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| **Project title:** | Restoration, management and utilisation of ecosystems services in farmland (BBSRC CASE Studentship) project |
| **Project number:** | CP 114 |
| **Project leader:** | Jane Memmott, School of Biological Sciences, University of Bristol |
| **Report:** | Annual report, December 2015 |
| **Previous report:** | |
| **Key staff:** | Samantha Ardin (PhD student) |
| **Location of project:** | School of Biological Sciences, Bristol University |
| **Industry Representative:** | Jon Knight, AHDB Horticulture |
| **Date project commenced:** | October 2013 |
| **Date project completed (or expected completion date):** | September 2017 |

# PROGRESS REPORT FOR BBSRC CASE/AHDB STUDENTSHIP

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DECEMBER 4, 2015

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# ABSTRACT

Ecosystems deliver numerous services central to our existence; the services of pollination and natural pest control fortify our food supply by contributing significantly to the productivity of agro-ecosystems, but the ecological networks from which they stem are being rapidly degraded. Promoting these natural services through targeted ecosystem restoration offers a way to unite the valuable, but seemingly disparate, aims of agricultural intensification and biodiversity preservation. The networks of species underpinning different ecosystem services interact in complex ways, and it is imperative that we gain a greater mechanistic understanding of these interactions if we are to successfully promote sustainable ecosystem service provision through restoration; however, this research avenue is limited by the infrequency of studies combining multiple ecosystem services. In this study, we establish a comprehensive, quantified, ecological network for an orchard agro-ecosystem, combining several types of trophic, mutualistic and parasitic networks relevant to the provision of pollination and natural pest control. In doing so, we hope to provide a platform from which better informed restoration strategies can be developed.


## Background

Natural ecosystems provide a wealth of services (Cardinale et al., 2012), with food production amongst those most fundamental for human survival. For instance, 87 of the world's leading crops, accounting for 35% of crop production globally, depend on animal pollination (Klein et al., 2007). Despite this, ecosystem degradation and biodiversity loss remain globally prevalent (Barnosky et al., 2012; Barnosky et al., 2011) with agricultural expansion and intensification amongst the key drivers (Foley et al., 2005; Krauss et al., 2010; Tilman et al., 2001). This seeming juxtaposition between global food security and biodiversity conservation has given rise to a large body of research, culminating in the advocation by many conservationists of 'land-sparing', in which areas of agricultural land are set aside for the sole purpose of biodiversity conservation, enabling indiscriminate intensification of the remaining agricultural land (Phalan, Onial, Balmford, & Green, 2011). Whilst in some scenarios this approach could enable optimisation for each land-use target, it overlooks the potential benefits of harnessing biodiversity-dependent services to simultaneously promote productivity and environmental health.

The dependency of robust ecosystem service provision on biodiversity has been demonstrated repeatedly (Albrecht, Schmid, Hautier, & Muller, 2012; Bartomeus et al., 2013; Biesmeijer et al., 2006; Brittain, Kremen, & Klein, 2013; Brittain, Williams, Kremen, & Klein, 2013; Carvalheiro et al., 2011; Garibaldi et al., 2011; Hoehn, Tscharntke, Tylianakis, & Steffan-Dewenter, 2008) with even greater levels of biodiversity required for the sustenance of multiple ecosystem services (Cardinale et al., 2012; Isbell et al., 2011; Maestre et al., 2012; Zavaleta, Pasari, Hulvey, & Tilman, 2010). Unfortunately, agricultural landscapes are often heavily degraded counterparts of their original system (Matson, Parton, Power, & Swift, 1997). Promoting fruitful ecosystem service provision in these habitats may therefore necessitate significant restoration of habitats and communities. Whilst there is increasing evidence that ecological restoration can successfully increase both biodiversity and ecosystem service provision, current restoration efforts are rarely able to fully reinstate either (Rey Benayas, Newton, Diaz, & Bullock, 2009), highlighting the need for a greater understanding of the restoration process.

It is not feasible mechanistically or economically to restore every element of a habitat; instead, we need to understand which elements of a network provide services and stability so that restoration efforts can be more focused. Crucially, for sustainable positive impacts to ensue, ecosystem restoration must ensure that the species and interactions necessary for service provision are fostered in the context of an equilibrated ecological network, resilient to perturbation and future environmental change. For this to be achieved, it is imperative that a greater mechanistic understanding of the resilience, dynamics and service provision of ecological networks is established, but the lack of detailed studies on complete agro-ecological networks renders this goal challenging.

In this project, we aim to develop comprehensive, quantitative ecological networks by sampling and collating trophic (plant-herbivore), mutualistic (plant-pollinator) and parasitic (herbivore-parasitoid) networks in ancient organic apple orchards and both mature and young commercial apple orchards. In doing so, we hope to overcome the limitations of studying networks of ecosystem service providers in isolation, and in doing so provide a platform from which to enhance our understanding of the relationship between network structure and the provision of multiple ecosystem services.

## The Role of Ecological Networks in Ecological Restoration

Ecological networks provide an excellent platform from which to develop an understanding of the relationship between biodiversity and ecosystem services as they allow us to interrogate not only individual species but the interactions between species that fundamentally underpin ecosystem service provision. By adopting a network approach, in which we construct and analyse a complete set of interactions between different species within a habitat, we create a theoretical encapsulation of ecosystem service provision; from this, we are able not only to understand the properties of the existing network but potentially make predictions about how the network can be manipulated to promote ecosystem service provision.

