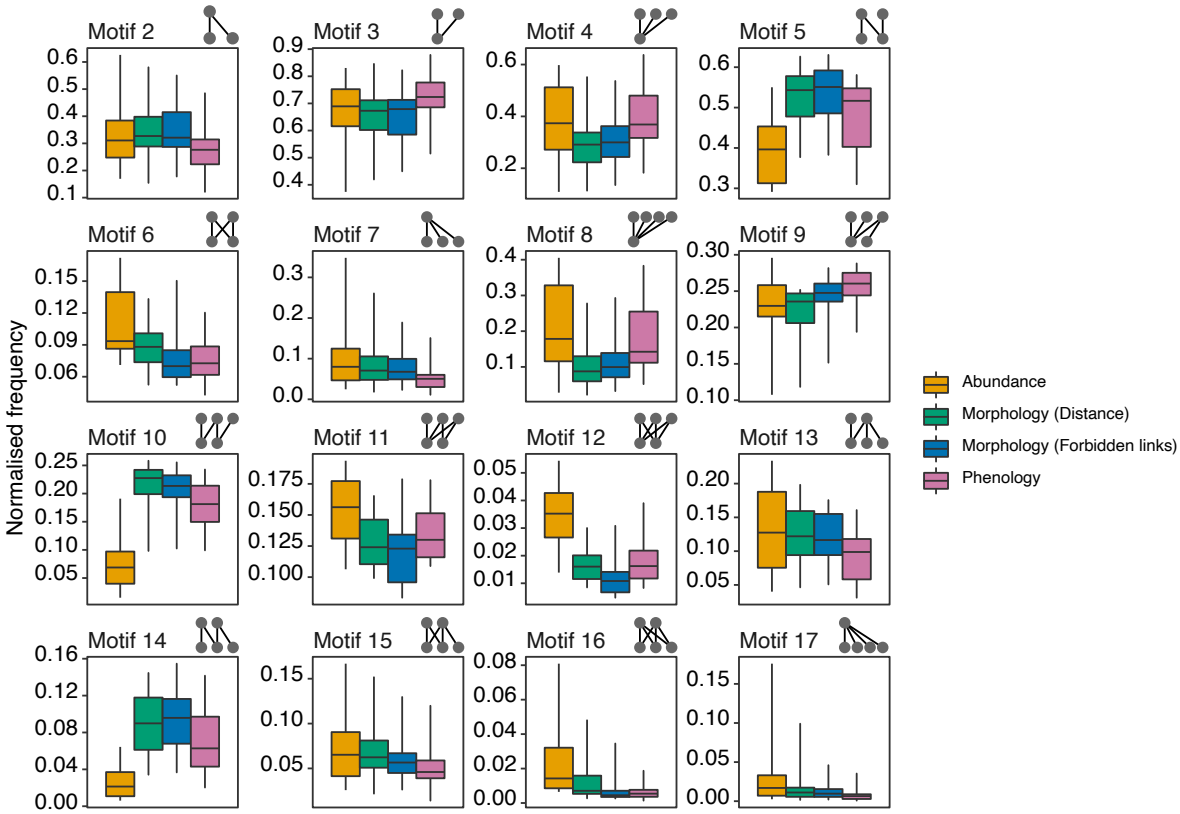

Figure 1: Normalised frequencies of each motif for networks generated using abundance (neutral processes) and morphological matching and phenological overlap (niche-based processes) for 24 plant-hummingbird interaction networks sampled across the Americas. Boxplots represent the distribution of mean normalised motif frequencies for generated networks across the 24 sets of abundance, morphology and phenological data. Upper whiskers represent 95% quantiles, the upper hinge is the 75% quantile, the middle line is the median, the lower hinge is the 25% quantile and the lower whisker is the 5% quantile. See Figure 2 for significance levels. In the motifs depicted above each boxplot, nodes in the bottom level of motifs are hummingbirds and nodes in the top level of motifs are plants.

