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David Bohan

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03



Networking Agro-Ecology – reconciling the different needs for ecological functions provided by biodiversity

David A. Bohan
UMR Agroécologie, Dijon

I am not going to enter into the details of ecosystem services, particularly not the political nature of ecosystem services. Rather, my aim is to try to propose a method that I think potentially in the future could become a way of identifying the bottlenecks, and the complexity in ecosystem services research that is a barrier to making things simpler.

I come at this problem very much from an ecological angle, as a researcher working in agriculture. Ecosystem services are, in actuality, ecological functions that have a socio-economic value. The ecological functions I study have that value and are therefore, candidate ecosystem services. I want to see them used by farmers so they can provide a service to the public. At the same time, this talk will also be a random walk through my research over the last 15 years or so.

The future of agriculture

It is now generally accepted that our requirements for food are going to increase in the future, with a continued rise in population. We have already seen over the last 60 years that our food system impacts directly what might be called service delivery; the things that we expect of our environment. One solution to this problem is the sustainable intensification of agriculture. The problem with this one solution is that there are at least two different ways of looking at the sustainable intensification of agriculture. One might be described as the techno-simple way, characterised maybe by extremes like GMO (Genetically modified organism). The other is the eco-complex, and in this talk I will present research to support eco-complex approaches to sustainably intensifying agriculture.

Biodiversity and regulation

I work with weeds, in part because I think they hold the key to delivering biodiversity-derived ecosystem services in farmland. Farmers spend an awful lot of time putting herbicides on fields to stop weeds affecting crop productivity. While being a disservice, in the sense that they impact crop productivity and that we have to use chemicals to control them, weeds also provide a very positive support to ecosystem service delivery in the form of weed biodiversity. What I am hoping is that we can better balance weed biodiversity and crop productivity, without putting the chemicals into the system, using ecological functions.

I work with a very beautiful – in my opinion –, carabid beetle, *Pterostichus melanarius* (figure 1). It is very abundant throughout Northern and Central Europe. Using a national-scale dataset, from the Farm Scale Evaluation (FSE) of the impact of GMO herbicide-tolerance on biodiversity in the UK, we examined the regulation of weeds by this beetle. There were four OGM crops - beet, maize, spring oilseed rape and winter oilseed rape - that were ready to be employed in Europe at the end of the 1990s, early 2000s, sown in 256 fields (figure 2). Each field was split, with the OGM crop grown on one side and the conventional crop grown on the other.

This talk is not about GMOs, and much of what I present today is of the conventional data. That is, conventionally grown beet, maize and rape from 256 half-fields across the UK. We sampled the weeds. Given that it was a herbicide-tolerant experiment, the aim was to study weed biodiversity under conventional GMO management. We followed a putative life cycle of a weed (figure 3) from the seed bank before the trial was sown (time t), through the seedling stages, early spring stages associated with the application of herbicide on one or other sides, the seed rain, what these weeds then put back into the system, at the end of the year (time $t+1$), the total amount of weed in terms of counts and biomass. Then in subsequent years, we went back and sampled the seed bank again.

For the invertebrates, we sampled using transect



Figure 1. The carabid beetle *Pterostichus melanarius*.

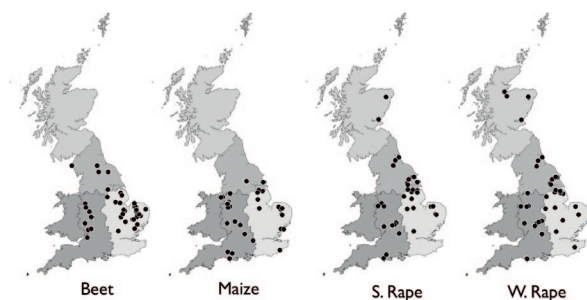


Figure 2. The FSE data.

walks for bees and butterflies, and pitfall and suction trapping for certain pests. This is the largest trial ever conducted in agriculture in the world that simultaneously samples plants and invertebrates.

- › 1.5 million weed plants counted
- › 1 ton (dried) plant biomass sorted
- › > 2.5 million invertebrates trapped
- › > 1400 km of pollinator transects walked

It provides a lot of information about what happens in farm fields in Northern Europe. What I am particularly interested in is the ecological functions (regulation) between the weeds and the invertebrates. In effect, ecologically what drives what?

For the carabids and weeds, we approached at this with a very simple model of regulation (figure 4). We said that the carabids, if they are going to be important, should change the size of the seed bank from time t to $t+1$. In other words, they should affect the long-term dynamics of the weeds. Now, what happens is that at t , some of these seeds germinate to become weeds in the field. Those weeds then set seed. The seed rains down onto the soil surface and some of those seeds then re-enter the seed bank at $t+1$. Carabids, however, only interact with the seeds on the soil surface before it re-enters the seed bank.

We had a number of hypotheses for the relationships between carabids and the seed bank. We looked at all of these relationships, but the one that really mattered is the one for an expectation of regulation: the change in the seed bank between t and $t+1$ should be negative, with increasing carabid abundance. The more carabids present in a field, the more the seed bank declines (figure 5). Happily, that was just what we found.