## Networks of Networks

It is rare for studies to combine multiple network types (e.g. consider pest control and pollination simultaneously), and it remains unclear how the dynamics and properties of different network types will interact when combined in larger networks of networks (Fontaine et al., 2011). Ecosystem services, which are underpinned by an intricate array of intra- and inter-guild interactions, are linked in complex ways (Bennett, Peterson, & Gordon, 2009; Nelson et al., 2009); hence, it is unsurprising that the behaviour of networks appear different when multiple network types are manipulated or analysed together rather than in isolation (Bewick, Brosi, & Armsworth, 2013; Pocock, Evans, & Memmott, 2012). Understanding the intricacies of cohesive, multi-interaction networks may enable us to more intelligently predict and manipulate ecosystems to the mutual benefit of biodiversity and ecosystem services.

## Network Analysis

Whilst multi-guild networks offer an excellent opportunity for understanding entire ecosystems, they bring with them the challenge of how to analyse such complex data sets. Each approach faces a trade-off between complexity, tractability and accuracy.

### *Simulation-based approaches to network analysis*

A recently popular approach has been to simulate species loss, deeming a species secondarily extinct when all of the species upon which it depends for a particular service (e.g. food, pollination) have gone extinct (see Pocock, Evans, & Memmott, 2012 for a recent example). Species that contribute significantly to the stability of the network can then be identified, as their simulated removal will cause a disproportionate increase in secondary extinctions; these species can be considered potential conservation targets.

However, the complexity of ecological networks means that these models are forced to make several simplifying assumptions. For example, behavioural plasticity may impact heavily on the nature of a perturbation (Brittain, Williams, et al., 2013; Brosi & Briggs, 2013; Kondoh, 2003), but is rarely incorporated into simulations due to the additional computational complexity this would add, as well as the difficulty of assigning appropriate parameter values. These models may also employ somewhat unrealistic extinction patterns. It seems unlikely for individual species to become extinct independently of any direct negative effect on other species in the community. Rather, we might expect more complex demographic changes in which subsets of species decline whilst others persevere, especially when we consider the breadth of impact of key extinction drivers such as climate change and habitat loss. Finally, these approaches tend not to account for functional extinction, in which the extinction of a species results from the increased mortality, but not extinction, of a second species (Saterberg, Sellman, & Ebenman, 2013). It is likely due to the necessary simplification typical of these simulation-based approaches that this method has not stood up to recent empirical testing (Brosi & Briggs, 2013).

### *Network metrics*

An alternative approach could be to calculate and compare the properties of a network that promote robustness and delivery of ecosystem services, and that this should inform conservation priorities (Kaiser-Bunbury & Blüthgen, 2015; Tylianakis, Laliberté, Nielsen, & Bascompte, 2010). High interaction diversity, for instance, may increase the rate of processes within an ecosystem (e.g. Hoehn et al., 2008). Nestedness, the tendency of specialist species within a network to interact with a proper subset of those with which generalist species interact, has also been proposed as a stabilising network property. For example, high levels of nestedness have been suggested to safeguard against secondary extinctions in mutualistic networks (Bastolla et al., 2009; Thebault & Fontaine, 2010). Evenness, a measure of the distribution of species abundances in an ecosystem, has been linked to better provision of ecosystem services such as pest control (Crowder, Northfield, Strand, & Snyder, 2010), whilst the distribution of interactions between species, degree distribution, has been linked to network robustness following random extinction (Albert & Barabasi, 2000).

Whilst network metrics provide a potentially straightforward method for network comparison, the causal relationship between a given metric and network function is often hard to validate.

For example, it has been suggested that the diversity of interacting partners, which correlates positively with nestedness, is, in fact, the true foundation of network robustness in mutualistic networks (James, Pitchford, & Plank, 2012). Furthermore, it is unclear how to promote sustained enhancement of particular network metrics without considering the network at a higher resolution.

### *The role of the community*

Community detection, which involves the identification of sub-communities within an ecological network could provide a unique viewpoint from which meaningful inferences can be made about network stability and ecosystem service provision, whilst avoiding oversimplification. Of the large body of computational methods used to detect communities in networks, many operate by optimising a quantity called 'modularity'. These modularity optimisation algorithms work on the premise that a collection of species and interactions within a network should be classified as a 'module' (or 'community') if the number of interactions between those species is greater than expected.

Most modularity optimisation community detection algorithms can be applied to both binary (presence/absence of interaction) and weighted (frequency of interaction) networks. In an ecological context, the outcome of community detection algorithms on a weighted network can be considered more robust as the additional frequency information reduces the influence of scarce or anecdotal interactions on community assignment. However, weighting may also disguise the importance of rare but influential interactions. This is because algorithms give consideration to how many times pairs of species interact, but not how abundant those species are. This is problematic as a frequent interaction between species i and j could be due to any mix of:

- High abundance of species i
- High abundance of species j
- Preferential interaction between species i and j (homophily)

Species distributions within an ecosystem are typically highly right-skewed such that most species are rare and a few species are highly abundant (Fisher, 1943). Highly abundant species are likely to be encountered more often and hence participate more frequently in interactions, masking the influence of more subtle factors on community structure. As a result, community detection can be disproportionately swayed by a few highly abundant species, to the extent that the underlying forces shaping the network are overlooked. However, if community detection methods can be tailored towards ecological networks (rather than the social networks for which they were originally developed), we may be able to identify key modules within networks that contribute highly to ecosystem service provision and can therefore be targeted for restoration efforts.