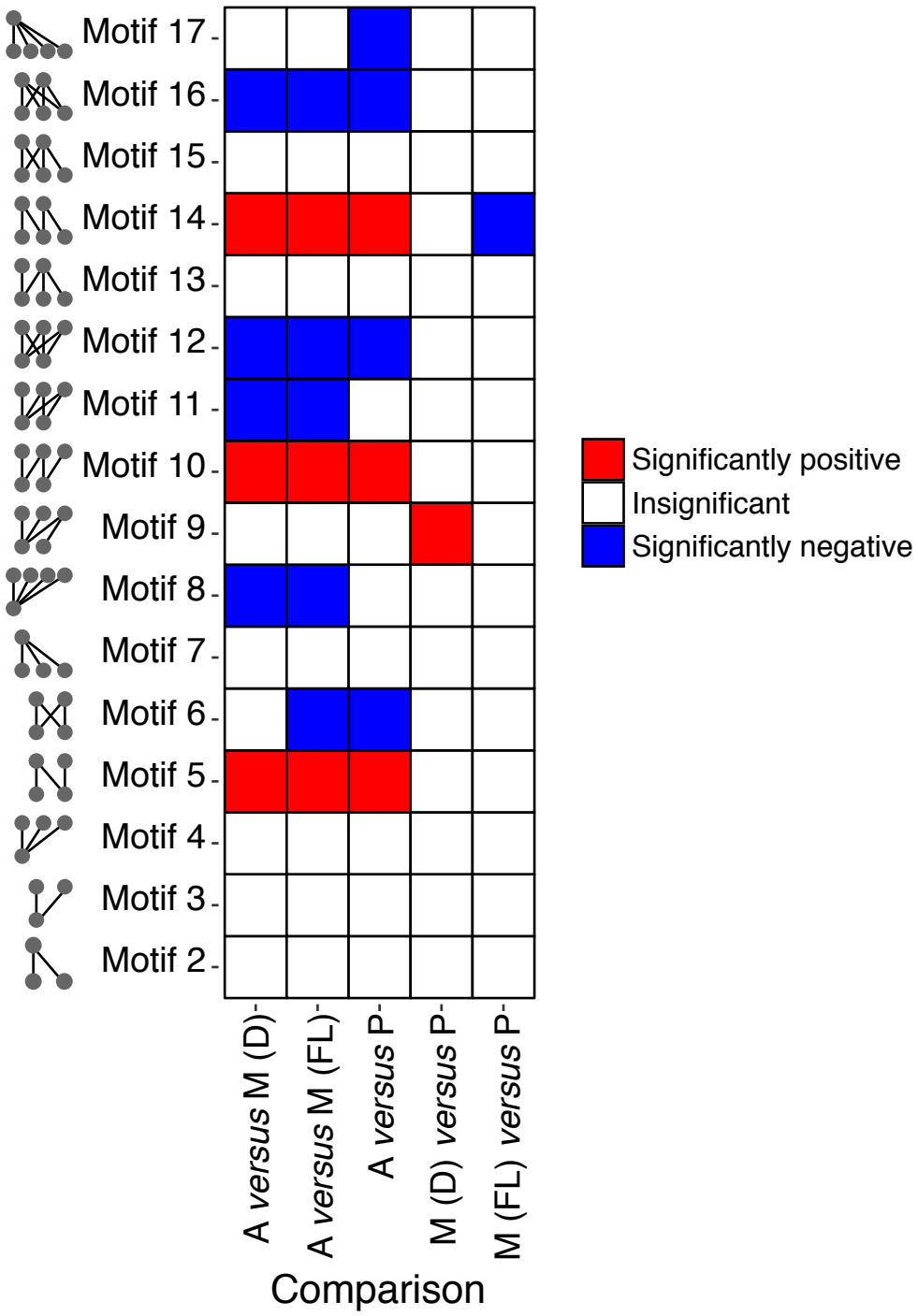

Figure 2: Matrix showing whether there are significant (adjusted $P < 0.05$) differences in normalised motif frequencies depending on the assembly processes (neutral processes like abundance, or niche-based processes like morphological matching or phenological overlap). Abbreviations for assembly processes are: 'A' is abundance, 'M (D)' is morphological matching based on distance between corolla depth and bill length, 'M (FL)' is morphological matching based on the forbidden link concept, and 'P' is phenology. Comparisons are relative to the first processes expressed. For example, if a cell in the A *versus* M (D) column is red, this means the motif frequency was significantly higher in the M (D) matrices than in the A matrices. Conversely, if a cell in the A versus M (D) column is blue, this means the motif frequency was significantly lower in the M (D) matrices than in the A matrices.

