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UNDERSTANDING THE DYNAMIC COMPLEXITY OF FOOD WEBS

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PROFESSOR PETER DE RUITER AND DR ANJE-MARGRIET NEUTEL

Stability of complex systems

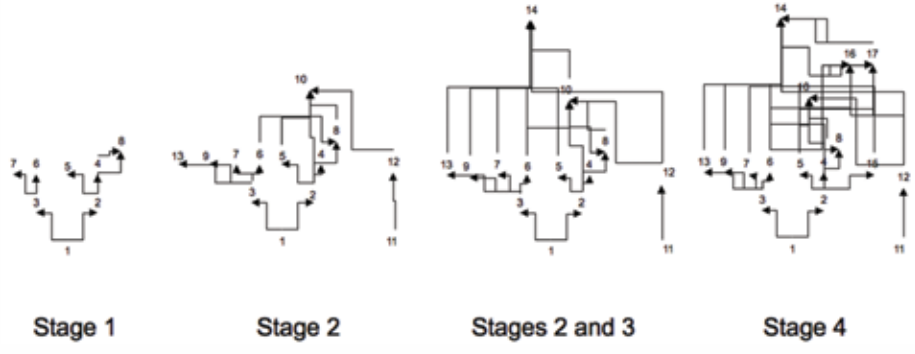
The Biometris group of Wageningen University and the British Antarctic Survey are using complexity science to consider the nature of food web systems and how they continuously adapt to changing environments

IN 1948, WARREN WEAVER postulated that a complex system could be classified as either disorganised or organised. In the former, the interactions between the component parts are largely random, so in order to consider the behaviour as whole it is necessary to use probability-based statistics. On the other hand, in organised complex systems interactions between components are not random but correlated; thus, differentiated behaviours can emerge within the system. If information about the nature of an organised system's interactions is known, computer modelling and simulation can be used to predict its behaviour.

COMPLEXITY IN THE REAL WORLD

A food web is an example of an organised complex system. It describes feeding interactions in an ecological community and can thus be used to understand the flow of energy and nutrients between organisms. Knowing, at each trophic level, 'what eats what' and their relative abundances, these multi-species interactions can be modelled using computer software to understand the underlying interactions and predict system outcomes under different conditions and external stimuli. This type of modelling provides a way to understand the persistence and dynamics of populations within an ecosystem and how these vary over time in response to factors such as the changing seasons or predator-prey relationship cycles.

Researchers in the Biometris group at Wageningen University in The Netherlands and the British Antarctic Survey in the UK apply mathematical and statistical methods to understanding the life sciences. Professor Peter de Ruiter leads a team of researchers that is using complexity- and stability-based models to investigate the interactions within the complex system of a soil-based food web. de Ruiter has been using a mathematical approach to understanding soil food webs throughout his research career, first working in a postdoctoral position at the DLO-Institute for Agrobiology and Soil Fertility before moving to Utrecht University for a Professorship in Environmental Sciences. Since 2006 he has been based at Wageningen, initially in the Soil Sciences Centre before moving to Biometris. Anje-Margriet Neutel has worked in close collaboration with de Ruiter, who was her former PhD supervisor, for many years. Since 2007, she has been conducting research at the British Antarctic Survey in Cambridge.



Development of soil food web structure along a vegetation successional gradient at the Island of Schiermonnikoog (NL). Numbers refer to trophic groups: 1, detritus; 2, bacteria; 3, fungi; 4, flagellates; 5, bacterivorous nematodes; 6, fungivorous nematodes; 7, noncryptostigmatic mites; 8, amoebae; 9, cryptostigmatic mites; 10, predatory nematodes; 11, roots; 12, phytophagous nematodes; 13, collembolans; 14, predatory mites; 15, bacterivorous mites; 16, nematophagous mites; and 17, predatory collembolans. Stage numbers refer to successional age: 1: 0 yr, 2: 10 yr, 3: 25 yr, 4: 100 yr. Adapted from Neutel et al. 2007, *Nature,* **449**, 599-602.