**Aims Of project**

1) To construct the first network of networks for an apple orchard habitat, combining key service providers such as pollinators and natural pest-controllers.
2) To disentangle the relationship between habitat management, ecological network structure and ecosystem service provision in apple orchards.
3) To identify ecological modules (communities) that are key for the provision of pollination and pest control in conventional and ancient apple orchards.
4) To predict suitable management/restoration actions, based on network modelling and community detection approaches, to promote both biodiversity and ecosystem function and to implement and evaluate one such action.

**Objectives for Years 1 & 2**

*1) Establish a comprehensive ecological network, containing key mutualistic and antagonistic interactions, for a pristine orchard habitat.*

Whilst apple orchards are reliant on both pollinators and natural pest control, no multi-guild ecological networks currently exist for apple orchards. Between April and September 2014, I therefore surveyed an organic, ancient cider orchard in the South West of England (Abbots Leigh, North Somerset, grid ref. 51.455, -2.665) for pollinators, leaf miners, caterpillars, aphids, bark-dwelling species, vegetation and birds, with a view to constructing the largest and most comprehensive apple orchard network to date.

The site comprised mature cider apple trees (*Malus domestica)*, grassland ground cover (partially grazed by sheep) and adjacent hedgerows. Surveys were carried out in each habitat type with sampling effort proportional to habitat area.

Pollinator surveys were carried out along randomly located 50m transects, resulting in a totalled sampled area of 7500m$^2$. Any individuals seen to contact the reproductive part of the flower were caught and the plant species and pollinator order/family for the interaction recorded.  Any species that could not be identified to species level in the field were captured for identification by professional taxonomists (this accounted for over 95% of all samples).

Vegetation and floral abundance, as well as leaf miners, caterpillars and aphids were surveyed in 50cm x 50cm quadrats placed at 10m intervals along each transect, resulting in a total survey area of 450m$^2$.  The underlying soil surface and all foliage to 2.5m was searched.  In the case where tree foliage extended above 2.5m, canopy height was measured and additional surveys were completed in the areas directly adjacent to the existing quadrat until an equivalent area had been surveyed.  In doing so, I made the assumption that species interactions were homogeneously distributed throughout the tree canopy.  The validity of this approach is questionable as abiotic (e.g. sunlight, wind) and biotic (e.g. predation) factors will vary between the upper and lower canopy; however, I expect that this variability also occurs between trees due to differences in canopy structure and location such that our method remains a relatively unbiased reflection of the true network.

Leaf miners, caterpillars and aphid mummies (parasitised aphids) were returned to the lab for rearing, resulting in the emergence of either Lepidopteran or Dipteran adults or parasitoid wasps.  Emerged species were identified by professional taxonomists.

*Malus domestica* trees were selected at random and the length and circumference of all primary and secondary branches up to a height of 2m were recorded.  For one randomly selected 50cm length of branch I recorded the percentage coverage of fruticose lichen, foliose lichen, crustiose lichen, moss and bark.  I collected all invertebrates associated with any surface type with greater than 10% coverage.

*[N.B. I am currently deciding on the best way to process these specimens, but they will most likely be grouped by order and then morphotyped and a literature search used to find information about the dietary habits of each group (enabling us to add this data to our overall network as a binary network).  Additionally, I may have the opportunity to assess their energy content using a bomb calorimeter, this being relevant to their value to predators such as birds during the winter].*

Birds were surveyed monthly throughout May-August at 2 point transects located at random points at least 100m apart.  Any birds seen or heard were recorded during a 15 minute period at each point.  As these surveys were done primarily to assess the feasibility of this survey method for years 2 and 3, I have only collected presence/absence data for each bird species rather than acquiring the quantitative data that can be collected using this method.

### *2) Compare ecological network structure and functionality across a range of apple orchards under multiple management regimes.*

I am currently compiling ecological networks for a range of commercial and ancient orchards, including key mutualistic and antagonistic interactions. As this project is highly exploratory in nature, with very little known already about ecological networks in orchards, it is essential that the orchards I survey offer enough breadth so that the scope for discovering interesting differences in community structure (potentially linked to different management strategies) is present, whilst also allowing for a structured test of our inferences (in year 3). I am therefore sampling 4 blocks of orchards, such that each block consists of: one pair of young, commercial orchards (trees aged 5-10 years); one pair of mature, commercial orchards (trees aged 20-30 years); and an organic, low intensity, ancient orchard, which will act as a reference site. Within each block, orchards are matched based on fruit use (e.g. cider or dessert apples), size, and geographical location, with all commercial orchards in a block matched additionally by their chemical (e.g. pesticides and herbicides) and management regimes (e.g. pruning and mowing)

Following similar methodology to year 1, I will construct a detailed network of networks for each orchard, including the following interactions:

***Table 1.*** *The different interaction types to be surveyed, including trophic, mutualistic and parasitic networks.*

| | ***Trophic*** | ***Mutualistic*** | ***Parasitic*** |
|---|---|---|---|
| ***Direct observation*** | Plant : Leaf-miner<br>Plant : Caterpillar | Flower : Pollinator | Leaf-miner : Parasitoid<br>Caterpillar : Parasitoid |
| ***Indirect observation*** | Invertebrate : Bird | | |

Unlike in year 1, bird species are being both identified and quantified. Birds will be surveyed a total of three times between May and September at 2 point transects located at random points at least 50m apart. At each point, I wait for 1 minute before recording the location and identity of any birds seen or heard over a 5 minute period. The literature will be used to infer the dietary preferences of each bird species and hence construct a binary bird-invertebrate network.

