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RESEARCH ARTICLE

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Use of Ecological Networks to Reveal Interspecific Fungal Interactions from 150 Years of Foray Records

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ABSTRACT

Fungal forays have been conducted for more than 150 years, providing valuable, but underutilized, sets of records for studies of fungal ecology. Although foray records have been used to study species composition and phenological change, their potential of revealing internal interactions within fungal communities has not been explored. This paper collates foray records conducted in Yorkshire over the past 150 years focusing on 12 autumn-fruiting, generalist ectomycorrhizal fungal species. Using network and co-occurrence analysis, the study has identified and characterized the community characteristics between the species, identifying highly influential species and significant interactions between species. The results demonstrate the potential of foray records in detecting interspecific fungal interactions and highlight their potential to contribute to future research in fungal community ecology.

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1. Introduction

Macrofungi (i.e. species that produce fleshy fruiting bodies visible to the naked eye) provide important ecological functions and services such as nutrient transportation, soil regulation [1] and food security [2,3]. Furthermore, they have been shown to be strongly affected by accelerating climate change with both earlier fungal fruiting times [4] and a latitudinal change in fruiting body abundance having been observed [5]. Importantly, these changes affect both the below-ground and above-ground fungal diversities [6].

Much recent research has focused on the impacts on below-ground fungal diversity [e.g. 7–9]. However, given that above-ground and below-ground communities are known to significantly differ in their composition [10,11] and responses to the disturbances [12], there is a clear need to better understand the impacts on above-ground fungal diversity. This need to enhance our understanding of above-ground fungal communities and interactions within is further supported by the importance of above-ground fungi diversity in mediating below-ground diversity [13] and interactions with fungivores [14,15]. A valuable, if underutilized, resource in this regard is foray records.

Fungal forays are a social and scientific activity involving one or more people engaging in the deliberate search for fungal sporocarps in a specific and predefined location over a defined period, generally followed by a period of communal discussion and microscope work to confirm identification and reach consensus. Indeed, it is this communal aspect that primarily differentiates fungal forays from other forms of field mycology and arguably ensures a higher fidelity of identification regarding the specimens collected.

Resultantly, fungal forays have remained one of the dominant forms of field mycology practiced over the past 150 years [e.g. 16,17], and accounts of forays are still published today. Traditionally, a full-list of sporocarp-forming fungal species found and identified (and thus a list of species not found) accompanies foray reports, with species identifications being based around community consensus and additional microscopical work. As such, foray records can provide snapshots of ecological communities which, due to a broadly consistent methodology, are comparable to each other. This comparability, combined with the abundance of data, makes the foray records invaluable for examining long-term changes in the fungal community–with other data sets, particularly for below-ground fungi, having much shorter series of data in terms of temporal length. Unsurprisingly, these records have found use in mycological research.

The first studies using foray records focused on examining relevance and reliability of using foray

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records in the study of local fungal species composition, Parker-Rhodes [18], for instance, suggested that erratic fruiting of the fungi could jeopardize the reliability of the foray records in representing the real composition of species, and smaller and more frequent fungal forays would be better. Additional research was broadly restricted itself to the statistical assessment of species distributions with a focus on estimating total species distribution and identifying abnormalities from the records from cumulative records: Rayner [19] summarized foray records over 12 years (1958-1970) assessed the frequencies of Basidiomycetes species, excluding rusts and smuts, being documented, concluding that the foray records provided a reasonably accurate estimate of the frequency of occurrence and the significant differences existing between the documented frequencies of different species. Building on Rayner's work, Hack [20] compared the differences between the frequency distribution of Agaricales from two types of foray records: single visits to many localities and repeated visits to one locality—finding substantial differences in species found. Orton [21] later expanded the use of foray records to examine the association between agarics and Caledonian pine and birch—with the aim of informing future field investigations—finding that grazing pressure reduced agaric abundance, while the presence of dead wood increased it. More recently, forays records, together with other forms of fungal records, have found a positive influence in the research of fungal ecology *via* 'citizen science' initiatives. This has resulted in successful projects at the local level [e.g. 22,23] and at the regional and global level [24]. Fungal foray records have also been utilized to assess long-term changes in species ecology by correlating species distribution and frequency with external factors. For example, foray records have been used to assess changes in sporocarp fruiting phrenology [25] and host affinity in fungi [4,26], and to examine population trends changes in distribution [27]. Fungal records from other sources have been used in similar studies [5,28–31].

Although fungal foray records have been used in scientific research for an extended period, particularly to assess long-term qualitative changes in species' response to their imminent environment; few, if any, have utilized forays to assess the internal structure of above-ground fungal communities quantitatively. Given the absence of a reliable and comprehensive sampling method to study the presence and interactions of every individual fungal species within an ecosystem, fungal forays represent one of the most extensive databases of above-ground fungal presence. This data can serve as a proxy for above-ground fungal interactions and holds significant potential to enhance our understanding of overall fungal dynamics through above-ground and below-ground linkages [13]. This is of note because fungal communities have complex and vital interactions within themselves (and with other organisms, see 32] and the importance of these interactions has become increasingly significant due to the current scale of global warming and rapid climate change [33].

Network analysis, or graph theory, uses nodes and edges to represent individuals and their interactions, respectively, within a complex system. This method originated in pure mathematics in the early twentieth century [34]. As biological networks began to emerge, early studies focused on ecological networks, such as food webs, where species were represented as nodes and their interactions as edges [35]. With advances in computational technology, network analysis has since been widely applied to study the internal structure and mechanisms of complex biological systems, including cellular processes [e.g. 36] and community ecology [e.g. 37]: the latter being the focus of this study. Similarly, co-occurrence analysis, which also emerged in the early twentieth century, became more structured with the development of association indices like Jaccard's and Sorensen's indices. More recently, with the development of null models and advanced computational methods, co-occurrence analysis has been integrated into more complex analyses, providing supplementary insights in areas such as metacommunity analysis [38] and trophic interactions [39]. Therefore, the combination of these two methods serves as an effective tool to identify and contextualize potential interactions between fungal species from fungal forays. Whilst these methods have not been previously used in the study of macrofungal interactions, they have been applied to other similar fields such as marine microbial interactions [40], intertidal food-webs [41], terrestrial bird-plant interactions [42], and soil-fungi-bacteria interactions [43].

Here we present an in-depth analysis of foray records conducted in Yorkshire over the past 150 years, a region with a particularly rich tradition of conducting forays and publishing the results [16,44,45]. Records of a group of 12 easily-identifiable, generalist, ectomycorrhizal species with relative consistency in their taxonomic concepts were isolated and transformed into a presence-absence matrix, which was qualitatively analyzed using co-occurrence analysis, followed by quantitative network analysis. In doing so, we show statistically significant interactions between species and identifying species with significant influence on group structures. In conclusion, we

highlight the utility of foray records and highlight their substantial potential for future research.