Each of the data-point shapes is one of the different crops. Across these conventional crops, grown in Britain, we find a national-scale pattern. The more carabids we sampled, the more the seed bank declined. In other words, we found something that looks like weed seed bank regulation.

Our simple model of regulation is satisfied and, because control of the seed bank is something that farmers might want in place of using herbicides, biodiversity-derived seed predation has all the hallmarks of an ecosystem service.

- › We found expected relationships between:
 - ›› seed rain amount and seedbank change
 - ›› seed rain amount and carabids
- › Simple 'regulation' model is satisfied
- › Seed predation has the hallmarks of an ecosystem service

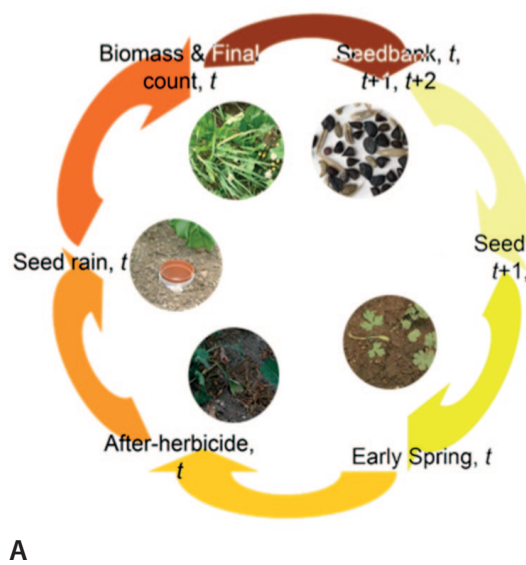


Figure 3. Weeds sampling.

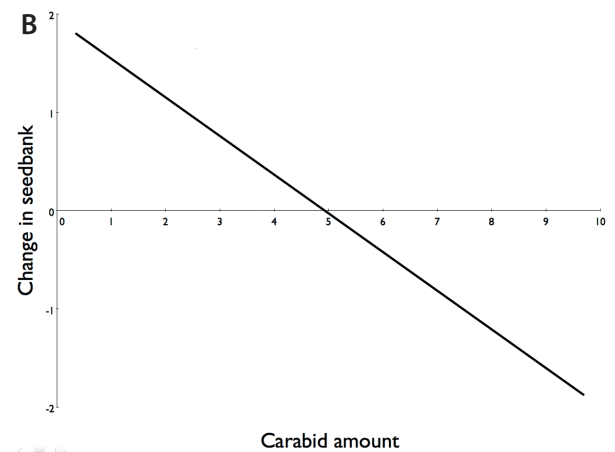
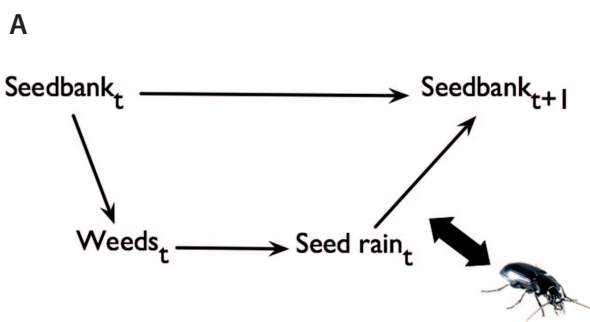


Figure 4. Simple model of regulation.

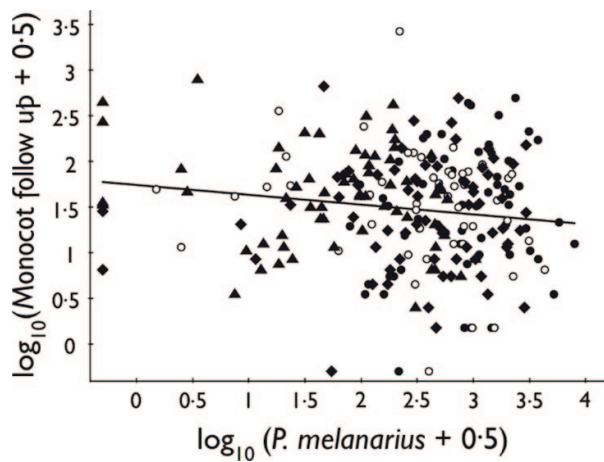


Figure 5. Evolution of the seed bank in relation to carabids abundance (Bohan et al. (2011) Journal of Applied Ecology 48, 888-898.).

The utility of ecological functions in agriculture

Ecosystem services often come with headline numbers – biocontrol by insects in farm fields in the USA was worth USD 5.5 billion per annum in 2013, or more local things, such as per hectare, biocontrol is worth USD 572 per annum globally (Naranjo *et al.*, 2015). These numbers are really big, but in reality they do not really work for farmers. The bottleneck for acceptability of ecological functions is convincing the people that are most primarily affected by it. What we need to do better is to convince farmers that we can actively replace their herbicides with ecological functions and services.