With each collated network, I will calculate key network metrics (including, but not limited to, community structure, evenness, degree distribution, modularity and interaction diversity). Ecosystem service provision will be evaluated by considering the frequency of beneficial interactions seen within the network (e.g. plant-pollinator interactions as a measure of pollination service), and species abundances (e.g. the abundance of natural enemies as an indirect measure of natural pest control). End of season apple production per unit area (available for all sites) and sale value of total crop (available for all commercial orchards) will act as metrics for the relative productivity and profitability of each orchard.

### *3) Develop improved methods for the detection of communities in ecological networks as an alternative analytical technique to simulation-based approaches.*

I used existing datasets to model the relationship between the abundance of two interacting species and the frequency with which they are observed interacting. By using a mixture of widely available non-parametric and parametric statistical techniques, I developed a new null-modelling approach for modularity-maximisation based community detection algorithms that enables species preference, regardless of species abundances, to be reflected in community allocation.

I will work collaboratively with my co-supervisor Dr. Steve Gregory (Computer Sciences Dept.) to evaluate the structure of these novel null models relative to a range of ecological networks (present in a large-scale farm network (Pocock et al., 2012), and in doing so assess their suitability for community detection in ecological contexts.

I hope to use the resultant community detection algorithms on our collected orchard networks to identify modules (communities) that contain high proportions of beneficial pollination and natural pest control interactions. It is these modules that I hope to restore in commercial orchards.

## Progress Made Towards Year 1 & 2 Objectives

1) *Establish a comprehensive ecological network, containing key mutualistic and antagonistic interactions, for a pristine orchard habitat.*

The flower visiting Diptera taxonomy is complete and these results are presented below. The Hymenoptera have been identified but are awaiting collection in Cardiff. The Coleoptera and leaf miner data (both the miners and their parasitoids), along with the aphids are still awaiting identification. As such, the below results are a subset of those that will be available by the end of this academic year.

## Results

Using existing community detection techniques, I was able to identify clear communities amongst the currently identified subset of pollinators (Figure 1). *M. domestica* was the only plant species within its module, and 43% of its pollinator visitors were not seen interacting with any other plant species.

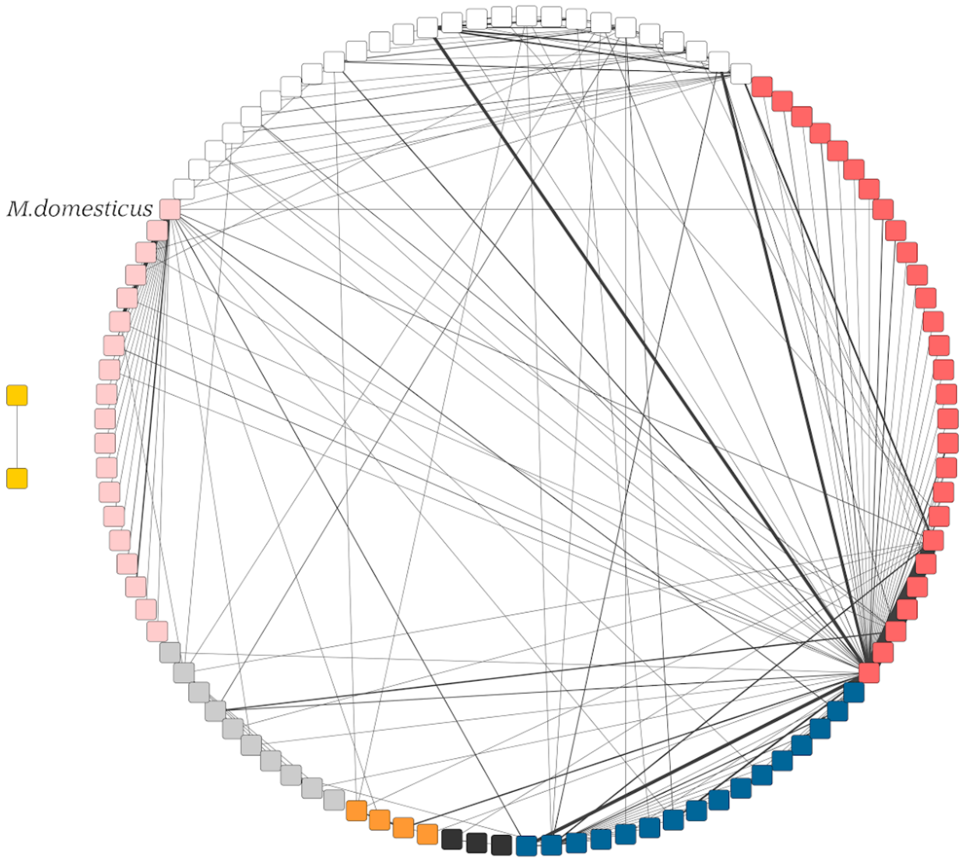



**Figure 1.** The pollinator network [for currently identified or morphotyped species] for the orchard. Each colour indicates a different community, identified using existing community detection techniques, with the community of M. domestica shown in light pink. The thickness of each link is directly proportional to the frequency with which the interaction was observed.

Within each community, there are clear network hubs: those species that are involved in a high proportion of interactions within their community (Figure 2). Three plants, buttercup (*Ranunculus acris),* apple *(M. domestica) and* cow parsley *(Anthriscus sylvestris)* are the most highly connected hub species, suggesting that increasing their abundance may promote disproportionate gains in biodiversity.