Discussion

We find that networks generated using different assembly processes have significantly different patterns of indirect interactions. Networks governed by neutral effects (species abundance) tend to have more densely-connected motifs where either (i) indirect interactions between plants/pollinators are mediated through a single pollinator/plant (motifs 8 and 17), or (ii) indirect interactions may be strong because there are multiple routes for indirect effects to travel at the same time (motifs 6, 11, 12 and 16) (Figures 1 and 2). Conversely, networks produced assuming niche-based processes – those determined by morphology or phenology – contain more motifs that comprise a core of interacting generalists, supported by peripheral specialists (motifs 5, 10, 14) (Figures 1 and 2).

Neutral processes produced two main types of motifs. First, they produced motifs, where specialists affect each other indirectly via a single generalist (such as motifs 8 and 17). These structures have been termed 'fan motifs' [18], and extend the classic apparent competition and exploitative competition structures from food webs (motifs 2 and 3) to having more than two specialists. Importantly, despite being generated by the same process, motifs 8 and 17 are likely to have different levels of competition between the specialist species. In motif 8, many plants compete for a single pollinator. In this situation, competition is likely to be low between the plants, especially if the pollinator is abundant, as the plants only need one successful visit from a pollinator to disperse their pollen and reproduce. Conversely, in motif 17, multiple pollinators are competing for a single plant. Here, competition is likely to be stronger, as pollinators are relying on the plant as a regular, limited food source. Importantly, however, these networks represent mutualistic interactions between species and thus it is also possible that 'fan motifs' represent indirect facilitative, rather than competitive, situations, where specialists indirectly benefit each other through interactions with a single generalist [21,22]. For example, the presence of a plant species could increase pollinator visits to one or more coflowering species, or multiple plant species could combine to form a large, shared floral display that increases pollinator visitation to all coflowering plants beyond what would be expected if each of the plants flowered in isolation. Whether indirect interactions are competitive or facilitative can depend on a range of factors, such as the distance between plants and their spatial configuration [35], however there is evidence that pollinator abundance can have an influence, with facilitation occurring above a threshold abundance, and competition occurring below the threshold [26]. Thus, combining motif analysis with independent abundance data, either collected empirically or simulated using population dynamics models, could give insight into the directionality of indirect effects.

The second type of motif produced by neutral processes is motifs with many links, where there are many possibly pathways through which indirect effects can flow (motifs 6, 11, 12, 16). This likely results from the neutral model's lack of consideration of 'forbidden links' [36,37]: as long as two species are of sufficiently high abundance, they are able to interact, resulting in more pathways [38]. This is in contrast to niche-based processes, where poor morphological matches or low temporal co-occurrence would prevent some interactions from being formed. This has important implications for whole-network dynamics, as it suggests that under neutral processes, the average length of the interaction chain between any two species will be lower, increasing the magnitude, and decreasing the localisation, of indirect effects. In turn this could allow the spread of perturbations through the community [10]. In motifs 6, 12 and 16 – known as 'complete' motifs – all plants interact with all pollinators. Here we might expect indirect interactions to be strong, as effects can be transmitted through multiple links simultaneously,

but also less predictable [18]. In motif 12, for example, if a pollinator decreased in abundance, this would remove the mutualistic benefit to the three plant species, but would also reduce competition between the two pollinators [18]; further research is necessary to examine the complex dynamics that could occur in these motifs. Motif 11 represents a slightly different situation to that in 6, 12 and 16, as motif 11 has a single specialist interacting with a completely connected set of generalists. In this 'asymmetric complete' motif, it has been suggested that generalists have a stronger effect on the specialists than the specialists have on the generalists, as the generalists are able to buffer changes in each other's abundances [18].