So what would we expect? What we might expect is that herbicides do the same thing to the seed bank that carabids; the seed bank would decline with more herbicides applied (figure 6). However, looking at what 200 farmers do on a daily basis in fields across the UK, we find that seed bank change is independent of the number of passes of herbicide. In other words, the form of the seed bank relationship we get with regulatory services and the form of the relationship we get with farmer behaviour are different. Qualitatively, services are doing different things to the seedbank and therefore we cannot replace things like herbicides with regulations. I think, however, that we should provide a better explanation than this because the “negative” regulation effect on the seed bank is probably something we would like.

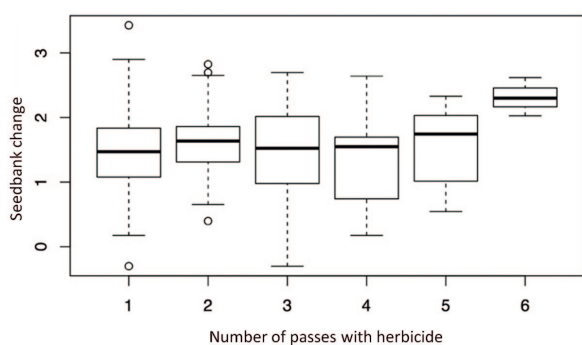


Figure 6. Herbicide services.

For myself, the question here has become ‘Given we have no relationship between seed bank change and herbicide, how do we test whether farmers could replace herbicides with carabids?’ What is needed is an experiment contrasted herbicide regimes. That is what we have in the FSE data because there are two regimes, the conventional and the GM regime. Thus, we can look for a signal of the carabid abundance and an interaction between herbicides and Carabids in the data.

In figure 7, seed bank change is plotted on the y-axis against the abundance of carabids on the x-axis, with 6 generalised linear model fitted curves, one each for up to six applications of herbicide. My interpretation of this graphic is that where there are high numbers of herbicide applications, there is no weed control effect attributable to carabids. In fields where there are low numbers of herbicide application, however, we find a significant and negative regulation relationship. Arguably, the carabids take over the regulation of seeds from the herbicides.

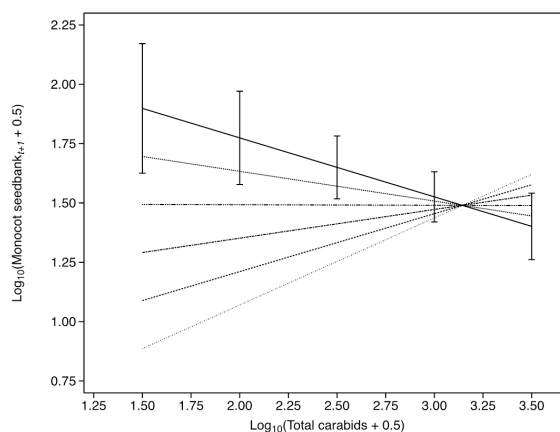


Figure 7. Herbicide replacement.

While we implicitly believe that current pesticide usage interferes with ecological functions and services, I believe that this is one of the first times that it has been shown in a great number of fields. Importantly, this does not mean that we can just stop using herbicides overnight. Rather this result suggests that should we be able to manage carabids, to increase their numbers in-field, by using landscape and better in-farm management, then carabids might be used to replace herbicides.

Regulation ecosystem services do not exist in isolation

I spent a part of my career working to control slugs using carabid beetles. Originally, I posed a very simple question, or used a very simple model. It is called the checkerboard model (Diamond, 1975). What the checkerboard model (figure 8) for a predator/prey dynamics postulates is that a patch, within a field of a crop, will initially be empty of pests and predators. Slowly over time, the pests will arrive and then increase in number. In parallel, predators may detect the presence of the pests and occupy the patch. Their populations may increase and eventually there may be a point where the predators regulate pest numbers.

Over this time course, we expect various discrete relationships in the checkerboard system. Early in the season, we expect a positive relationship between predator and prey abundances. Later, the relationship should be negative. Between these two time points, there should also be a change in prey population that is negatively related to the predator abundance. The checkerboard model gives exactly the same regulation graph that I presented for the weeds earlier. We tested the model in a field of winter wheat, across a grid of sampling points throughout the field (figure 9). The grid measures 16 metres between points, eight metres and four metres, and at each one of these sampling points, we had two pitfall traps for carabids and took soil samples for the slugs in June and July.

This produces abundance maps for the slugs and Carabids in June and July (figure 10). In June, where we found slugs, we also found Carabids. In July, however, where we observed the carabid predators,

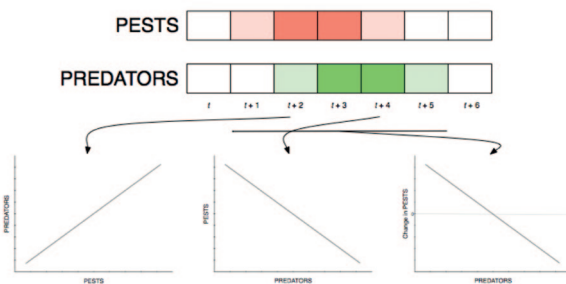


Figure 8. The checkerboard model.