Many species within each module act to link two modules, with 16 pollinators of *M. domestica* fulfilling such a role. These species form 57% of the pollinators of *M. domestica,* suggesting that promoting floral diversity in orchards may have ecosystem service benefits through promoting the pollinator services to apple.

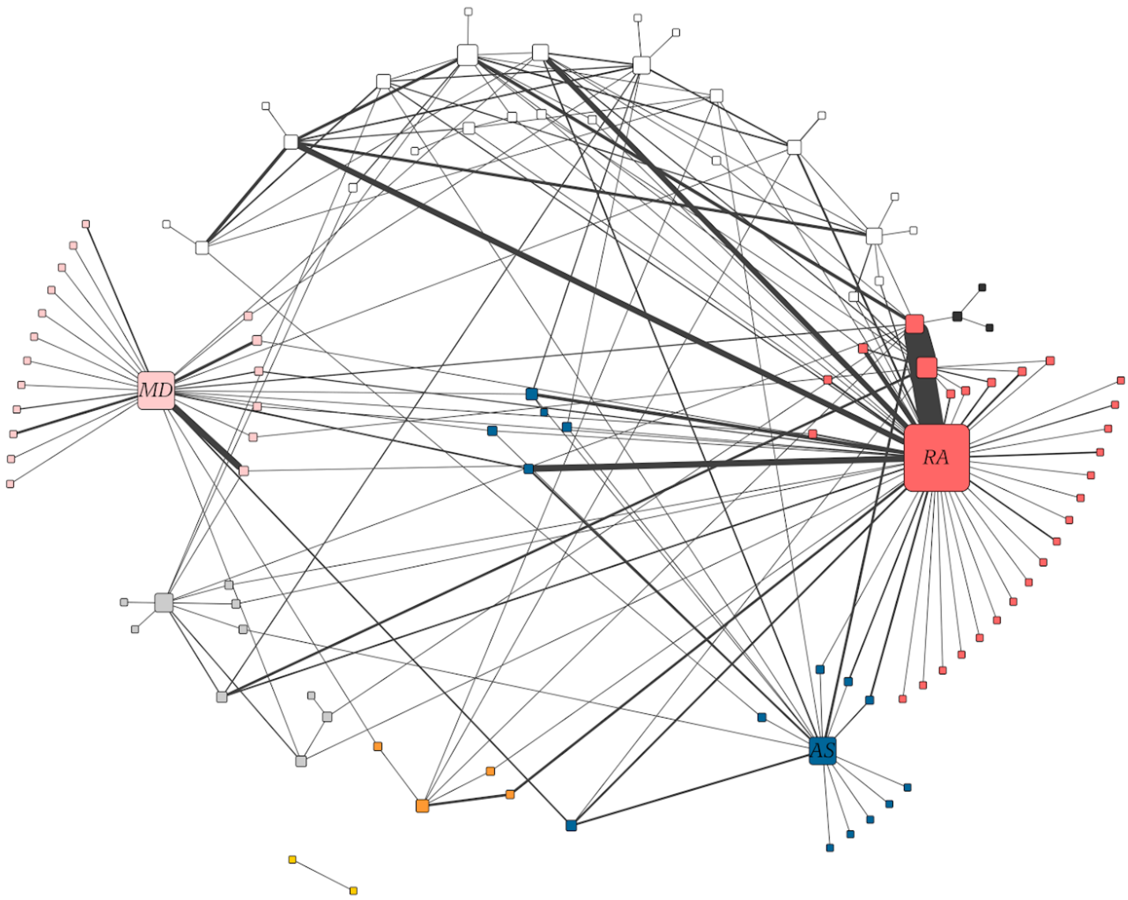



***Figure 2.*** *The pollinator network, with key hub species Ranunculus acris (RA), M. domestica (MD) and Anthriscus sylvestris (AS) labelled. The most highly connected species are found in the exterior of this network view, with species that act to form links between 2 specific modules found in the interior.*

When considering the sub-network of *M. domestica* pollinators and their associated plant species, one can see that *R. acris* and *A. sylvestris* are the most highly connected to *M. domestica* pollinators (Figure 3), suggesting that management approaches that foster these two plant species may act to promote *M. domestica* pollination.

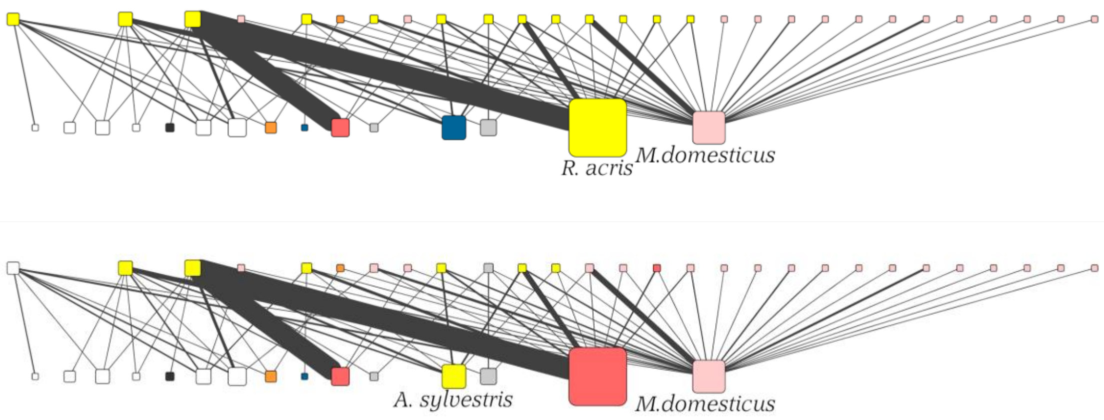



**Figure 3.** The sub-network of M. domestica pollinators and their associated plant species, with (a) R. acris and associated pollinators and (b) A. sylvestris and associated pollinators highlighted in yellow. The thickness of line corresponds to the number of times the interaction was observed.