Niche-based processes resulted in motifs with a core of interacting generalists, connected to peripheral specialists (motifs 5, 10, 14). The indirect interaction pathways in these motifs can be highly complex. For example, in motif 5, there are four species: two plants in the top left (P_L) and top right (P_R), and two hummingbirds in the bottom left (H_L) and bottom right (H_R). One possible pathway is that P_L can negatively affect H_R indirectly, by providing a mutualistic benefit to H_R's competitor H_L, and by competing with P_R, reducing the mutualistic benefit to H_R [18,39]. While a complete study of the dynamics of each motif is beyond the scope of this work, our results do suggest that niche-based processes restrict the sharing of interaction partners, thus forcing pathways between species to be longer and more indirect. Given that longer pathways likely have smaller effects, niche-based processes likely reduce the level of indirect effects in the community [40]. In turn, this could limit the spread of perturbations through the network [10].

While there were few differences between different niche-based processes, networks based on phenological overlap had significantly higher frequencies of motif 9 (two generalists interacting) and significantly lower frequencies of motif 14 (three generalists interacting) than morphological matching models. This could reflect the degree of constraint between these two processes. *A priori*, it is difficult to say whether phenological overlap or morphological matching represents a greater constraint on species interactions. Phenological overlap requires species to co-occur in time to interact, but ignores species morphology, while morphological matching only allows species to interact if the hummingbird bill length and floral corolla depth are sufficiently matching, regardless of temporal co-occurrence. For our data, the phenological overlap model produced significantly more motifs with two generalists, and significantly fewer motifs with three generalists, than the morphological matching model. This suggests that interactions between generalists are rarer under phenological overlap, indicating that phenology may impose a greater constraint on species interactions than morphology in plant-hummingbird pollination systems.

Here we shed light on the different assembly processes associated with individual bipartite motifs. As well as being ecological interesting in its own right, we hope this study contributes to filling the 'interpretation gap' that has so far limited the uptake of bipartite motifs in analyses of mutualistic networks [18]. Notably, our results are useful for interpreting the results of motif analyses and for generating motif-driven hypotheses. For example, networks with a high proportion of invasive species may be expected to have higher frequencies of motifs associated with neutral effects, as invasive species lack the coevolutionary associations of native species [41]. Our results, combined with the availability of motif analysis software [19], allows the advantages of motifs to be more fully realised, paving the way for motifs to become an important component of the network ecologist's toolbox.

Funding

BIS and APB are supported by the Natural Environment Research Council [NE/S001395/1]. BIS is also supported by a Royal Commission for the Exhibition of 1851 Research Fellowship. BD thanks the Danish National Research Foundation for its support of the Centre for Macroecology, Evolution and Climate (grant no. DNRF96).

References

1. Strauss SY. 1991 Indirect Effects in Community Ecology - Their Definition, Study and Importance. *Trends Ecol. Evol.* **6**, 206–210. (doi:Doi 10.1016/0169-5347(91)90023-Q)

2. Wootton JT. 2002 Indirect effects in complex ecosystems: recent progress and future challenges. *J. Sea Res.* **48**, 157–172. (doi:10.1016/S1385-1101(02)00149-1)

3. Wootton JT. 1994 The Nature and Consequences of Indirect Effects in Ecological Communities. *Annu. Rev. Ecol. Syst.* **25**, 443–466. (doi:10.1146/annurev.es.25.110194.002303)

4. Bailey JK, Whitham TG. 2007 Biodiversity is related to indirect interactions among species of large effect. In *Ecological communities: plant mediation in indirect interaction webs* (eds T Ohgushi, TP Craig, PW Price), pp. 306–328. Cambridge: Cambridge University Press.