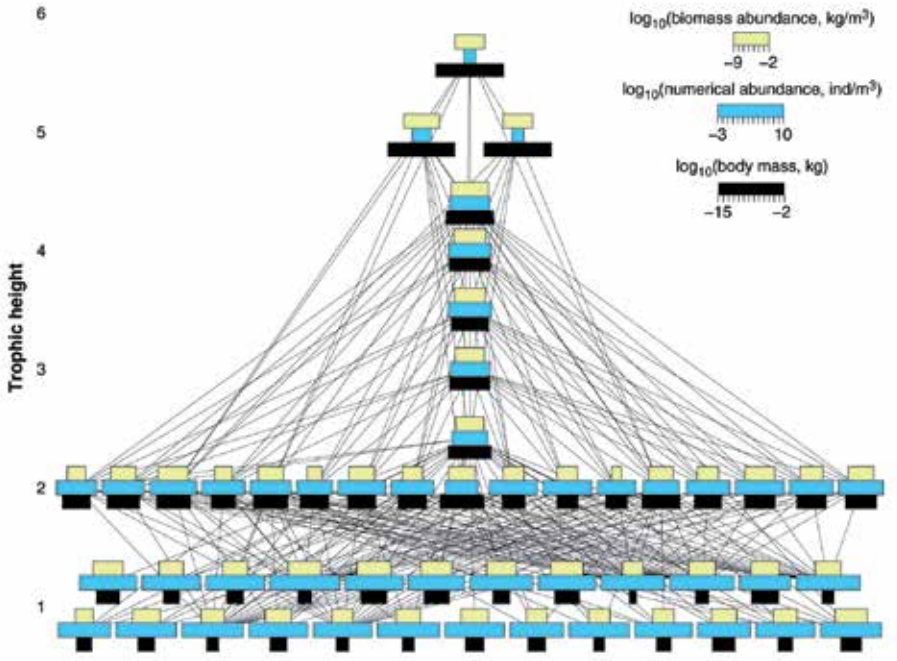
THE IMPORTANCE OF SOILS

de Ruiter and Neutel have focused their research mainly on the soil food web, which has been called the poor man's rainforest. It contains a significant proportion of the world's biodiversity, organised in highly complex networks. These include protozoa, bacteria and fungi, as well as nematodes, arthropods and higher order species of animals and birds. Soil communities are vitally important for their contribution to ecosystem services; particularly the decomposition of soil organic matter. Given the volumes of material continually being processed, the soil food web is thought to be responsible for a significant proportion of the total global cycling of materials, energy and nutrients. Consequently, it is important to develop an understanding of the stability of this complex system; determine the effectiveness of its functioning for the entire ecosystem; and consider its interaction with other types of food webs.

STABILITY OF THE WEB

The concept of food web stability is an important one, as de Ruiter and Neutel explain: "It is fundamental to understanding how species-rich communities will respond to environmental change and disturbance". This entity is immensely complex as, in order to understand how the system responds as a whole, it is necessary to consider a large number of small scale interactions between species, within species, and between species and the environment. Despite this complexity, the nature of food webs lends itself to both theoretical and experimental study, as de Ruiter elaborates: "The combination of theoretical food web models and field observations has led to tremendous insight in recent decades in patterns and principles that govern food web structure, stability and ecological functioning".

The most recent work carried out by de Ruiter, Neutel and their collaborators involves building on a framework based on the concept of 'maximum loop weight' as a new way to approach the stability of complex systems. The



The food web of Tuesday Lake, 1984. The width of the horizontal bars shows the body mass (log_{10} kg), number (log_{10} individuals/m^3) and biomass (log_{10} kg/m^3), respectively, of each species. The vertical positions of the species show trophic height. Despite a major change in species composition, following a manipulation, this energetic setup of the food web remained roughly the same . Reprinted with permission from Johnsson et al. 2005, *Advances in Ecological Research,* **36**, 1-84.

theory underlying this investigation was put forward by Neutel. It posits that in ecosystems the strength of feedbacks – the stabilising and destabilising forces in a network – resulting from chains of interactions is strongly patterned in a way that increases the stability of the system. The longer the feedback loops, the weaker the 'weight' of these feedbacks on the system. Weak links in long chains form the basis of this pattern. Through modelling, de Ruiter and Neutel have shown how it is possible to demonstrate that in more complex ecosystems – with more species and connections and, as a consequence, a larger number and length of feedbacks in these systems – the stability of the systems is preserved. This is in contradiction to classic theoretical ideas based on purely abstract models which lack the typical feedback 'signatures' found in empirical models.

CONSIDERING DYNAMICS

Regarding the current theory involved in modelling food webs, there are two issues that the researchers at Biometris and the British Antarctic Survey feel need to be considered: the dynamic nature of food webs and how they are affected by a changing environment. Food webs are highly dynamic in terms of species composition and abundance in space and time, which alters their ecological functions and ecosystem-service delivery. Thus, in order to understand their contribution through modelling, it is important to take such variability into account.