If we considers all plant species that are visited by the pollinators of *M. domestica*, we find that they form an even temporal spread between May and July (Figure 4). [N.B. Inferences beyond this period cannot be made as the ground flora was heavily trampled by 250 sheep (dotted line, Figure 4)]. The temporal spread suggests that increased floral diversity may promote temporal stability of food for key pollinator species, at least in the absence of grazing.

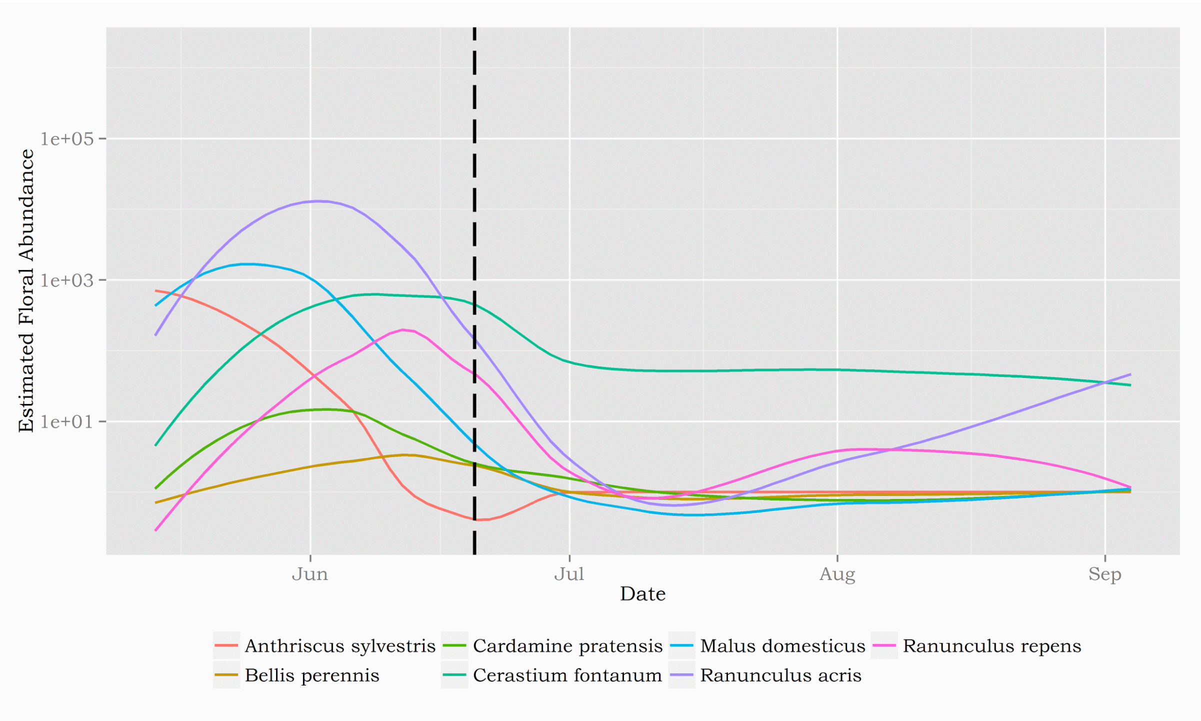



**Figure 4.** The relative abundances of all plant species that are visited by M. domestica pollinators throughout the entire season. The dotted line represents the introduction of over 250 sheep, an example of extreme mismanagement, which resulted in the almost complete destruction of the ground flora.

Whilst drawing inferences from an incomplete network is potentially misleading, there do appear to be key plant species that promote both biodiversity and ecosystem service provision. These species, all common weeds in agricultural landscapes, provide food for a very wide range of pollinators whilst also extending the availability of food for pollinators of *M. domestica* outside of the *M. domestica* flowering period. It is these win:win scenarios that I hope to find when considering both pollination and pest control simultaneously.

## 2) *Compare ecological network structure and functionality across a range of apple orchards under multiple management regimes.*

Working with a full time field assistant, I have completed 3 rounds of sampling (as of $1^{st}$ August 2015) and hope to complete 1-2 more by mid-September, although this may be impeded by my currently broken hand (in a cast).

### *Potential problems*

Most of the networks I am surveying develop over the course of the season (e.g leaf miners and caterpillars), which should ensure that sample sizes are good. Due to the very short season over which *M. domestica* flowers, I have some concerns that I have observed only a small subset of the associated pollinator network. Furthermore, the variability in weather over the few days I was able to sample each site will have introduced some bias to this network, with cooler weather suppressing pollinator foraging and shifting pollinator composition towards larger, more robust groups such as *Bombus sp.*. There is a possibility of obtaining more pollinator data next year for these field sites. Alternatively, my future work may need to incorporate an element of probabilistic network reconstruction.

## *3) Develop improved methods for the detection of communities in ecological network as an alternative analytical technique to simulation-based approaches.*
*Develop improved methods for the detection of communities in ecological network as an alternative analytical technique to simulation-based approaches.*

By modelling the relationship between species interactions and attributes, I was able to develop a novel null model that can now be used to establish tailored, ecosystem-based modularity optimisation algorithms for the identification of compartments in my networks. This part of the project has already been subject to a focused report as part of the BBSRC SWDTP scheme, consequently the results below are a summary of my main findings.