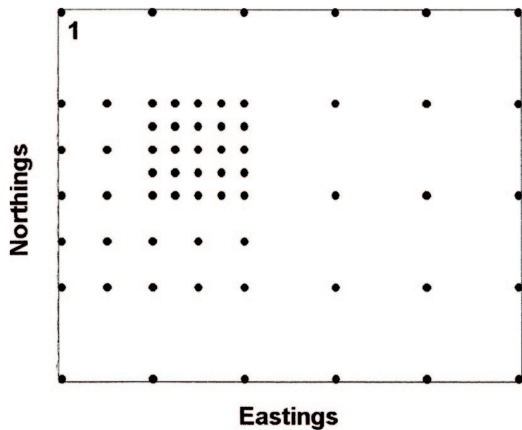


Figure 9. The grid of sampling points in a field of winter wheat.

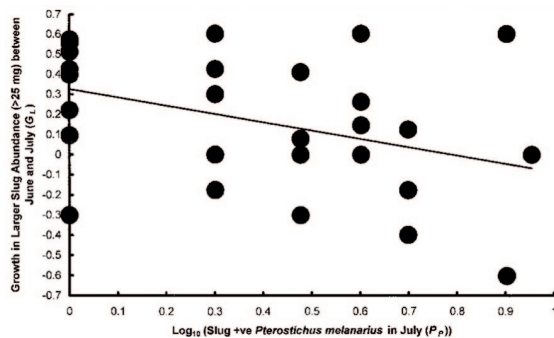


Figure 12. (Bohan et al., 2000).

there was now an absence of slugs.

When we look at these data in terms of simple graphics, in June (figure 11a), we find the positive relationship expected between the abundance of slugs and Carabids. In July (figure 11b), we get the negative relationship between Carabids and slugs.

Over the course of the two months, (figure 12) the change in slugs is negatively related to the carabids, a pattern consistent with regulation. Subsequently, we analysed the stomach contents of these carabids and identified slug DNA, so we know they have eaten slugs. Slug predation by carabids is therefore consistent with checkerboard model and regulation, and given the economic importance of slugs to farmers could be described as an ecosystem service.

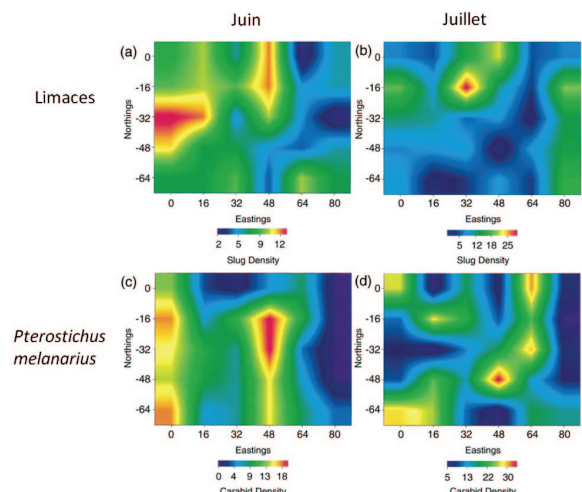


Figure 10. Abundance maps for slugs and Carabids in a winter wheat field. (Bohan et al., 2000).

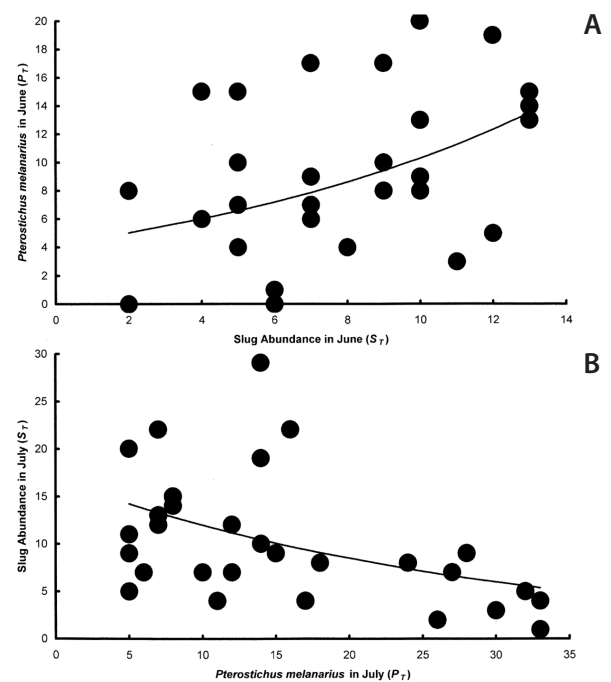


Figure 11. Relationship between the abundance of slugs and Carabids in a winter wheat field (a) in June (b) in July. (Bohan et al., 2000).