2. Methodology

2.1. Data collection

Foray records from forays conducted in Yorkshire were collated from a range of online and print published sources. Records where collated from *British Mycological Society Centenary Autumn Foray, Bulletin of the British Mycological Society, East Yorkshire Fungus Group, Harrogate & District Naturalists' Society, Mid-Yorkshire Fungus Group Yearbook, MYFG Foray Record, MYFG Extended Case Study, MYFG News, Ryedale Natural History Society Foray Record, The Naturalist, The Transactions of the Yorkshire Naturalists' Union, Transactions of the British Mycological Society, Transactions of the British Mycological Society, Whitby Naturalist's Annual Report*. These represented the collective efforts of numerous individuals associated with the Yorkshire Mycological Committee, the British Mycological Society, the Mid-Yorkshire Fungus Group, East Yorkshire Fungus Group, the Whitby Naturalist and others (Supplementary Appendix 1.1). The records included both professional and amateur mycologists, students, and non-specialist members of the general public.

Records from iNaturalist, GBIF, FRDBI, CATE2, and other conglomerate sources were not used for several reasons. Firstly, the peer-review (formal and otherwise) associated with published records is a closer representation of community consensus regarding specimen identification in comparison to individual records which may be uploaded by any member. Secondly, the individual nature of fungal records uploaded to these databases means that records may not be complete records of a foray activity, duplicates of other records uploaded by other individuals (including those not associated with the foray). Published full-species lists, in contrast, provide distinct snapshots of fungal diversity identified by a group operating under a consistent methodological procedure.

In order to minimize errors from misidentification, species were selected with relatively stable taxonomic concepts and that are easily identifiable without excessive microscopic or genetic work. Species were also selected with a broad host range that included both broad-leaved and coniferous species in order to ensure maximum potential habitat crossover. In total, twelve ectomycorrhizal species were selected: *Amanita muscaria* (L.) Lam., *Amanita pantherina* (DC.) Krombh., *Amanita phalloides* (Vaill. Ex Fr.) Link., *Amanita rubescens* Pers., *Boletus edulis* Bull., *Cantharellus cibarius* Fr., *Imleria badia* (Fr.) Vizzini., *Paxillus involutus* (Batsch) Fr., *Russula cyanoxantha* (Schaeff.) Fr., *Russula fragilis* Fr., *Scleroderma citrinum* Pers., *Xerocomellus chrysenteron* (Bull.) Sutara. As synonyms were widely present within the foray records collected, the study cross-referenced the foray records with Index Fungorum (www.indexfungorum.com) and Species Fungorum database (https://www.speciesfungorum.org/) to ensure the fidelity of the data collected.

Published records of autumn forays giving whole species lists were identified. Although the selected foray records contained presence-only data, they represented a comprehensive list of species observed and identified during the foray. Therefore, we relied on the assumption of pseudo-absences to infer presence-absence data for the selected species—a method widely used in ecological studies of community structure, including species distribution models [e.g. 46]. Forays records that only gave partial lists of species (such as those listing only rare, interesting, or new species) and those that included but didn't differentiate specimens that were brought to the gathering by participants from different dates or localities [e.g. 47,48] were not included in the curated dataset. Spring forays were also discounted due to the well-documented seasonality of sporocarp fruiting and different taxonomic groups targeted by the two forays [see, for instance, 49]. In total, 412 suitable foray records were identified and collated, ranging from 1885 to 2023 (Supplementary Appendix 1.2). Notably, as demonstrated in Figure 1, due to the existence of a comprehensive list of foray records in *MYFG Yearbook 1997*, there was a huge number of foray records coming from the year 1997. Since the foray records were independent from each other and the nature of species interaction did not change over a short time frame, the overrepresentation of 1997 would be unlikely to introduce bias to the dataset.

2.2. Data analysis

Co-occurrence analysis was conducted in RStudio (2023.09.1 + 494) with R version 4.3.2., using the R packages: cooccur (v1.3 [50];), dplyr (1.1.4 [51];), metacom (1.5.3 [52];), and ggplot2 (3.5.1 [53];). The network analysis was conducted in Jupyterlab (4.0.6.) with python version (3.11.5), using NumPy (2.1.0. [54];), Pandas(2.2.2. [55];), Matplotlib(3.9.2. [56];), and NetworkX (3.12. [57];). Detailed code is shown in Supplementary Appendix 2.1 and 2.2.

2.3. Co-occurrence analysis

Co-occurrences between two species were documented if they appeared in the same foray records.

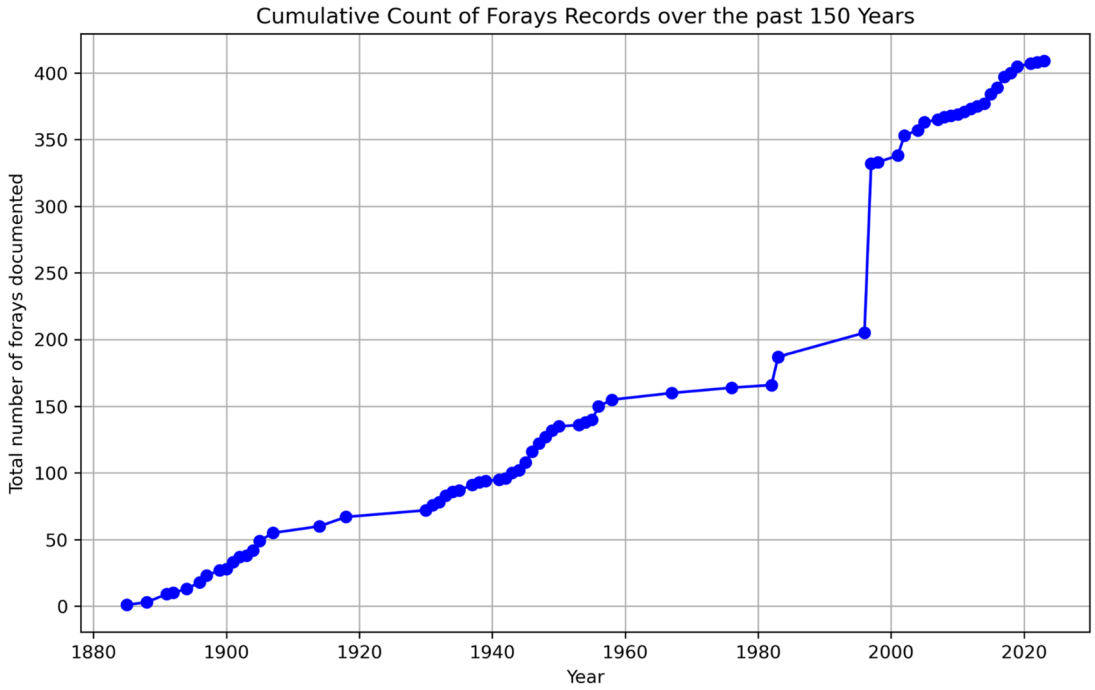

Figure 1. The cumulative count of foray records carried out in yorkshire, the United Kingdom, over the past 150 years, the huge amount of records in 1997 was due to the comprehensive list of records in MYFG Yearbook 1997.