It was with their stability insights that the researchers were able to study food web dynamics on the Dutch Wadden Island of Schiermonnikoog. The entire Schiermonnikoog ecosystem is moving east at a rate of 1 m per year, resulting in new successional habitats continually developing on the eastern side, whilst ecosystems on the western side become increasingly mature and developed. de Ruiter and Neutel explain the significance of this for soil food webs: "Along with the development of aboveground succession driven by the generation of organic matter in the soil, the soil food web develops along the succession gradient in terms of longer food chains, a higher frequency of trophic interactions and hence a higher complexity". The development of the soil food web was studied by taking stability 'snapshots' over ecological time. Changes in stability properties gave insight in the response of the soil community to the build-up of organic matter.

CONSIDERING A CHANGING ENVIRONMENT

There are two main properties of ecosystems that play a key role in habitat variability: ecosystem productivity – the rate that available resources are used to produce plant biomass – and the quality of resources, which has a significant impact on the structure of a food web and thus influences its stability and complexity. de Ruiter's team is currently investigating whether it is possible to improve their complexity and stability models by considering resource availability, not simply in terms of quantity but, more specifically, in terms of composition and nutritional quality.

de Ruiter and Neutel hope that by meeting the challenge of incorporating empirical data about the quantity and quality of resources; variation in community dynamics and stability along environmental gradients; and the consequences of dynamics and stability on ecosystem functioning and services, modelling the behaviour of food webs can be improved so they can give insight into how ecosystems will respond to changing environmental conditions.

INTELLIGENCE

UNDERSTANDING THE DYNAMIC COMPLEXITY OF SOIL FOOD WEBS

OBJECTIVES

To investigate complexity and stability in food webs, which are treated as open and dynamic systems continuously adapting to a changing environment.

KEY COLLABORATORS

Professor Dr Hans Heesterbeek, Utrecht University, The Netherlands • **Professor Dr John Moore**, Colorado State University, USA • **Dr Lia Hemerik**; **Drs Cassandra van Altena**, Biometris, Wageningen University, The Netherlands • **Professor Richard Law**; **Dr Jon Pitchford**, University of York, UK • **Michael Thorne**, British Antarctic Survey, UK

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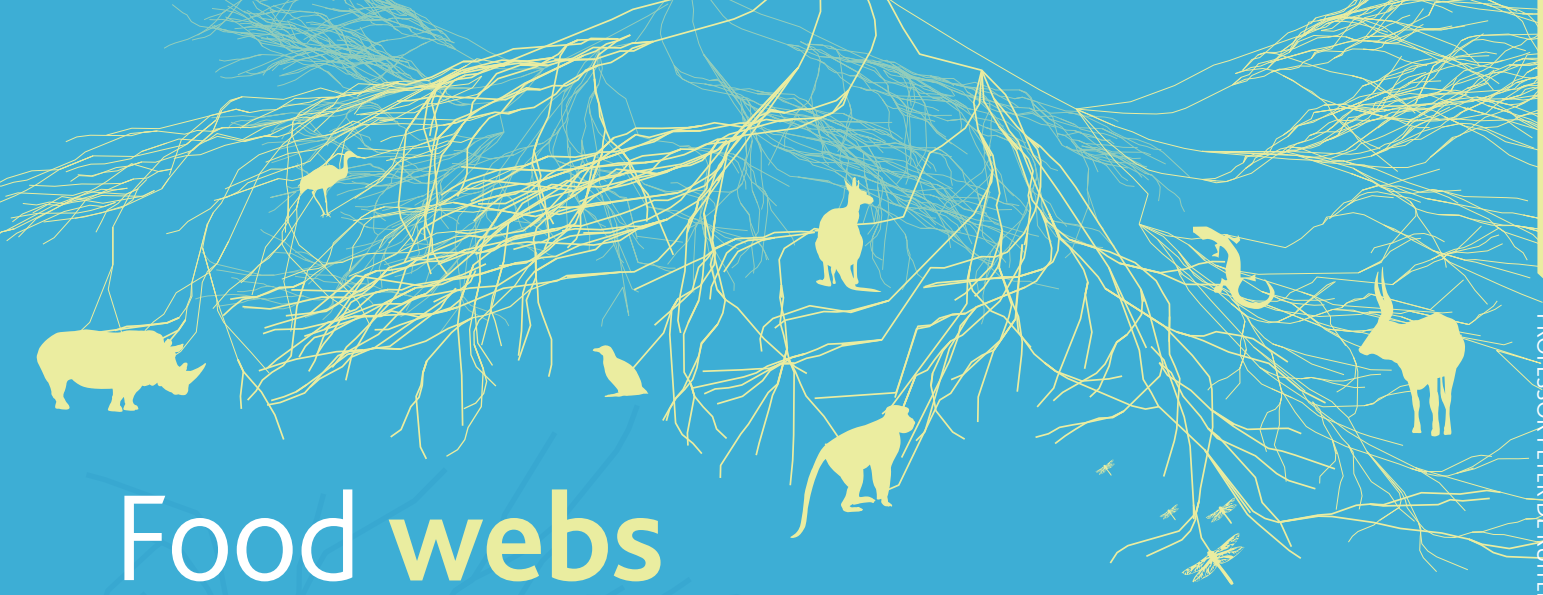
PROFESSOR PETER DE RUITER is a food web ecologist. He has written 70 peer-reviewed articles, edited the book *Dynamic Food Webs* (2005), co-written with John C Moore the monograph *Energetic Food Webs* (2012), is subject-editor of scientific journals, organised symposia and workshops, acted a keynote speaker, and participated in numerous international research activities.