5. Martínez D, García D, Herrera JM. 2014 Consistency and reciprocity of indirect interactions between tree species mediated by frugivorous birds. *Oikos* **123**, 414–422. (doi:10.1111/j.1600-0706.2013.00558.x)

6. Vandermeer J, Hazlett B, Rathcke B. 1985 Indirect facilitation and mutualism. In *The Biology of Mutualism: Ecology and Evolution* (ed DH Boucher), pp. 326–343. New York: Oxford University Press.

7. Morales CL, Traveset A. 2009 A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecol. Lett.* **12**, 716–728. (doi:10.1111/j.1461-0248.2009.01319.x)

8. Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM, Karron JD. 2009 New frontiers in competition for pollination. *Ann. Bot.* **103**, 1403–1413.

9. Carvalheiro LG *et al.* 2014 The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecol. Lett.* **17**, 1389–1399. (doi:10.1111/ele.12342)

10. Thébault E, Fontaine C. 2010 Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science (80-.).* **329**, 853–856. (doi:10.1126/science.1188321)

11. Bastolla U, Fortuna MA, Pascual-García A, Ferrera A, Luque B, Bascompte J. 2009 The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018–1020. (doi:10.1038/nature07950)

12. Vázquez DP, Chacoff NP, Cagnolo L. 2009 Evaluating multiple determinants of the structure of plant-animal mutualistic networks. *Ecology* **90**, 2039–2046. (doi:10.1890/08-1837.1)

13. Simmons BI *et al.* 2019 Abundance drives broad patterns of generalisation in plant–hummingbird pollination networks. *Oikos* **128**, 1287–1295. (doi:10.1111/oik.06104)

14. Olito C, Fox JW. 2015 Species traits and abundances predict metrics of plant-pollinator network structure, but not pairwise interactions. *Oikos* **124**, 428–436. (doi:10.1111/oik.01439)

15. Maruyama PK, Vizentin-Bugoni J, Oliveira GM, Oliveira PE, Dalsgaard B. 2014 Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network. *Biotropica* **46**, 740–747. (doi:10.1111/btp.12170)

16. Dalsgaard B *et al.* 2013 Historical climate-change influences modularity and nestedness of pollination networks. *Ecography (Cop.)*. **36**, 1331–1340. (doi:10.1111/j.1600-0587.2013.00201.x)

17. Olesen JM, Jordano P. 2002 Geographic patterns in plant-pollinator mutualistic networks: Comment. *Ecology* **83**, 2416–2424. (doi:10.1890/03-3016)

18. Simmons BI, Cirtwill AR, Baker NJ, Wauchope HS, Dicks L V., Stouffer DB, Sutherland WJ. 2019 Motifs in bipartite ecological networks: uncovering indirect interactions. *Oikos* **128**, 154–170. (doi:10.1111/oik.05670)

19. Simmons BI, Sweering MJM, Schillinger M, Dicks L V., Sutherland WJ, Di Clemente R. 2019 bmotif: A package for motif analyses of bipartite networks. *Methods Ecol. Evol.* **10**, 695–701. (doi:10.1111/2041-210X.13149)

20. Jordano P. 2016 Chasing Ecological Interactions. *PLoS Biol.* **14**. (doi:10.1371/journal.pbio.1002559)

21. Moeller DA. 2004 Facilitative interactions among plants via shared pollinators. *Ecology* **85**, 3289–3301. (doi:10.1890/03-0810)

22. Sotomayor DA, Lortie CJ. 2015 Indirect interactions in terrestrial plant communities: Emerging patterns and research gaps. *Ecosphere* **6**, 103. (doi:10.1890/ES14-00117.1)

23. Chittka L, Schürkens S. 2001 Successful invasion of a floral market: An exotic Asian plant has moved in on Europe's river-banks by bribing pollinators. *Nature* **411**, 653. (doi:10.1038/35079676)

24. Flanagan RJ, Mitchell RJ, Karron JD. 2010 Increased relative abundance of an invasive competitor for pollination, Lythrum salicaria, reduces seed number in Mimulus ringens. *Oecologia* **164**, 445–454. (doi:10.1007/s00442-010-1693-2)