Foray records with less than two of the target species present were removed from the analysis to prevent disproportionate effects [58] that may introduce a bias. As an established protocol [50], the co-occur package computed observed and expected frequency of co-occurrence between every pair of species to identify nonrandom positive and negative associations (i.e. co-occurrences that occur at a consistent enough level to be statistically significant and thus unlikely to be the result of coincidence). Results were expressed as a percentage of nonrandom co-occurrence relative to total co-occurrence as well as a plot showing the nature of nonrandom co-occurrences.

Since the results indicate that the *Amanita* species interrogated, as a group, exhibit a range of co-occurrences within the group and with other species in the network–and are the only group showing a negative co-occurrence with *Scleroderma citrinum* Pers.–they would represent a distinct local group containing valuable ecological information. As such, both co-occurrence and following network analysis were repeated for this group to examine its characteristics as a local network.

2.4. Network analysis

Conventionally, networks were generated using the binary result from the co-occurrence analysis *via* using an edge to represent the positive co-occurrence [e.g. 59]. However, this method fails to differentiate random and negative co-occurrence which may also be informative under various ecological context [60]. Hence, this study used the presence matrix to generate a weighted edge list (Supplementary Appendix 2.3), in which the weighted edges represent the rate of co-occurrence between each pair of connected species among all 418 foray records. The distances of the edges were calculated using the reciprocal of the weight [61]. The weighted edge list was used to construct an adjacency matrix and a network. For the entire network, the distribution of weighted degree was calculated to present an overview of the network structure [62].

For each node in the network, the weighted degree and the weighted clustering coefficient were calculated using the weighted edge between nodes, and the weighted betweenness centrality were calculated using the distance between nodes as requested by the package [57]. The weighted degree of a node is the sum of the weights of the edges connected to it, reflecting how strong the targeting node was connected to its neighbors [62]. The weighted clustering coefficient of a node measures how strongly targeting nodes' neighbors are connected to each other, revealing how closely neighboring nodes are clustered [63]. There were multiple ways of calculating weighted clustering coefficients and the method used here was adapted from Lopez-Fernandez et al. [63]. The weighted betweenness centrality is the percentage of shortest paths between all pairs of nodes that involve the targeting node (excluding the ones that start or end with the targeting node), indicating the importance of the node within the network [64,65].

To demonstrate the purpose of the metrics, Figure 2 presents a simple complete weighted network with

4 nodes. Each node in Figure 2(A) represents a species; the edges and respective weights represent the rate of co-occurrence between the targeting nodes. The edges' weight in Figure 2(B) represents the distance between nodes, it is calculated using the reciprocal of the weight in Figure 2(A). Figure 2(A) is used to calculate the weighted degree and weighted clustering coefficient of every node and Figure 2(B) is used to calculate the weighted betweenness centrality of the nodes. Using the highlighted node (node 1) as an example, it has a weighted degree of 0.7 as the sum of weights of all the edges connecting to it is 0.7. It has a weighted clustering coefficient of 0.133. The node is connected to 3 neighbors that are connected to each other with 3 edges. The sum of weights of all three edges are 0.4, hence the weighted clustering coefficient of node 1 can be calculated *via* 0.4/3 = 0.133. Lastly, node 1 has a betweenness Centrality of 0.333. In total, there are 3 possible shortest paths that do not involve node 1 as a starting or ending node. Among the identified paths, the shortest route between nodes 2 and 4 passes through node 1. Therefore, the weighted betweenness centrality of node 1 is calculated as 1/3 = 0.333 (for more on biological networks [66]:).

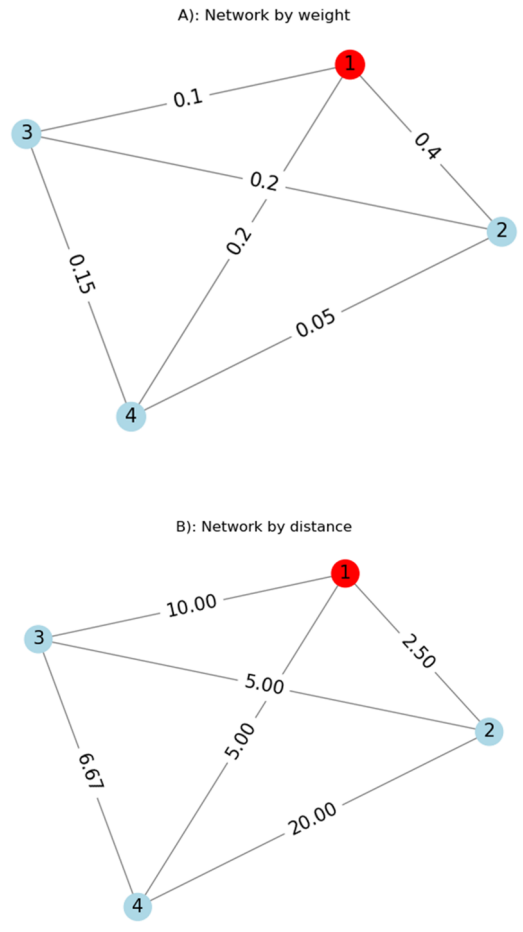

Figure 2. A sample network used to explain the metrics.

To evaluate these three characteristics statistically, 5000 null networks were generated using weight shuffling [67] and a bootstrap analysis was conducted using the null networks.

Lastly, the overall community structure of the network was evaluated using the Girvan-Newman method [68], which involved a consecutive removal of the most influential edges followed by the identification of significant community structures.

3. Results

3.1. Co-occurrence analysis

For the entire datasets, after the removal of foray records that contain 1 or fewer species, a total of 214 foray records were analyzed. As shown in Figure 3, there were 28 statistically significant positive co-occurrence and 2 statistically significant negative co-occurrences, which together accounted for 45.5% of the total 66 possible co-occurrence between the 12 species. As shown in Figure 3(A), *Amanita rubescens* had the highest amount of positive co-occurrence: it demonstrated positive co-occurrence with 8 out of 11 species; the 3 exceptions were *Cantharellus cibarius*, *A. pantherina*, and *Scleroderma citrinum*. Comparably, *Paxillus involutus* and *A. muscaria* showed the lowest amount of positive co-occurrence with 3 species only. Lastly, both negative co-occurrences involved *S. citrinum* with *A. phalloides* and *A. rubescens*.

For the *Amanita* subset, after the removal of foray records that contain 1 or less species, a total of 94 foray records were analyzed. As shown in Table 1, there were 0 positive co-occurrence and 3 negative co-occurrences, which together accounted for 50.0% of the total 6 possible co-occurrence between the 4 possible species. The three negative co-occurrences were between *A. muscaria* and *A. pantherina*; *A. muscaria* and *A. phalloides*; and *A. rubescens* and *A. pantherina*.