## RESULTS

Relative to the existing null models used in community detection algorithms, my null models more closely represent the properties of the existing network in terms of network density and connectivity (Figure 5). The original networks have low edge density (mean=0.017) and a mean average path length (a measure of connectivity) of 4.783. The existing null models (developed for use with social networks) include many unfeasible interactions (e.g. plant-plant), and have high density (1.000) and connectivity (average path length = 1.000). All novel null models show similar network properties to the original network with low edge density (mean = 0.014) and connectivity (mean average path length = 4.425).

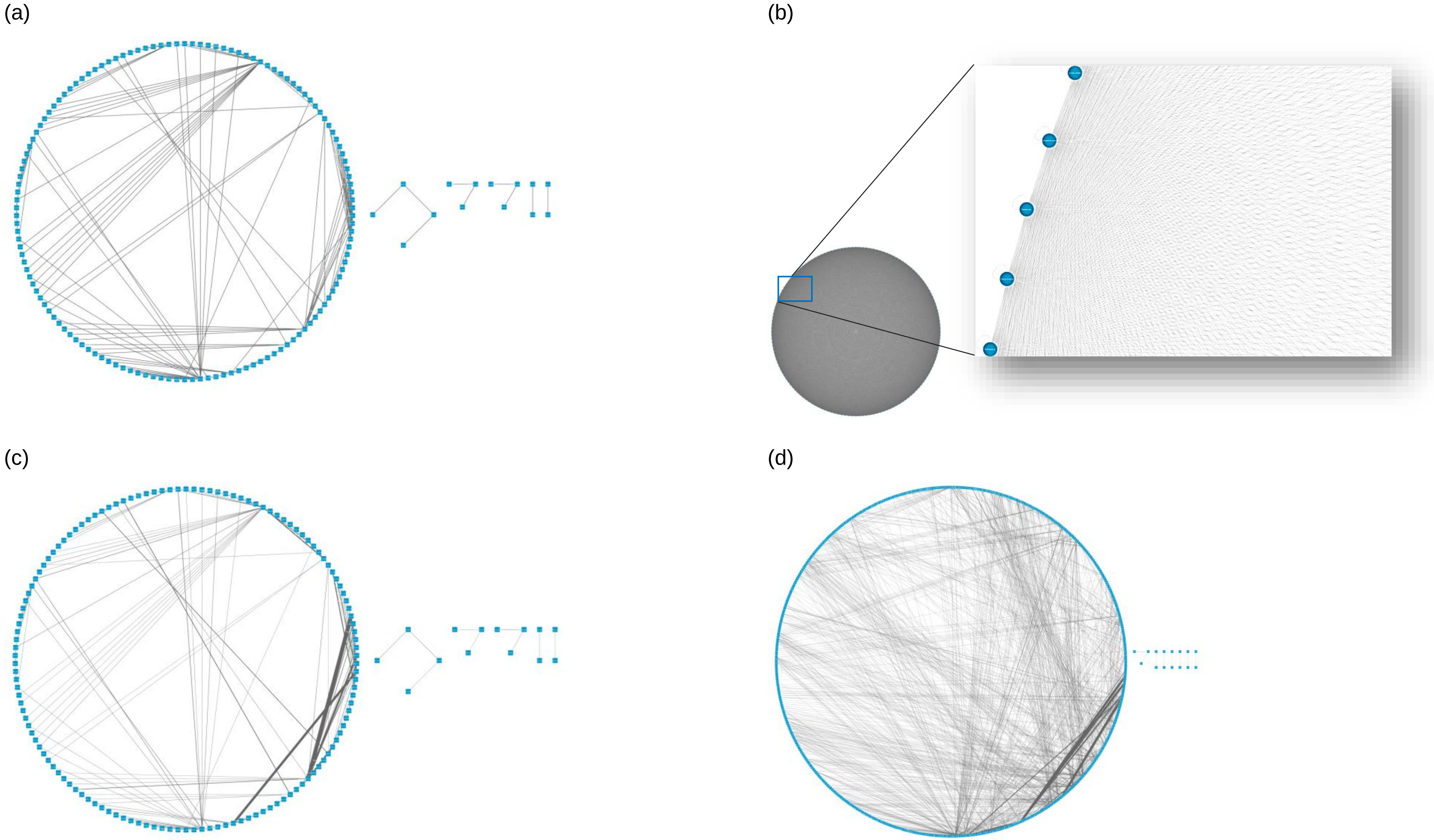



**Figure 5.** (a) The original network for an organic farm (Pocock et al., 2012), (b) a typical existing null model (note the extremely high linkage density), (c/d) novel null models developed during this project (note the closer resemblance to typical ecological network structure in terms of linkage distribution).

**Objectives for year 3**

Year 3 objectives will depend heavily upon the findings from my first two field seasons and these are still incomplete; the objectives below provide a direction of travel and were part of the original proposal. They will be revisited and refined as analysis for the first two years nears completion.