The system described in figure 13, which is only a small piece of the whole ecosystem, has already become quite complex. I have shown that there are two prey groups, slugs and weeds, regulated by the same predator grouping, the carabid beetles. In effect, these are two ecosystem services in competition for the same ecosystem service provider. In miniature, therefore, we have many of the problems of interacting ecosystem services in this one small system.

Knowing this, can we really say to farmers, ‘Okay, we have shown that carabids regulate slugs and weed seeds and if you have lots of carabids in your fields they will control your slugs and weeds’? Or, is it more likely the case that they will prefer one of these groups to the other? I do not know. What I would like to do is build up from these findings to food webs that explicitly include all the links between all the biological elements of the agricultural ecosystem.

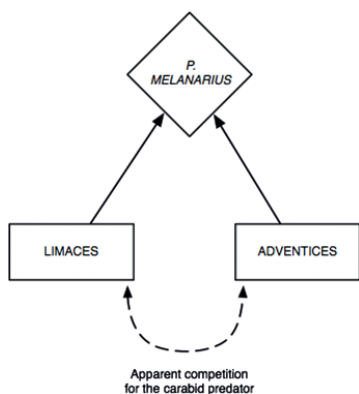


Figure 13 : Scheme of the weeds-slugs-Carabids system.

Luckily, some of this work has already been done. Pocock and colleagues published a multi-network of many different types of ecological network, in 2012 in Science, in wheat crops in the UK (figure 14). These are pollinators, pests, parasitoids, seed-feeding insects and birds all linked together. The important thing is that they are all linked together via the plant nodes at the centre of the network. The dark green nodes are the weeds and the light green ones are the crop. Most links are through the weeds.

What we have done by moving to a multi-network approach is complexify. From a single ecological function, via a two prey / one predator system, we have gone to multiple species all interacting. It is a lot more complicated. But one thing that comes out of these kinds of approaches, when done properly, is an identification of the simplicities in the system. One of the simplifications that emerges from the myriad of interactions is that they typically interact through the weeds. The weeds are therefore central to the functioning of the ecosystem. Management of the weeds could deliver services.

An analysis of this network shows that management for any one function will likely be at the cost of others. There is therefore no optimistic scenario, where we can adopt one single management and everything improves. Thus, moving to a richer description also allows us to touch the social and economic domains of agriculture. In some ways, complexifying the problem, but doing it correctly, allows us to actually simplify the problem and allows us to generate clear statements.

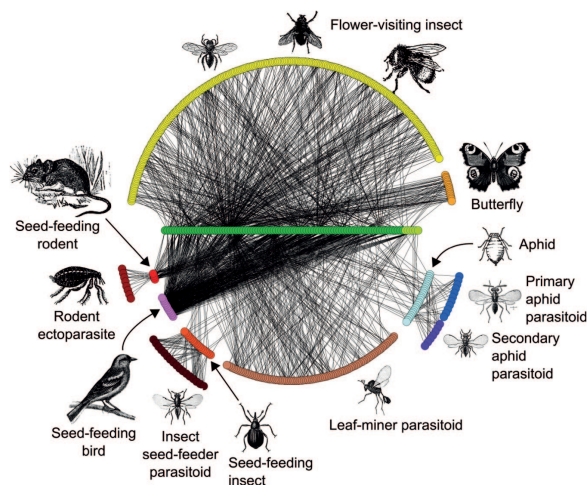


Figure 14 : Multi-network approaches. (Pocock et al., 2012 and Bohan et al., 2013).

Constructing networks of function

We have a problem though. There are very few networks in agriculture. So we posed the question, 'How do we get more networks in agriculture so that we can actually do something?' There are quite a lot of data out there – could we use it? Our reasoning was that in observed abundance and diversity data there is the imprint of past interactions. Could we take a dataset and learn the network of interactions hidden within it?

To test this idea, we again used the FSE GMO data that I introduced earlier. Imagine one of the 256 fields in the dataset. The field was cut in two, and on one side of the field we put the conventional treatment and on the other side we put the GMO treatment, each with distinct herbicide regimes. Now, imagine that a herbicide application goes on one side or other - it does not matter which. That herbicide will remove weed plants that are food and shelter for invertebrates. So for a herbivore, species Y, if its food has just disappeared, it is going to respond in one of two ways. It will either die in place or it will move. We can, after the application of a herbicide on one side or the other, calculate a ratio change of species Y between the two sides – and so on for all of the herbivore species. With regard to species X (a predator that feeds on the invertebrate species Y), if species Y has just died or moved, species X will respond by dying or moving. Thus, our expectation is that if two species are linked by a trophic interaction where we get a change in the ratio of species Y we also should have a correlated change in the ratio for species X. In other words, for two species that are linked, there should be a correlation.