3.2. Network analysis

The visualized network is shown in Figure 4. The constructed network is a complete weighted network meaning that every node is connected to the other 11 nodes. The summary of each node's characteristics and the relevant statistical tests' results are demonstrated in Table 2.

From the bootstrapping, the expected weighted degree for a node is 1.01. A value higher than that indicates a possible node with stronger-than-average link to the rest of the network, vice versa. As shown in Table 2 A, *Amanita pantherina, A. phalloides*, and *Cantharellus cibarius* have weighted degrees that were

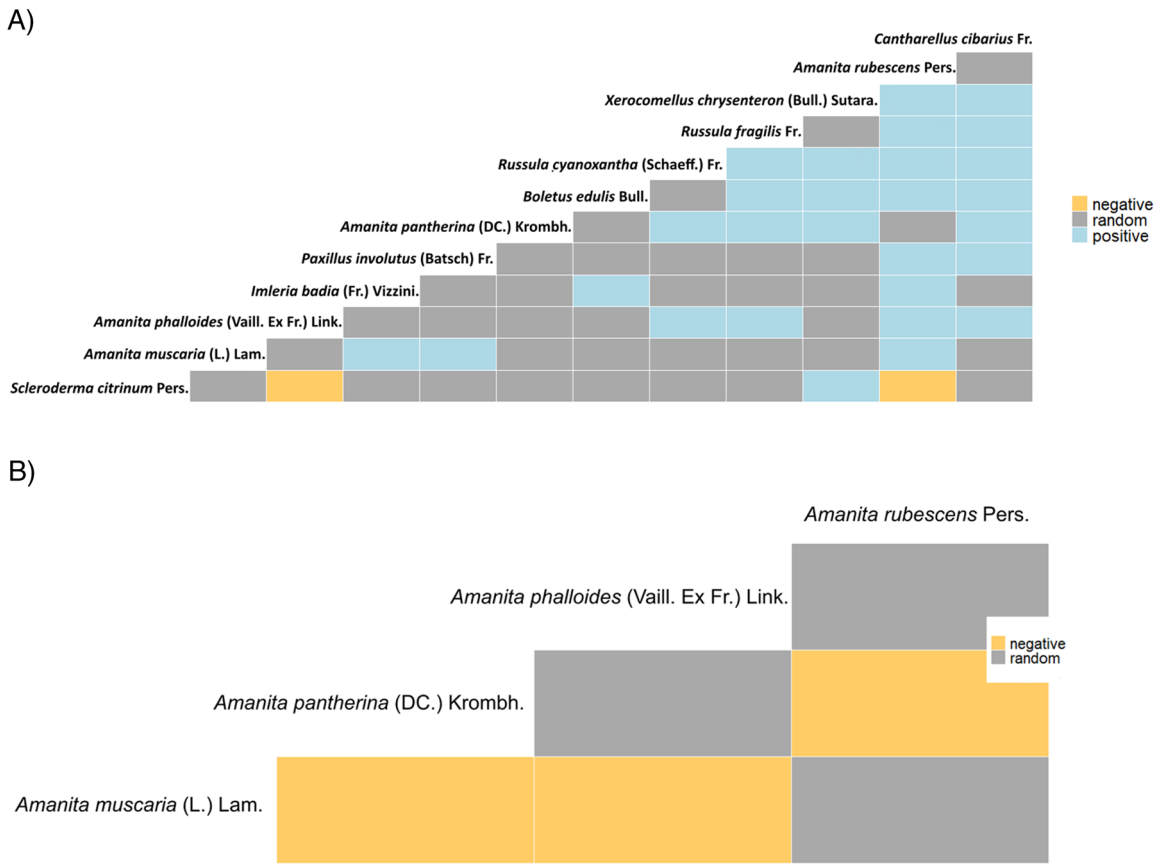

Figure 3. Co-Occurrence matrices for different datasets; a the full dataset, B the subset focusing *Amanita* species. Positive co-occurrence existed widely among the fungal species studied. When isolated, the *Amanita* species demonstrated solely negative and random co-occurrence. The localized co-occurrence (B) was different from that in the global group (a), due to the fact that when considering the *Amanita* species only, more records would contain one or less occurrence hence removed from the analysis as mentioned in the section of methodology (network analysis).

Table 1. The number of positive co-occurrence (+), negative co-occurrence(-) and the percentage of nonrandom co-occurrence for the full dataset and subset focused on *Amanita* species.

	Number of co-occurrence		Percentage of nonrandom co-occurrence
Dataset	+	–	
Full	28	2	45.5
Amanita species only	0	3	50.0

significantly lower than the expected value (*A. pantherina*: weighted degree = 0.247, *p*-value < 0.001 *A. phalloides*: weighted degree = 0.645, *p*-value = 0.0172; *C. cibarius*: weighted degree = 0.0464, p-value < 0.001). *A. rubescens*, *Paxillus involutus*, and *Xerocomellus chrysenteron* have weighted degrees that were significantly higher than the expected value (*A. rubescens*: weighted degree= 1.633, *p*-value < 0.001; *P. involutus*: weighted degree= 1.53, *p*-value = 0.00220; *X. chrysenteron*: weighted degree = 1.34, *p*-value = 0.0236).

From the bootstrapping, the average expected weighted clustering coefficient for a node is 0.0914. A value higher than that indicates a possible node with neighbors that were clustered more closely than average, vice versa. As shown in Table 2B), *A. pantherina, A. phalloides*, and *C. cibarius* have weighted clustering coefficients that were significantly higher than the expected value. (*A. pantherina*: weighted clustering coefficient = 0.104, *p*-value < 0.001; *A. phalloides*: weighted clustering coefficient= 0.0969, *p*-value = 0.0158; *C. cibarius*: weighted clustering coefficient = 0.100, *p*-value < 0.001;). *A. rubescens*, *P. involutus*, and *X. chrysenteron* have weighted clustering coefficients that were significantly lower than the expected value. (*A. rubescens*: weighted clustering coefficient= 0.0789, *p*-value < 0.001; *P. involutus*: weighted clustering coefficient= 0.0808, *p*-value < 0.001; *X. chrysenteron*: weighted clustering coefficient = 0.0842, *p*-value = 0.0282).

