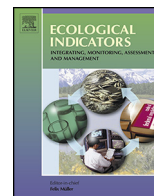




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# Interspecific networks in ground beetle (Coleoptera: Carabidae) assemblages

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### ABSTRACT

Although changes to interspecific relationships can significantly alter the composition of insect assemblages, they are often ignored when assessing impacts of environmental change. Long-term ground beetle data were used in this study to analyse ecological networks from three habitats at two sites in Scotland. A Bayesian Network inference algorithm was used to reveal interspecific relationships. The significance and strength of relationships between species (nodes) were estimated along with other network properties. Links were identified as positive relationships if co-occurrences of beetles correlated positively, and as negatives relationships if there was a negative correlation between the occurrences of the species. Most of the species had few links and only 10% of the nodes were connected with several links. *Calathus fuscipes*, a common carabid in the samples, was the most connected, with nine links to other species. More interspecific relationships were found to be positive than negative, with 48 and 23 links, respectively. The modular structure of the network was assessed and eight separate sub-networks were found. Habitat preferences of the species were clearly represented in the structure of the sets of those five sub-networks containing more than one species and were in line with the findings of the indicator species analysis. In our study, we showed that generated Bayesian networks can model interspecific relationships between carabid species. Due to the relative ease of the collection of field data and the high information content of the results, this method could be incorporated into everyday ecological analysis.

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## 1. Introduction

Networks are around us everywhere, from our body's biochemical processes through social interactions to transportation or power systems and certainly in ecology. Although several attempts were made earlier in the last century to analyse large and complex networks, this challenging task only recently became possible as a result of the availability of modern computer technology. Despite the fact that analysing social networks has recently become a routine tool (Borgatti et al., 2009) for instance in epidemiology (e.g. Christley et al., 2005), the advertising industry (e.g. Yang and Lin, 2006) or for the security services (e.g. Ressler, 2006), the use of ecological networks is still a great challenge for ecologists. Although food webs are generally considered as ecological networks (Ings et al., 2009), there are many other ways in which species can be linked to each other, for instance mutualism, competition or, indirectly, through an environmental factor to which they are equally

sensitive. The presence or absence of these links can play an important role in defining communities or separating them from each other on temporal or spatial scales (Ohgushi, 2008). In spite of their importance, interspecific networks of communities are often neglected in ecological studies that aim to compare assemblages or to assess environmental impacts.

One of the reasons why such interactions are not incorporated in these projects may be the complexity of networks or the lack of sufficient data to construct them. Milns et al. (2010) described the usefulness of Bayesian networks (BNs) to reveal ecological links between bird species, using only species count data, discretized to four coarse levels. They argued that recording species abundances even on a coarse level might provide us with useful insights into the associated ecological networks and thus improve the quality of environmental assessments. However, this method has not been tested thoroughly with other organisms and the ecological implications of certain network properties have not been discussed.

In common with other networks, ecological networks consist of nodes and links between them. In most of these networks, species are the nodes and various types of relationships (e.g. energy flow, mutualism or predation) connecting them are the

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links in the network. We know from the analysis of social networks that several factors can influence the topology of a network (Kossinets and Watts, 2006). Network properties derived from different topologies can also be measured in ecological networks (Proulx et al., 2005), such as the number of links connecting one node to others (degree), various measures of centrality and betweenness (Freeman, 1977), or the strength of the links. Similar to social networks, ecological networks are likely to depend on various environmental factors, therefore reflecting environmental changes or perturbations caused by human impacts. Moreover, exploration of the subsystems of complex networks can enable scientists to gain deep insight into the underlying mechanisms stabilizing ecosystems (see Solé and Montoya, 2001). Likewise, there is evidence that the complexity of a network, with respect to taxonomic or functional diversity, also stabilizes communities (Ives and Carpenter, 2007), making it a matter of importance to conservation. Species that have more, or stronger links to other species, or bear greater eigenvector or betweenness centrality may play a critical role in networks and their decline. They can therefore play a crucial part in the alteration of communities (Benedek et al., 2007). In spite of the importance of ecological network analyses, sufficient data to allow the technique to be used are not frequently available. It is only in the last decade that network analysis has been used to understand the complexity of ecosystems. Although pollination networks are regularly discussed (e.g. Olesen et al., 2007; Campbell et al., 2011), comparable analyses of insect assemblages have not yet been carried out. The networks we used are causal networks, based on species co-occurrences, therefore they should not be interpreted as food webs. Neither should the interspecific links found in the model routinely be interpreted as direct, species-to-species interactions (e.g. plant–pollinator relationships) but more as the likelihood that two species are in some way interdependent. It is however difficult to define the nature of these relationships. In spite of the known limitations, BNs, built using species occurrence data, can be important tools for ecologists to gain deeper insights into the structure of assemblages, whilst incorporating possible species interactions into models.