25. Hochkirch A, Mertes T, Rautenberg J. 2012 Conspecific flowers of sinapis arvensis are stronger competitors for pollinators than those of the invasive weed bunias orientalis. *Naturwissenschaften* **99**, 217–224. (doi:10.1007/s00114-012-0888-2)

26. Ye ZM, Dai WK, Jin XF, Gituru RW, Wang QF, Yang CF. 2014 Competition and facilitation among plants for pollination: Can pollinator abundance shift the plant-plant interactions? *Plant Ecol.* **215**, 3–13. (doi:10.1007/s11258-013-0274-y)

27. Kaiser-Bunbury CN, Mougal J, Whittington AE, Valentin T, Gabriel R, Olesen JM, Blüthgen N. 2017 Ecosystem restoration strengthens pollination network resilience and function. *Nature* **542**, 223–227. (doi:10.1038/nature21071)

28. Sonne J *et al.* 2020 Ecological mechanisms explaining interactions within plant-hummingbird networks: morphological matching increases towards lower latitudes. *Proc. R. Soc. B Biol. Sci.* **287**, 20192873. (doi:10.1098/rspb.2019.2873)

29. Sonne J *et al.* 2020 Ecological mechanisms explaining interactions within plant-hummingbird networks: morphological matching increases towards lower latitudes, v5, Dryad, Dataset. (doi:https://doi.org/10.5061/dryad.dncjsxkw2)

30. Vizentin-Bugoni J, Maruyama PK, Sazima M. 2014 Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird-plant network. *Proc. R. Soc. B Biol. Sci.* **281**, 20132397. (doi:10.1098/rspb.2013.2397)

31. Weinstein BG, Graham CH. 2017 Persistent bill and corolla matching despite shifting temporal resources in tropical hummingbird-plant interactions. *Ecol. Lett.* **20**, 326–335. (doi:10.1111/ele.12730)

32. Dormann CF, Frund J, Bluthgen N, Gruber B. 2009 Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. *Open Ecol. J.* **2**, 7–24. (doi:10.2174/1874213000902010007)

33. Baker NJ, Kaartinen R, Roslin T, Stouffer DB. 2015 Species' roles in food webs show fidelity across a highly variable oak forest. *Ecography (Cop.).* **38**, 130–139. (doi:10.1111/ecog.00913)

34. Hothorn T, Bretz F, Westfall P. 2008 Simultaneous inference in general parametric models. *Biometrical J.* **50**, 346–363. (doi:10.1002/bimj.200810425)

35. Charlebois JA, Sargent RD. 2017 No consistent pollinator-mediated impacts of alien plants on natives. *Ecol. Lett.* **20**, 1479–1490. (doi:10.1111/ele.12831)

36. Jordano P. 2016 Sampling networks of ecological interactions. *Funct. Ecol.* **30**, 1883–1893. (doi:10.1111/1365-2435.12763)

37. Canard EF, Mouquet N, Mouillot D, Stanko M, Miklisova D, Gravel D. 2014 Empirical evaluation of neutral interactions in host-parasite networks. *Am. Nat.* **183**, 468–479. (doi:10.1086/675363)

38. Simmons BI *et al.* 2018 Abundance drives broad patterns of generalisation in plant-hummingbird pollination networks. *bioRxiv* (doi:10.1101/339762)

39. Vázquez DP, Ramos-Jiliberto R, Urbani P, Valdovinos FS. 2015 A conceptual framework for studying the strength of plant-animal mutualistic interactions. *Ecol. Lett.* **18**, 385–400. (doi:10.1111/ele.12411)

40. Guimarães PR, Pires MM, Jordano P, Bascompte J, Thompson JN. 2017 Indirect effects drive coevolution in mutualistic networks. *Nature* **550**, 511–514. (doi:10.1038/nature24273)

41. Vizentin-Bugoni J, Tarwater CE, Foster JT, Drake DR, Gleditsch JM, Hruska AM, Patrick Kelley J, Sperry JH. 2019 Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawai'i. *Science (80-.).* **364**, 78–82. (doi:10.1126/science.aau8751)