From the bootstrapping, the average expected weighted betweenness centrality for a node is 0.0466. A value higher than that would indicate the node demonstrates a higher-than-average influence on the rest of the network. For each node's betweenness centrality, since have a complete weighted network, most of the node have a weighted betweenness

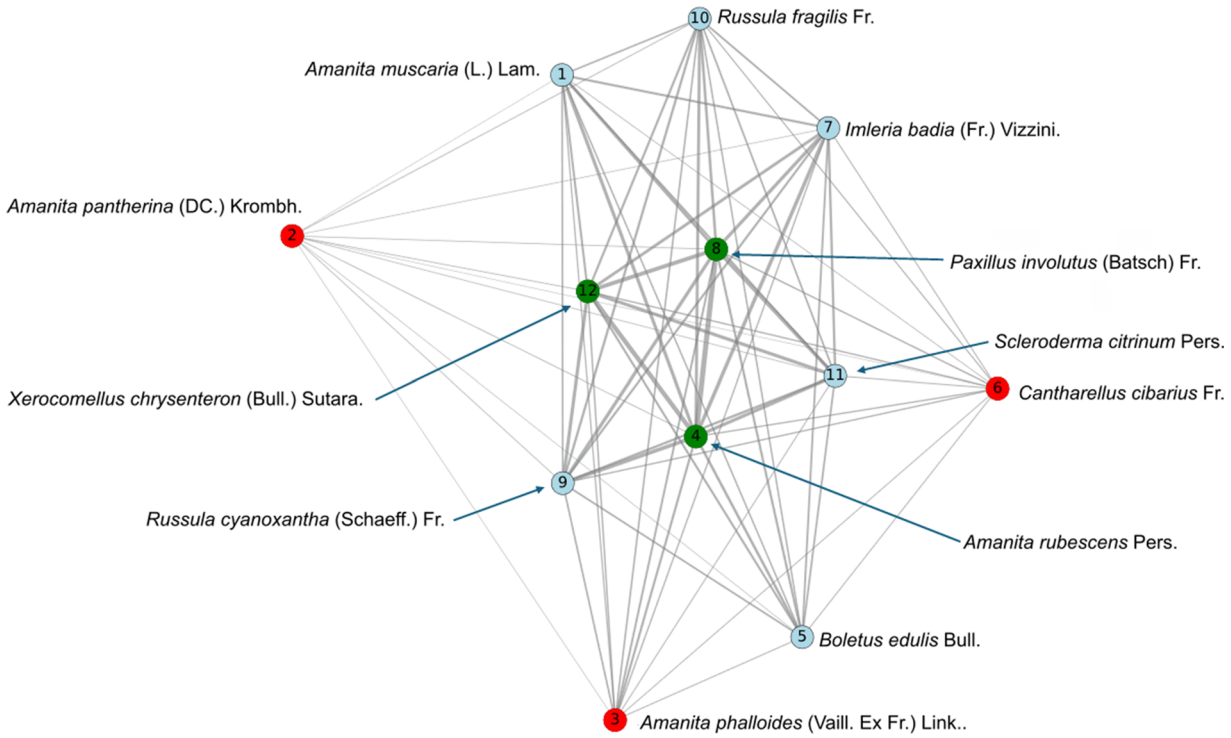

Figure 4. The fungal network. The width of the edge represents the rate of co-occurrence, hence, the strength of interaction. The nodes labeled red were the ones with a weighted degree that is significantly lower than the expected value. The nodes labeled green were the ones with a weighted degree that is significantly higher than the expected value.

centrality of 0.00, which is the lowest possible value. Therefore, each node's weighted betweenness centrality was statistically tested only to determine whether it is significantly greater than the expected value (Table 2C). Among all 12 nodes, 3 nodes have a positive weighted centrality: *A. rubescens* (0.245), *P. involutus*, *X. chrysenteron* (0.0273). Within the three, only *A. rubescens*' value was significantly larger than expected (p-value = 0.00760).

Lastly, as shown in Supplementary Appendix 2.4, there were 5 edges with relatively higher weighted betweenness centrality (weighted betweenness centrality > 0.05). Therefore, the Girvan-Newman method was repeated 5 times to generate 5 iterations of community structures. All 5 iterations were shown in Figure 5. After each iteration, one species was isolated from the population in the following order: *A. muscaria*, *A. phalloides*, *A. pantherina*, *C. cibarius*, and *A. rubescens*.

4. Discussion

4.1. Species' identities in the community

If extensive interactions existed within the fungi examined, the nodes in the network constructed from the foray records would be expected to have different identities such as bridges, hubs, and peripheral nodes [69]. The network constructed was a complete weighted network: a network in which all the possible edges are present, and each edge possessed a specific weight to indicate the relationship (rate of co-occurrence) between the nodes [70]. As a result, certain community structures and node characteristics, such as modules and node degree, calculated using the typical method, were innately hard and meaningless to measure and interpret, as these algorithms assume only a subset of all possible edges are present [70]. Still, some characteristics of the node remain informative. Although most of the nodes (6 out of 12) had non-significant characteristics, as shown in Table 2, this did not imply a lack of interactions within the community. Studies using various algorithms have shown that in networks, both influential and peripheral nodes typically make up a minority, even in communities with extensive interactions [71,72]. Besides these 6 non-influential nodes, the remaining 6 nodes could be categorized into 2 groups of 3 nodes: the highly influential nodes and the peripheral nodes.

The three peripheral nodes represent *Amanita pantherina, A. phalloides*, and *Cantharellus cibarius*. All demonstrated similar characteristics: a significantly lower weighted degree and a significantly higher weighted clustering coefficient than expected. The weighted degree would normally suggest that these three species generally have a weaker-than-expected connection to the rest of the network as conventionally a high weighted clustering coefficient indicates the target species is involved in a tightly-knit

Table 2. The value and relevant statistical results of the three metrics measured for every node: A) weighted degree, B) weighted clustering coefficient, C) weighted betweenness centrality.

A

		Weighted Degree		
			p-value	
Node	Species Name	Value	+	-
1	***Amanita muscaria* (L.) Lam.**	0.932	0.657	0.342
2	***Amanita pantherina* (DC.) Krombh.**	0.245	>0.999	**<0.001**
3	***Amanita phalloides* (Vaill. Ex Fr.) Link.**	0.670	0.979	**0.0210**
4	***Amanita rubescens* Pers.**	1.638	**<0.001**	>0.999
5	***Boletus edulis* Bull.**	0.830	0.843	0.158
6	***Cantharellus cibarius* Fr.**	0.490	>0.999	**<0.001**
7	***Imleria badia* (Fr.) Vizzini.**	1.11	0.282	0.734
8	***Paxillus involutus* (Batsch) Fr.**	1.55	**0.00140**	0.999
9	***Russula cyanoxantha* (Schaeff.) Fr.**	1.17	0.162	0.814
10	***Russula fragilis* Fr.**	0.968	0.580	0.419
11	***Scleroderma citrinum* Pers.**	1.10	0.289	0.716
12	***Xerocomellus chrysenteron* (Bull.) Sutara.**	1.36	**0.0226**	0.974