There are, however, many reasons why you might get correlation. Any two species could be correlated to a third species that has changed. They are also both subject to the same, correlated weather. There is also just pure chance. To select the meaningful, trophic correlations, what we actually need is some background information. The background information we supplied for each one of the species in the system was: i) that they had appropriate mouth parts for doing the type of trophic interaction we were looking for, so if they were predators, they had predator-like mouth parts; ii) that they co-occurred in the same sample; and, iii) their body size - generally predators are bigger than prey "Big things eat small things".

With this set of rules, we set out to learn food webs and produced the first learned food web that we are aware of (figure 15). Of something like 160 species that were originally in the dataset, we found that only 45 of those species were actually implicated in the food web. That is only about 25% of the species, but these species account for over 75% of the individuals, so the majority of individuals were implicated in this network. In terms of structure, the network actually did what we thought it should. Collembola detritivores are important prey. Carabids are the dominant predators. Carabid larvae also come out extremely strongly in these systems as being predators of a wide variety of prey. There is also, of course, lots of intraguild predation, with predators feeding on other predators.

We validated the food web using the literature. We searched, by species, for papers that contained information about trophic interactions. It showed that there was a very strong correlation between what we found through the learning and what was found in the literature. In other words, we had high certainty that this network was real. There is an important point here – methods of constructing networks by going to the literature and looking for links, is actually quite standard in trophic ecology. But it is also very partial. I am a very limited human being. I know only certain parts of the literature. I may also search in the grey literature, which is not actually properly validated. There needed to be more objective ways of doing this validation. We developed a tool for actually learning trophic networks from publication search engines, such as Google Scholar. We take a food web, for example the one we have learned, and we parse it into

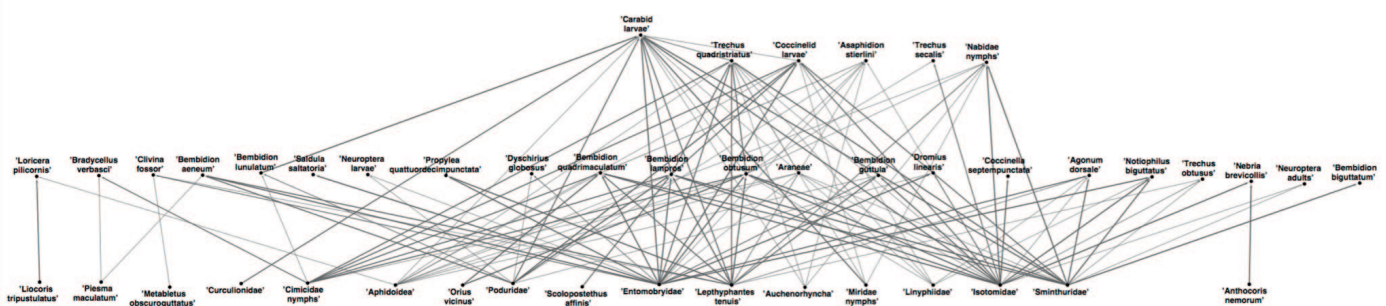


Figure 15. Food web involving 45 of the species (75 % of the individuals), in the studied field. (Bohan et al., 2011 and Tamaddoni-Nezhad et al., 2012).

Google Scholar (figure 16). Using text mining we then produce networks that look like figure 17. We use this network to test the learned food web using “frequency of a hypothesis” approaches. For this we treat each link in the learned food web as a hypothesis, which occurs with a given frequency in the data. We can then examine this frequency of the presence of the hypothesis and compare it to the number of “hits” we get from the literature (figure 18). There was a high correlation.

It seems that through this process, we learned a network for agriculture that is consistent with the literature and our expectations. However, it still produces some illogical links. One of these is the spiders as prey. Now, there are lots of species of spiders in the world and I only know of one that is not an obligate predator and it eats mushrooms – spiders should be predators. The question was, ‘are spiders really prey in this food web or is there a basic problem with the learning?’ In the learning rules, all prey are small. Given the spiders are small, then might the learning actually generate artefactual prey?

To test whether spiders are prey in this food web and, therefore, that the network as we have learned is correct, we tested the predators implicated in spider predation using DNA approaches. Using stored gut samples of *Pterostichus melanarius*, we found the presence of DNA of spider species. Seemingly, spiders are important prey for these predators. The links we were learning, even though they appeared illogical, were actually present as feeding links in reality. Thus, through learning approaches using existing data, we can produce validated ecological networks quickly and cheaply.

Building synthetic ecosystem networks

The final part of this talk is about building ecosystem scale networks. To this point I have talked about a network learned from a single ecological protocol – the Vortis suction sample protocol. Ecologists typically work with many different protocols: pitfall traps, suction samples or whatever. What the protocol-centric view tends to do, however, is cut the ecosystem up. We don’t have a full picture of what is going on in these ecosystems. The networks this produces through learning will therefore only be a representation of a small part of the ecosystem. So, one of the aims of my work on learning networks is to see whether we can knit together all these different protocols to build a much fuller picture of what is going on in these ecosystems, and so the question is, ‘Can we link data from different sampling protocols into networks?’