*1) Implement and evaluate a management manipulation in orchards with a view to promoting both biodiversity and ecosystem service provision.*

I will use community detection approaches to identify modules within the network that offer net benefits in terms of pollination and pest control. I will interrogate each of these ecological modules to answer questions such as: are there key 'hub' species within this module and are the species within this module associated with particular micro-habitats, such as deadwood or ground flora? I will conduct manipulations on orchard pairs (one experimental, one control) to see if I can reinstate or reinforce a specific module. These manipulation will be informed by the findings of years 1 and 2, but may consist of: alteration of floral composition through introduction of specific plants (for example adding cow parsley or reducing grazing pressure to allow greater flowering), removal of a specific species to promote increases others, addition of bird boxes to promote pest control by birds, or addition of bark-reserves as shelter for natural predators. I will evaluate the effect of the manipulation on network structure and ecosystem service provision. Our evaluation method will depend on the manipulation chosen, but could involve measuring the abundance of focal individuals (those within the key module) or the impact on ecosystem service provision (by surveying for key interactions and/or species).

Due to our paired design, I will be able to evaluate the manipulated network relative to: the same network in the previous year (this allows us to ask if the network has improved); the network of the paired orchard (this asks how the network has changed relative to the control network, which allows us to account for the effects of inter-annual climatic differences); and the pristine network (this asks how well the network is performing relative to a pristine reference orchard, allowing us to evaluate how well the manipulation performs from both biodiversity and ecosystem service perspectives).

*2) Develop novel modelling approaches, incorporating pollinator preferences and plant phenology, to predict which plant communities will best support pollination and natural pest control.*

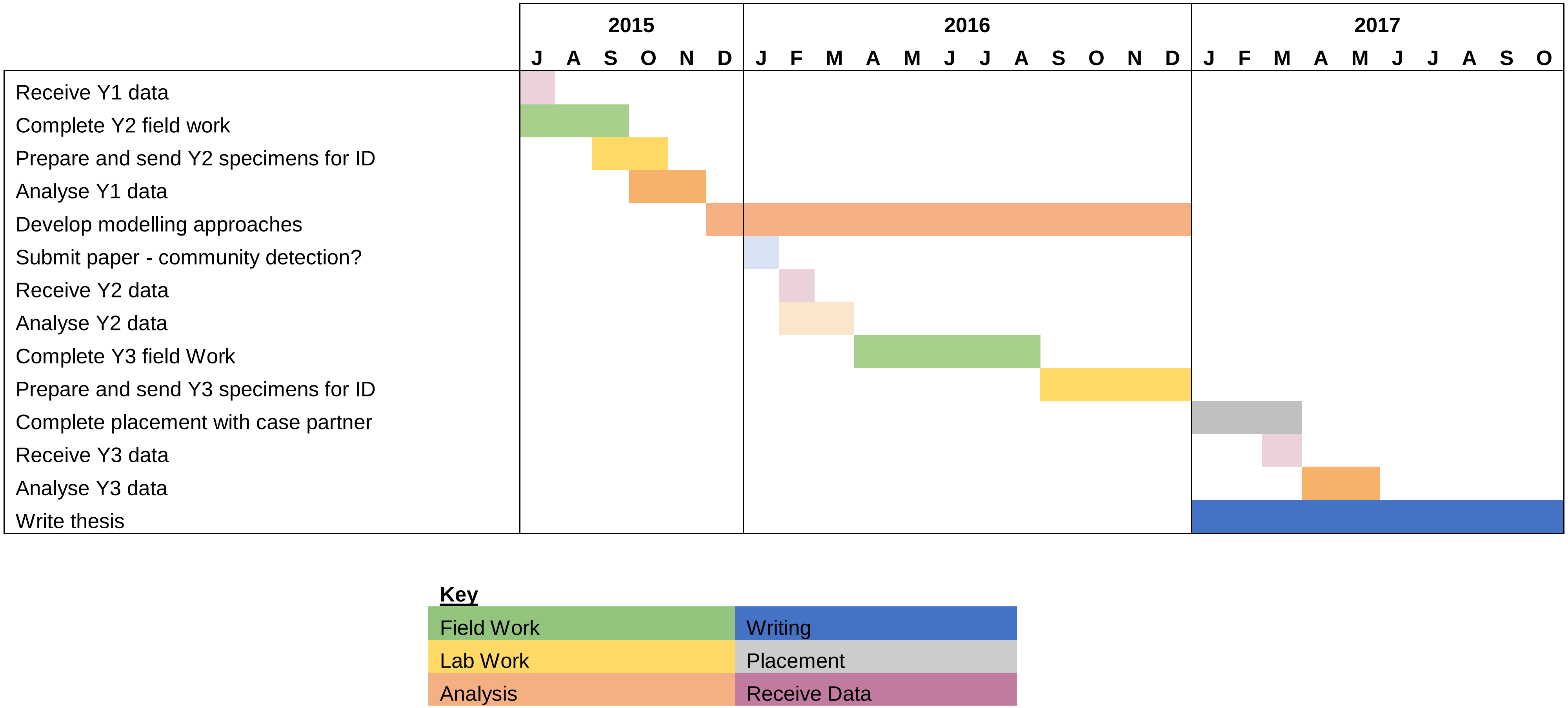
This element of the project is still in its infancy and, as such, will be outlined in a future report.

## Outline thesis plan

*Provisional Chapter Ideas*

1. Structure and functionality of a network of networks in apple orchards.
2. Network structure and functionality across varying management regimes in apple orchards.
3. Community detection in ecological networks.
4. Network modelling, incorporating pollinator preferences and plant phenology, to optimise community composition for ecosystem service provision in apple orchards.
5. Manipulation of ecological networks for the promotion of ecosystem services.

# Gantt chart




*Pale colours indicate uncertainty over dates*

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