B

		Weighted Clustering Coefficient		
			p-value	
Node	Species Name	Value	+	-
1	***Amanita muscaria* (L.) Lam.**	0.0928	0.345	0.664
2	***Amanita pantherina* (DC.) Krombh.**	0.105	**<0.001**	>0.999
3	***Amanita phalloides* (Vaill. Ex Fr.) Link.**	0.0975	**0.0216**	0.980
4	***Amanita rubescens* Pers.**	0.0799	>0.999	**<0.001**
5	***Boletus edulis* Bull.**	0.0946	0.159	0.845
6	***Cantharellus cibarius* Fr.**	0.101	**<0.001**	>0.999
7	***Imleria badia* (Fr.) Vizzini.**	0.0895	0.738	0.270
8	***Paxillus involutus* (Batsch) Fr.**	0.0816	>0.999	**0.00180**
9	***Russula cyanoxantha* (Schaeff.) Fr.**	0.0883	0.835	0.165
10	***Russula fragilis* Fr.**	0.0921	0.433	0.578
11	***Scleroderma citrinum* Pers.**	0.0897	0.712	0.286
12	***Xerocomellus chrysenteron* (Bull.) Sutara.**	0.0850	0.980	**0.0230**

C

		Weighted Betweenness Centrality		
			p-value	
Node	Species Name	Value	+	
1	***Amanita muscaria* (L.) Lam.**	0.00	>0.999	
2	***Amanita pantherina* (DC.) Krombh.**	0.00	>0.999	
3	***Amanita phalloides* (Vaill. Ex Fr.) Link.**	0.00	>0.999	
4	***Amanita rubescens* Pers.**	0.218	**0.0160**	
5	***Boletus edulis* Bull.**	0.00	>0.999	
6	***Cantharellus cibarius* Fr.**	0.00	>0.999	
7	***Imleria badia* (Fr.) Vizzini.**	0.00	>0.999	
8	***Paxillus involutus* (Batsch) Fr.**	0.0910	0.199	
9	***Russula cyanoxantha* (Schaeff.) Fr.**	0.00	>0.999	
10	***Russula fragilis* Fr.**	0.00	>0.999	
11	***Scleroderma citrinum* Pers.**	0.00	>0.999	
12	***Xerocomellus chrysenteron* (Bull.) Sutara.**	0.0364	0.523	

+ indicates the proportion of values from the bootstrapping that are equal or larger than the observed value. - indicates the proportion of values from the bootstrapping that are equal or smaller than the observed value.

group which has the potential to be a module that is isolated from the rest of the network [73,74]. However, given that the network is a complete network, the conventional interpretation of clustering coefficient is less applicable. Since the three species nodes are connected to all the remaining nodes and all the neighbors are connected, every node's neighborhood is already a complete weighted subgraph. Furthermore, the algorithm employed only involved the weight of edges between the neighbors but not the edges that connect the target node to the neighbors. Therefore, the measured weighted clustering coefficient fails to demonstrate the involvement of the nodes within the local cluster. Instead, a higher weighted clustering coefficient simply indicates that the neighbors were strongly connected and closely clustered [75: 70]. Furthermore, as the three nodes demonstrated weak connections toward their neighbors, it suggests that the three species were not involved closely in the whole network while the neighbors of them were much more strongly clustered [76]. This argument is further supported by

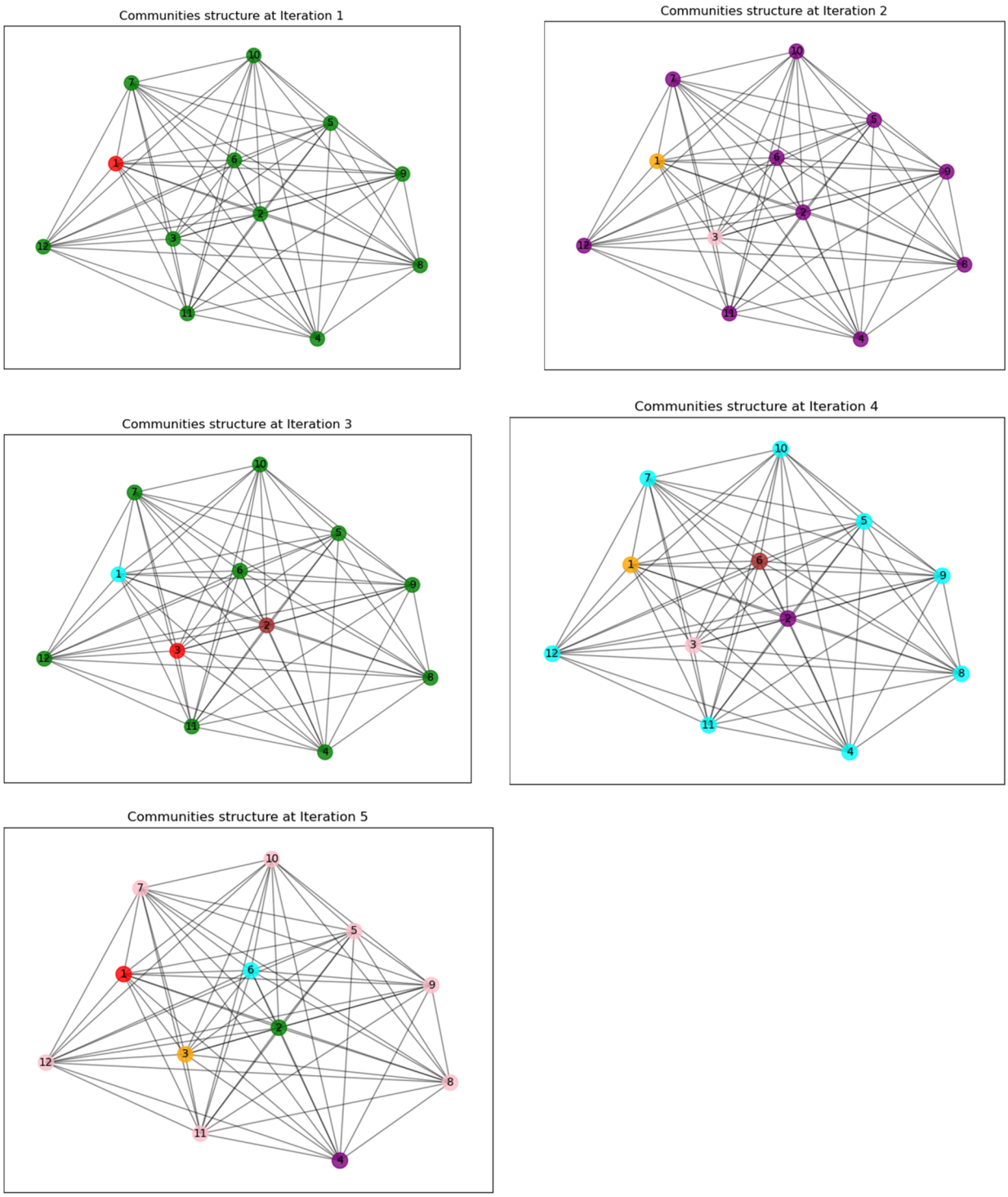

Figure 5. The community structure of the fungal network after each iteration (1: *Amanita muscaria* (L.) lam., 2: *Amanita pantherina* (DC.) krombh., 3: *Amanita phalloides* (vaill. Ex Fr.) Link., 4: *Amanita rubescens* Pers., 5: *Boletus edulis* Bull., 6: *Cantharellus cibarius* Fr., 7: *Imleria badia* (Fr.) vizzini., 8: *Paxillus involutus* (batsch) Fr., 9: *Russula cyanoxantha* (schaeff.) Fr., 10: *Russula fragilis* Fr., 11: *Scleroderma citrinum* Pers., 12: *Xerocomellus chrysenteron* (Bull.) sutara.) after each iteration, only one species was isolated. Among four of the five species isolated were from the genus *amanita*.

the fact that all three species have a 0.0 betweenness centrality indicating a lack of participation in structuring the shortest path within the community and that the three species were peripheral nodes in the network constructed.

