

Distribution of emergent phytoplankton biodiversity in a global ocean circulation model. Areas in red are predicted to contain a higher diversity of traits and more species.  
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# Trait-based ecosystem models

Scientists are now modelling ocean ecosystems in unprecedented detail. Here, collaborators from both sides of the Atlantic share some recent achievements of their trait-based modelling approach



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What are the core goals of the trait-based ecosystems modelling approach?

ØF: In general terms, it is to make sense of the existence of diversity, and how the diversity of organisms is formed and shaped by the environment, including interactions with other organisms in an evolutionary game.

Can you spell out why the development of conceptual and simulation models of ecological systems is considered such an important task?

ØF: Ecosystems are complex and coupled systems in which we only know fragments of the chemistry and ecology of various groups of organisms, from bacteria to mammals. Models of different kinds are tools to understand how interactions among all these elements come together and lead to different ecosystem structures.

Basically, models give us the opportunity to investigate the logical outcome of our assumptions of how the world works – and the scientific thrill of putting together what is known to learn about the unknown.

There is growing scientific concern that ocean ecosystem modelling might be on a wrong track. Why is this so, and how is the project working to reverse this perception?

ØF: Traditional ecosystem models have received a wide range of criticism recently. Some think the models too complex and others think they are too simplistic – but the essence may be that the models are more rigid than the real world they portray.

Modellers have defined the structure of the models in the first place, instead of letting the diversity in them be an emergent property, determined by the environment and the



interactions among actors. The core of the trait-based approach is to use the principles of Darwinian selection to determine which forms are successful – enabling the model structure to emerge freely, much like in nature. We hope this strategy will lead to better ecosystem models in the future.

Can you provide a brief overview of how trait-based modelling has accelerated over recent years?

SD: Increased discussions between ecologists and modellers have helped fertilise new projects and approaches. The increase in computer power over the years has meant that we can now model larger (even global) levels with more complex models. Some 10 years ago

it would have been impossible to have done the simulations we are doing now.

**Can you offer insight into the emergent biogeography framework? What scientific challenges does it present?**

**MF/SD:** One way to help us conceptualise the global ocean, and help us understand how it might change over time, is to break the oceans down into smaller domains with specific sets of characteristics: we refer to these as biogeographical provinces. Such provinces can be described by a variety of metrics, including the types of organisms that inhabit them.

Models can help understand why such provinces exist and what sets their boundaries. Our findings to date emphasise how important the physical processes in the oceans are at setting these provinces.

**Why do trait-based modelling activities require an interdisciplinary approach?**

**TK:** The short answer is that understanding the traits and trade-offs of marine organisms is more than just biology; they are also strongly influenced by the physics and chemistry of the environment. How organisms search for food, find mates and detect predators are all fundamental life processes, each with physical and chemical aspects.

The other factor is complexity, and I mean that in a technical sense. This is where we need clever mathematicians. Complexity is not only seen in ecosystems, but in many different disciplines, from physics and chemistry to economics.

**What do your present activities involve?**

**ØF:** I am curious to understand the implications of a trait-based model of nutrient uptake in phytoplankton, what it means to classical competition theory and what the trade-offs are between growth and survival in microbes.

**What would you highlight as your primary achievements to date?**

**ØF:** We have developed a coherent theory explaining why some fish have altered their use of spawning grounds (a life-history trait) along the Norwegian coast as a result of increased fishing pressure. And we have developed a size-structured pelagic ecosystem model with adaptive spatial behaviour of fish and zooplankton! It will be exciting to see the patterns emerging from this model.

**What long-term impact do you foresee the trait-based models will have?**

**SD:** Models grounded in traits and trade-offs are more flexible and can be used to examine what might happen in the future as the ocean's change, or how ecosystems might have been structured in the past.

# A new approach to ecosystem modelling

Current models describing ecosystems are not sophisticated enough to cope with some of the complexities found in nature. But new approaches will shed fresh light on ecosystems and the way we think about them

**MUCH OF SCIENCE** concerns breaking down the complexity of processes found in the real world to simpler systems that can be understood and examined more easily. Modelling the real world has been the primary task of scientists for hundreds of years and many systems, such as the Solar System, are now so well modelled that their real-world behaviour can be predicted with incredible accuracy.

Much more difficult to model, however, is the group behaviour of a population of organisms (plants, microbes, animals) or the interactions between different populations. An ecosystem is a complicated biological system, enveloping all life in a particular area as well as that which life interacts: air, minerals, water, sunlight, etc. Developing conceptual or simulation models of these ecological systems is not an easy task. One of the main barriers to progress in developing accurate models for ecosystems is their complexity. There are simply too many varieties of plants, animals and microbes to keep track of and many of those organisms often defy the general laws of ecology. Yet such models are urgently needed to make sense of how ecosystems respond to environmental and manmade changes.