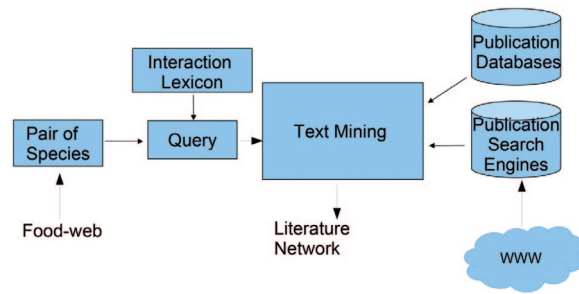


Figure 16. A tool for automatic literature verification.

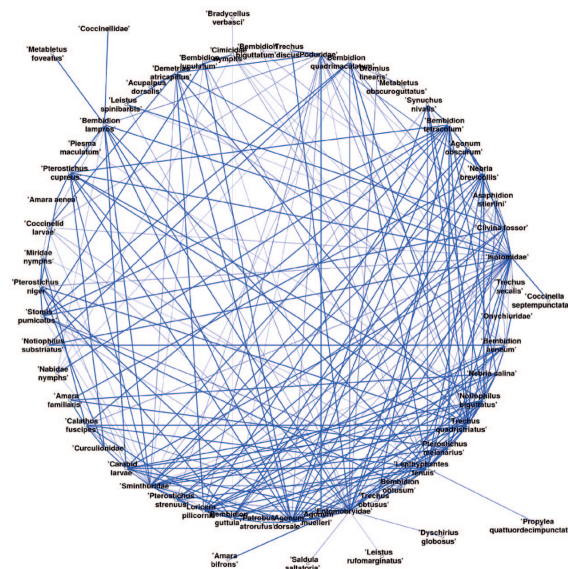


Figure 17. An automatic literature verification. Example based on the food web of figure 15. (Spearman’s $r_s = 0.821$ with p -value 0.01).

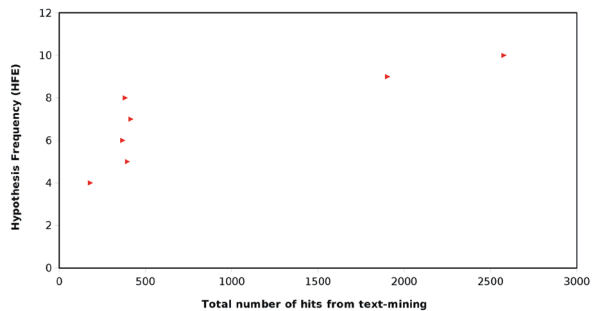


Figure 18. Relation between the frequency of the presence of the hypothesis and the number of “hits” we get from the literature.

After we developed the initial Vortis food web, we then went on and learned this one using data from pitfall traps. figure 19 a and b represents two protocol-specific networks from the same ecosystem. The networks contain many different species, so to knit these two together we isolated those species the networks have in common. There are some species that occur in both of these networks and we would expect that the interactions learned between those species should be similar in both networks. On figure 19c, we represent this common-species network. The strong lines here are the ones where the link occurs in both of the networks, and the

thin lines are where it occurs only in one of the networks. What you can see is that we learn very similar networks from two very different protocols. The networks between the common species are actually quite similar and what this means is we can merge these two datasets and learn what we have called the master web (figure 20); the global web of interactions across the two protocols in agricultural fields.

Progress towards ecosystem-scale representations of ES

So, have we made any progress? Previously, if we were to construct networks in agriculture, in a system with something like 600 species, we would have had to have looked at all of the interactions individually, tested those interactions, either using the literature or in the laboratory. It would have come up with an extremely large number of links to look at. This is both a lot of work and an awful amount of time. What we have done is, with an appropriate dataset, build a network automatically. Now, we can use automatic learning, using datasets that already exist, and just observation of those unknown or illogical links with specific testing that we did with the DNA. This increases the rate of network construction and reduces the cost.