From an ecological perspective, multiple explanations for the existence of peripheral nodes exist: niche specialization [77], relatively low ecological importance (as demonstrated in food webs by Jordán et al. [78]), and limited abundance. Existing studies support the argument of low ecological importance. Both *A. pantherina,* and *A. phalloides*, have demonstrated redundant ecological roles with, at least, *A. muscaria* and *A. rubescens*. in their host

ranges [79], nutrient cycling as ectomycorrhizal fungi [80], and toxin release [81]. This could make *A. pantherina* and *A. phalloides* peripheral nodes as they bear limited ecological importance and their replacement, *A. muscaria* and *A. rubescens*, limited their abundance due to chance and reasons that will be explained in later sections. Similar argument might also be applied to *C. cibarius*. Unfortunately, too little research currently exists to meaningfully explore the potential role of niche specialization in explaining the peripheral nodes in the constructed networks.

The influential nodes represent *A. rubescens, Paxillus involutus, and Xerocomellus chrysenteron*. All three species nodes had a significantly higher weighted degree and a significantly lower weighted clustering coefficient than expected. These three nodes were the opposite of the previous three. They had a very strong connection toward the rest of the network and their neighbors were only weakly linked to one another. Therefore, these three were the highly influential nodes that kept the network connected and stable [82]. This observation was further supported by the fact that the three species listed were the only three that had a positive weighted betweenness centrality while that of all the other species was 0.0.

A highly influential node usually represents the ecologically important species, abundant species or indicators of ecosystem's health. Rineau et al. [83], has shown that *P. involutus* is able to convert organic matter in plant litter to mobilize the entrapped nutrients. This is an activity that has been lost in ectomycorrhizal fungi as an adaptation to the dependence on host photosynthate [84]. Together with saprophytic microbes, *P. involutus* could increase the turnover of nutrient and carbon in the ecosystem which facilitate the growth of other ectomycorrhiza [83]. The identification of *P. involutus* a central node in the network supports these claims of its wider ecological importance.

A. rubescens also demonstrated additional interesting network characteristics. As well as being a highly influential node within the network, it was the only node that demonstrated a weighted betweenness centrality that is significantly higher than expected. Its weighted betweenness centrality has reached 0.245, meaning that approximately ¼ shortest path existed within the network would involve *A. rubescens*. Therefore, it is not only a highly influential node, but a central node of the network. The importance of *A. rubescens* was further supported by the result of co-occurrence analysis shown in Figure 3(A) as it demonstrated the most positive co-occurrence with the rest of the species (8/12). The implications of such a finding are discussed below.

4.2. Localized interactions

As shown in Figure 5, using the Girvan-Newman method, when the five edges with the highest influence were removed sequentially, only one species was removed from the whole community after each iteration. This demonstrated a high robustness of the network as the network could maintain homogeneity even after the removal of the most influential edges [85], which showed that strong fungi-fungi interactions did exist within the fungal community studied. Focusing on the nodes that were isolated during the 5 iterations, 4 of them were from the genus *Amanita*. Therefore, instead of only *A. pantherina*, and *A. phalloides* being isolated from the group, the whole *Amanita* genus seems to be isolated to the rest of the network and connected to it with a few highly functional edges. Similar network structure has been demonstrated in other biological processes such as the plant-pollinator interactions [86]. However, the isolation of *A. rubescens* in iteration 5 contradicts the previous argument that *A. rubescens* was the central node, which should demonstrate a relatively strong connection to every single node within the complete weighted network [87]. This contradiction could be resolved by the fact that the *Amanita* genus, as a whole, was isolated from the rest of the network. As shown in Supplementary Appendix 2.3, besides *A. rubescens,* all the other species from the *Amanita* genus demonstrated a low weight (<0.1) edge with most of the species from the other genus. Comparably, *A. rubescens* has demonstrated a relatively strong link to the species from the other genus. Furthermore, except for *A. pantherina* which was an established peripheral node, the other two *Amanita* species had strong links to *A. rubescens*. Therefore, *A. rubescens* was a connector hub [88] that linked the isolated *Amanita* genus to the rest of the network. Most of the shortest paths between other species and the species from the *Amanita* genus had to go through *A. rubescens* which provided it with the highest weighted betweenness centrality among all the nodes. The whole argument could be further supported by Supplementary Appendix 2.4 which showed that among the 5 edges removed, the only two that involved species not from the *Amanita* genus were between *A. rubescens* and *Boletus edulis* and betweent *Cantharellus cibarius* and *Paxillus involutus*. Therefore, although there is relatively strong connection within the *Amanita* genus, the connection between the *Amanita* genus

and the rest of the networks was largely maintained by the edge between *A. rubescens* and *B. edulis*. This sits in line with the common belief that *B. edulis.* Is usually found with A. *rubescens* and *A. muscaria* [89], further supported by evidence that found of *Amanita* and *B. edulis* hyphae and rhizomorphs often closely interwoven and forming composite mycorrhizas [90,91]. However, the exact reason behind this strong correlation is not yet understood. A similar conclusion can be applied to *C. cibarius*, which was an isolated node and connected to the rest of the network *via* the edge between itself and *P. involutus*. However, there is little documentation noting an extensive co-occurrence between the two species.

Furthermore, when considering the main community (Figure 3(A)), the *Amanita* genus seems to demonstrate mainly positive co-occurrence, especially between A. *rubescens* and the rest of the *Amanita* species interrogated. When isolated from the main community (Figure 3(B)), the species in the *Amanita* genus seemed to demonstrate mainly negative and random co-occurrence. One possible explanation for the latter is the existence of intra-genus competition. As mentioned previously, the *Amanita* species assessed demonstrated ecological redundancy which could result in a competitive interaction [92]. As demonstrated in other species such as plants, a competitive interaction would cause negative co-occurrence [93]. The positive co-occurrence observed in the full community suggested the existence of indirect interaction between the *Amanita* species tested and the other species which helps to stabilize the interaction within the *Amanita* genus. Similar interactions have been widely demonstrated in the real-world such as the interaction between predator and prey [94] and facilitation species [95]. As mentioned, the *Amanita* species were connected to the main group *via B. edulis*, which could act to stabilize the interaction within the *Amanita* genus, yet little research has focused on characterizing the interaction between *Amanita* species and *B. edulis*. There also exists studies that suggest the negative co-occurrence being the results of other factors such as different microhabitats and different climatic responses [60]. However, few studies have compared the microhabitats and climatic responses of *Amanita* species and the work by Barzeau and Schamp considers only indirect competition and not direct competition. Therefore, with all the current information, the intra-species competition remains an effective explanation of the observation.