DR ANJE-MARGRIET NEUTEL is a theoretical ecologist. Her work focuses on the relationship between the structure and stability of ecosystems. Based on field observations, she has introduced the concept 'loop weight', identifying key feedbacks in the stability of ecological networks.



Food webs

Professor Peter de Ruiter and **Dr Anje-Margriet Neutel** are experts in food webs and their dynamics which, as they explain, are essential components of healthy ecosystems and environmental processes

Could you give a synopsis of your research interests and explain how your work can help create a better understanding of the relationship between soil ecosystem processes and the structure of biological communities?

PdR: We are both interested in the structure and stability of complex communities and the relationship between biological diversity, ecosystem functioning and environmental quality. Most of my studies have focused on soil ecosystems. Soils are particularly interesting because they contain extremely diverse, complex and dynamic communities that govern processes such as the decomposition of organic matter, carbon sequestration and nutrient cycling. Thus, they are major components of the global cycling of materials, energy and nutrients.

AMN: My research interests are closely connected to those of Peter. I am specifically interested in the general rules that shape ecosystems. The dominant process in an ecosystem is the transfer of energy from primary producers, plants, through food chains to top predators, and the cycling of nutrients – it is about eating and being eaten. Ecosystems can be described as networks of interacting populations that feed on each other, called trophic networks or food webs. Until recently, ecological theory has largely neglected the strengths of the interactions in ecological networks. Our work has focused on how observations of the energy flow in ecosystems reveal characteristic patterns in interaction strengths underlying system stability.

PdR: Fundamental to our approach is the linking of empirical information (mostly from field surveys) to mathematical models. This has enabled us to study the mutual relationship between ecosystem functioning; for example, in terms of carbon sequestration and nutrient cycling, and the structure and stability of the food webs, the biological communities.

You devised a theoretical framework along with colleagues to empirically analyse stability in food webs. What is stability in this context and how did you capture this in your framework?

AMN: Stability in our approach is the ability to return to a steady state after some disturbance. We study relative stability. Traditionally, the speed of return to its original state is such a relative measure. But this is dependent on the timescale of the systems. In our approach the models are made time-independent, so that we can compare organisms and systems across scales. What we measure is the self-damping force of the individual network components that we have to assume for the model to be stable. This is very abstract, but in biological terms it is very concrete: it is a level of competition. It is an energetic cost for the individual populations, the loss in production due to competition within the population. This 'intra-specific' competition is a stabilising force that can counterbalance the net positive feedback resulting from the interactions in the network.

What kind of patterns do you see emerging when analysing food webs?

AMN: At the basis of our model analysis lies the detailed study of many different organisms. On the one hand, the information used for the models is detailed, but the patterns emerging do not depend on the, often very uncertain, exact numbers of population size and energy flow. They have been shown to be broad patterns, and are very robust. That is what makes the approach worthwile, because we are looking for strong signals, not dependent on variability and uncertainty in measurements. The patterns in feedbacks and stability depend on orders of magnitude in energetic properties, and on very common regularities in ecosystems.

Will the resulting complex models of food webs help to prepare us for changing environments?

AMN&PdR: Our study of soil food webs in the process of vegetation succession has been the starting point of using food web stability models to analyse the process of environmental change, and we are both strongly motivated to continue these studies. What we need are ecological models grounded in reality which will help us think about the behaviour of the systems, without the expectation of providing exact predictions, but with the aim of shedding light on the vulnerability of our systems.

And finally, do you plan to attend any forthcoming events, conferences or workshops?

PdR: Along with Volkmar Wolters (Germany) and John Moore (USA) I am organising the Food Web Symposium 2013 in Schloss Rauischholzhausen, Giessen, Germany on 13-15 November 2013. This conference continues a decadal conference series that started in 1973.

AMN: At the forth biannual meeting Mathematical Models in Ecology and Evolution, this time held in York, UK (MMEYORK2013, 12-15 August 2013) I am organising a mini-symposium on food webs, together with main organiser Jon Pitchford (York, UK).