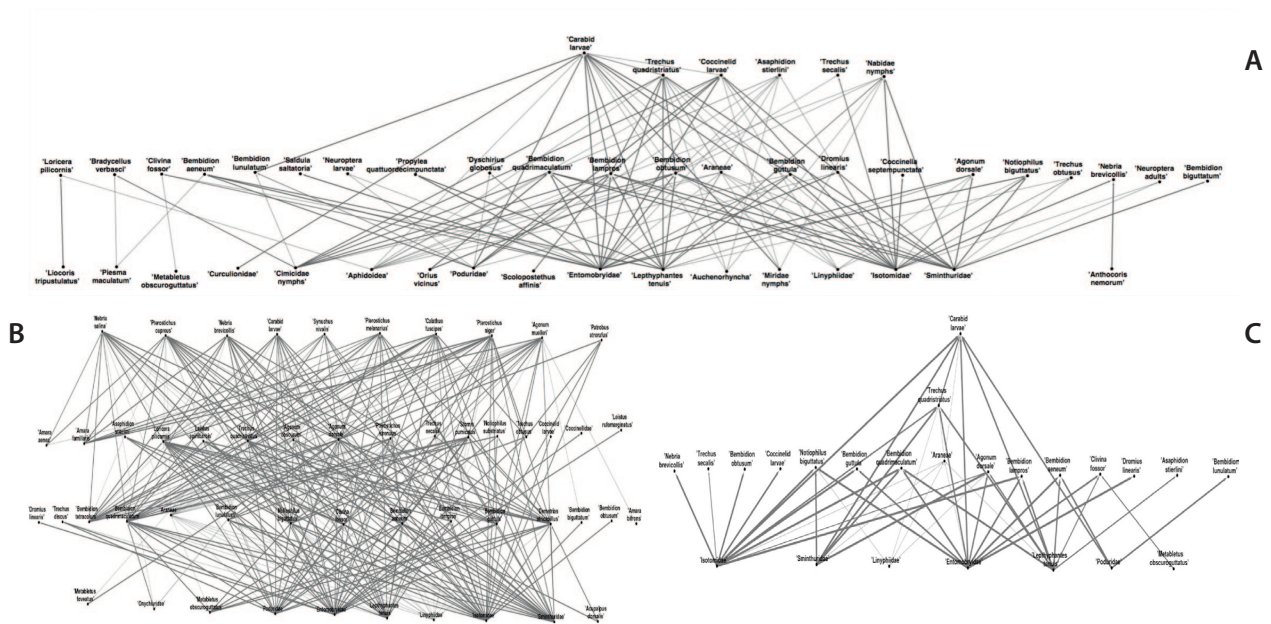


Figure 19. a) and b) two protocol-specific networks from the same ecosystem. c) network with species that are common to (a) and (b) network.

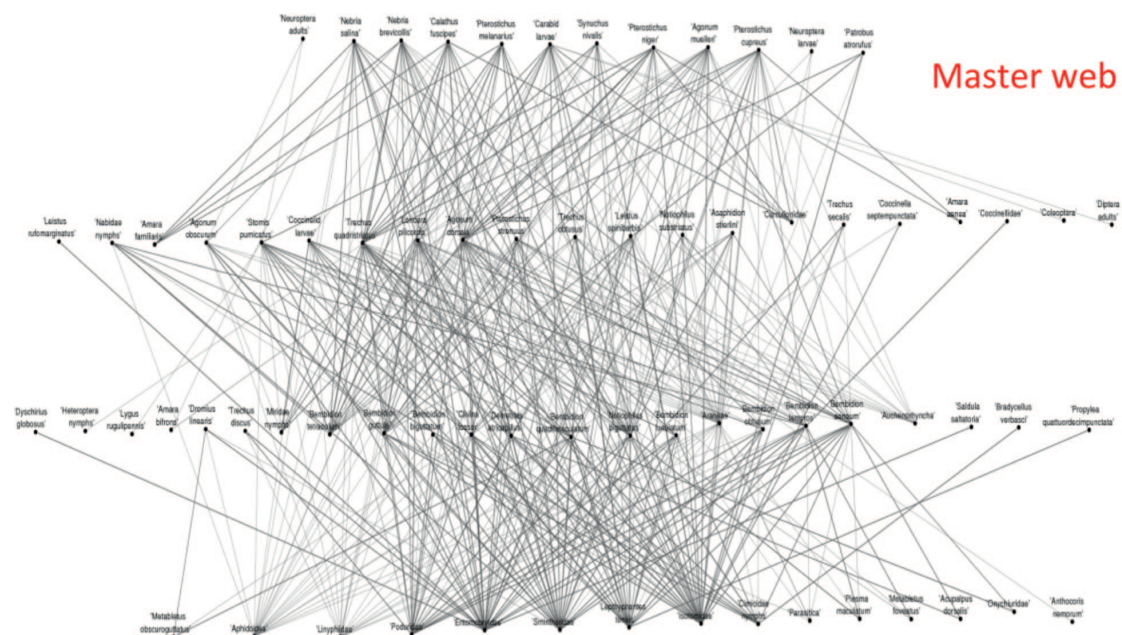


Figure 20. (Bohan et al., 2011 and Tamaddoni-Nezhad et al., 2012).

The questions we are now moving onto are questions of analysis and simplification. 'What do these networks mean for us in agriculture? What do they tell us about the way that we manage? What should we manage? What are the things that are sensitive to management? What should we preserve or conserve?' One future aim may be to try and identify those species that occur in all situations. If we are going to use regulation functions, as ecosystem services, maybe we could prioritise those species we work on to be sure, when discussing with farmers and other stakeholders, they will be present in fields and will do the job we need.

FINAL REMARKS

This presentation is a work in progress. Many of us are trying to understand more and more about this agricultural system. My contribution is in studying regulation services mainly through this lens of networks and complexifying the system, in the sense that we move to a richer description of regulation functions, but that this ultimately leads to simplification and identification of solutions to problems of ES delivery.

Thank you very much.

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