In this study, we aimed to construct the probable ecological network of ground beetle (Coleoptera: Carabidae) assemblages, using Bayesian Networks (BN), to analyse the key features characterizing these networks and also to test how well BNs can describe the assemblages studied here. Our focus was mainly on whether BNs can reveal differences in assemblages between sampling locations, or habitat types. Since BNs map statistical links between species occurrences, we hypothesized that (1) our constructed networks represent legitimate ecological patterns (Milns et al., 2010) and therefore show similar characteristics to real-life networks such as one of the best known ones, the Ythan Estuary food web (Huxham et al., 1996). Consequently, we predicted that (a) links between species in more similar assemblages will be denser than those that are less similar to each other, thus forming a modular structure (consisting of sub-networks), and that (b) the modular structure will model the differences between sites and habitats, similar to the groupings obtained using hierarchical clustering (Pozsgai et al., 2015). Moreover, since mutualistic relationships were suggested to be more important in ecological networks, and direct competition between carabid species in nature has not been proved (Lövei and Sunderland, 1996; Niemela et al., 1997), we also hypothesized that (c) there will be more positive than negative interspecific relationships in line with the findings of Aderhold et al., 2013 and Fath and Patten, 1998).

We also hypothesized that (2) some species' properties were correlated with certain network characteristics. Hence, we predicted that (d) although a few species will have numerous links, most would have low numbers of connections and hence the degree

of nodes will follow the power-law distribution (Barabási and Albert, 1999). It is also logical to presume that (e) species characteristic of certain groups in terms of transect, habitat and site, appear in the network as “hub” species. In these cases, they may show numerous in-group links and only a few out-group links and, based on their individual properties in the network, they are likely to be the species most responsible for the stability of the networks. Besides these, we expected (f) the most dominant species to occupy a relatively central position, bearing numerous links to other species and therefore being ideal candidates as indicator organisms. We also anticipated (g) a direct indication of changes in population densities based on some individual network properties; explicitly whether there is any correlation between species having more links and how susceptible they are to decline.

## 2. Materials and methods

### 2.1. Sampling sites and protocol

Carabid beetles were sampled at two Scottish locations, Glensough (latitude/longitude: N 56° 53' 43.3", W 2° 32' 29.4") and Sourhope (latitude/longitude: N 55° 28' 52.3", W 2° 14' 42.1"), for 18 years, from 1994 until 2011. At each site, three transects were established in three different vegetation types, namely acidic grassland, dry heather moorland and blanket bog. Since both sites participate in the UK Environmental Change Network, all sampling was carried out using the ECN Ground Predator Protocol (Rennie et al., 2015; Sykes and Lane, 1996). In each transect, 10 pitfall traps with a diameter of 8 cm were used. Metal mesh cones, with a mesh size of 2 cm, were placed in the base of each trap to assist the escape of small mammals and frogs. Traps were emptied fortnightly from the first week of May to the last week of October. All adult carabids were identified to species level using the works of Lindroth (1985, 1986), Hürka (1996) and Freude et al. (2004). Due to discrepancies in earlier identifications, *Patrobus atrorufus* and *Patrobus assimilis* were merged to *Patrobus sp.* 'pseudospecies' and *Pterostichus nigrita* and *Pterostichus rhaeticus* were also treated as one species, *P. nigrita*, due to the difficulty of their identification. Species for which fewer than 10 individuals in total were caught were excluded from the analysis. Data were pooled by year for each transect, resulting in 108 recording events of 40 species.

### 2.2. Statistical analysis

The Bayesian networks we used for further analysis were identified using the Banjo software (Hartemink, 2008). Aside from minor changes, we followed the method applied by Milns et al. (2010) and only the major steps are therefore listed. Since Banjo is optimized for handling discrete data, carabid counts were discretized in four levels, namely zeros (0), one or two specimens (1), individual counts between three and the mean abundance for the whole dataset, excluding zeros (2) and number of captured individuals greater than the mean abundance of the dataset, excluding zeros (3). A total of 1,000 'greedy' search algorithms (Cormen et al., 1990), with random starts, were executed in Banjo based on discrete species data to generate each network, and 100 networks were generated. The time of each search was maximized as 10 min which resulted in an average of  $6 \times 10^7$  ( $SD = 3.5 \times 10^5$ ) iterations. This method analyses the co-occurrence of the species using Bayesian network interference algorithms, whilst estimating the strength of a link between species (influence score, IS). Links between species pairs correlating negatively in their occurrences were marked as negative links, whilst positively correlated co-occurrences were scored with positive values.

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