The fungal community structure shown by this research shows that the species assessed cluster into three principal communities with the *Amanita* genus and *C. cibarius* being the two peripheral groups and the rest of the species being the core group. Within the core groups, *B. edulis* and *P. involutus* are the two most important nodes—serving as the respective links to the two peripheral groups respectively. Among the peripheral groups, *A. rubescens.* was highly influential as the main connection between the main group and the *Amanita* genus group. Lastly, the interaction between *Amanita* species and species in the core group help to stabilize the community structure of the *Amanita* genus. All of these, again, suggested that the ectomycorrhizal fungal community demonstrated sophisticated interactions within it.

4.3. Fungal interactions as insight into fungal community ecology

When considering the stability of an ecosystem for an extended period of time, diversity has been thought to be a prerequisite [96]. A higher diversity usually means a higher redundancy and more diverse reaction traits, meaning that the ecosystem is able to weather certain external disturbances to a larger extent [97]. Based on that, many studies of fungal ecology have focused on external factors, such as climate and fungal and non-fungal species diversity. For example, the models of Martínez-Peña et al. [98] used to predict the relationship between the yield of *Boletus edulis* and *Lactarius* group *deliciousus* and multiple environmental variables such as rainfall, temperature and stand age of the wood. These existing fungal studies usually considered species or genus as independent and isolated groups in an ecosystem, which explain the increase in stability, resistance and resilience of the community when there is an increase in fungal diversity [99].

However, when considering the interaction between species within a community, rather than isolated species, a more diverse ecosystem tends to be less stable as important connection increases and average interaction strength increases [100]. Therefore, besides isolated groups, fungal species should be considered as a community, and the interaction between species should continue to be studied extensively.

In order to identify interacting species out from millions of random species pairing, a method to detect interaction signals at the community level is required. In this study, it has been proved that foray records have the capability of detecting signals of interactions within local communities in the forms of co-occurrence, special nodes, and edges such as the positive correlation between *Amanita* species and *B. edulis.* Certain signals can be detected without

physical interaction if the correlated species share a similar habitat [101], or one species is a strong ecological indicator [102]. These instances need to be differentiated to prevent the over-estimation of interaction levels within fungal communities. Yet understanding interspecific fungal interactions remains vital for wider understandings of ecology and conservation.

Recent climate change and environmental pollution have introduced an unexampled level of disturbances to global ecosystems [103]. Under the circumstance, understanding how external factors would affect different fungal species is simply not enough for the prediction of future community structures [104]. Species interaction with one another is also crucial. For example, it has been long known that in other communities that two mutualistic species are more likely to experience simultaneous decline in population [105]. In the case of fungal communities, if the positive co-occurrence signal between the *Amanita* species tested and *B. edulis* is shown to be caused by a real physical mutualistic interaction–as suggested by some microscopical studies [90,91]–then population changes in *Amanita* species are no longer solely dependent on their own response to external disturbances and the responses of *B. edulis* need also to be investigated.

Indeed, despite the importance of ectomycorrhizal networks to wider forest ecology, fungal community ecology remained an under-studied field–primarily due to subjective bias and difficulties in investigation [104]. Here, we suggest that the methodologies employed in this study are applicable in future studies of within-community fungal interactions as a preliminary study to guide the more specific and detailed investigations. Whilst it must be kept in mind that the signals detected do not guarantee the presence of interactions, the signals do shed light into the possible directions to detect where interactions are likely to be located. With more interactions being qualified, the future network and co-occurrence analyses could also be more informative and fruitful—allowing us to accelerate our understanding of fungal interactions and power further studies of fungal ecology and conservation.

4.4. The future of fungal forays

Despite being viewed by many as an antiquated practice, we hope to have demonstrated here the utility of fungal forays to modern fungal ecology–in addition to their wider educational and social benefits. Previous research has demonstrated that fruiting bodies' formation could be affected by external factors such as environmental disturbances [12], climate factors [106], and human activities such as forest floor trampling [107]. The long-term impacts of such factors are still relatively unknown and fungal forays provide a set of baseline records which can be used to monitor these impacts.

However, it must be recognized that fungal fruiting is a time-sensitive event and this can impact on the reliability of foray records to indicate general trends: Parker-Rhodes [18] suggested that due to erratic fruiting, only 25% of the local species composition is documented by foray records and foray records need be smaller and more frequent to be more accurate; Halme and Kotiaho [108] demonstrated that time is a crucial factor affecting the accuracy of foray records in reflecting local species composition; similar conclusion was drawn by Fadnes [109], who also noticed that fungi's phenological change. As such, it is important to be aware of these factors when using foray data. As in this study, using a restricted set of species and using multiple foray records can help to minimize the impacts caused by seasonal variation whilst looking at wider ecological trends [108,110].

Looking forward, modern techniques such as environmental DNA can complement foray records and offer a more precise picture of the local fungal community. However, due to the risk of contamination and the degradability of extracellular DNA, relying solely on environmental DNA is nearly impossible for constructing a comprehensive and continuous fungal community profile of an area (with exceptions for specific environments such as permafrost, see [111]). Therefore, long-term foray records are likely to remain a key dataset for examining and understanding long term changes in local fungal community structure and composition.

5. Conclusion

In using foray records from Yorkshire spanning the past 150 years, this study has successfully identified species within the fungal community that possess different identities, revealed substructures, and uncovered extensive localized interactions that were previously unknown. These findings not only highlight the complexity of interactions within fungal communities but also demonstrate the potential of foray records as a valuable resource in fungal ecology.

Foray data collected by amateur groups provides a rich, if underutilized, resource for the global scientific community, particularly those seeking to understand the impacts of environmental change. With established forays occurring and being recorded

from the late nineteenth century, foray records provide high resolution snapshots of fungal community structure across a substantial time period. Whilst care needs to be taken to ensure a selection of species with stable species concepts, the benefits of such data far outweigh its limitations. Many of these limitations, particularly regarding concerns of accurate identification, are likely to be minimized if the use of foray data can be combined with genetic analysis of historic and contemporary specimens. This, particularly, remains an unexplored horizon with substantial potential to further our understanding of the complex long-term interactions between fungi and their response to global change.

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Data availability statement

The authors confirm that the data supporting the findings of this study are available within its supplementary materials.

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