## TRAIT-BASED MODELLING

A new approach to capturing real-world ecosystems is 'trait-based' modelling. These models organise life according to 'functional traits' – properties of a group of organisms that are essential to its success and functioning in a particular environment. Typically, one such trait, for example body size, will give an organism an advantage in one environment but a disadvantage in another. So organisms face 'trade-offs', where they have to sacrifice one benefit to obtain another.

By quantifying and mapping trade-offs it is possible to construct a large space of potential organisms according to functional traits. Computer software can then simulate competition between the different organisms to see which ones persist and coexist. Different models of how organisms grow as a function of the abundance of their prey or nutrients have been around for some time; simple predator-prey models have been around since the 1920s.

However, Øyvind Fiksen from the Theoretical Ecology Group in the University of Bergen, Norway explains that these models are not adequate in describing the full complexity of ecosystems: "These parameters tell you nothing about the traits of the organism – which particular properties of the organism determine its competitive strength at high or low resource abundances or how environmental factors influence competitive strength". He continues: "Trait-based models should be formulated in real traits of an organism, such as its size or how many uptake sites for nutrients it has on the cell surface".

## THEORETICAL ECOLOGY GROUP

The core aim of trait-based ecosystem modelling is to better understand ecosystems, says Fiksen: "The goal is not to build one single grand model, but to shed more light on the amazing interactive and dynamic oceanic ecosystem, and the way we think about it". Today, it is possible to run global models of ocean currents and productivity with a large number of state variables.

In the Theoretical Ecology Group, the team is working on a project called 'Trait-based ecosystem models' (TBECO), which looks to create and develop trait-based models and apply them to previously unexplored ecosystems. One of the main achievements of the project so far has been the development of a new model of nutrient uptake in microbes, which will be important in specifying trade-offs in growth and competitive interactions. Through the model, it is now possible to specify nutrient uptake in terms of real properties of a cell, such as its size, density of pores and the chemical process

## INTELLIGENCE

# TBECO

### TRAIT-BASED ECOSYSTEM MODELS

#### OBJECTIVES

Future marine ecosystem models will predict the structure of pelagic communities as a game between competitors and predators where each player will carry a set of traits and behavioural responses that determine their success. Our aim is to quantify and model traits, trade-offs and behaviours of microbes, plankton and fish, and prepare ground for such models.

#### KEY COLLABORATORS

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#### FUNDING

Research Council of Norway

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**DTU Aqua**  
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Massachusetts Institute of Technology

of transporting nutrient molecules through the cell membrane.

#### FROM MICROBES TO FISH

The greatest challenge to TBECO is applying the method to larger organisms. For example, the open water masses of the ocean cover a large fraction of the Earth, and are the field of a continuous life-and-death game between predators and prey. For zooplankton, the predators are mainly larger zooplankton or fish. Fish depend on light to detect their prey, and because light is absorbed and scattered in water it gets dark in the deeper layers of the ocean. This provides a safe refuge in daytime, giving the rise to one of the largest animal migrations on Earth: the daily vertical migration of zooplankton. Fish are particularly dangerous to larger zooplankton, and they tend to swim deeper in daytime. Since the foods of zooplankton – the phytoplankton – grow better in sunlight near the surface, this migration is a trade-off between feeding and survival chances for the zooplankton. The smaller zooplankton, however, which are eaten more by larger zooplankton than by fish, may benefit from the migration of larger zooplankton to the surface layers in daytime. Fiksen and the team have managed to model this complicated system: "We have developed a model of the spatial game between fish and zooplankton, and even one where fish react to their environment through feelings... of fear and hunger!" he enthuses.

#### MODELLING CHALLENGES

Much work remains in determining the trade-offs and essential traits, and formulating meaningful models with the essential traits and responses embedded. The best way to determine these trade-offs is to gain a deep understanding of the biochemistry and physiology discovered through laboratory experiments. Fiksen goes into more detail: "The organism traits will be real, inherent properties and the ecological interactions will be formulated mechanistically with adaptive responses to environmental and internal cues". From this basis, he says, structure and function will emerge from an evolutionary algorithm.

Another challenge to ecological modellers has been the ability of larger animals to swim

and the complex behavioural and life-cycle repertoires they possess. In TBECO, modellers have tried to include such traits and behaviours in the framework of a mass-balanced ecosystem model. The new model assumes all actors respond immediately to changes in the ambient

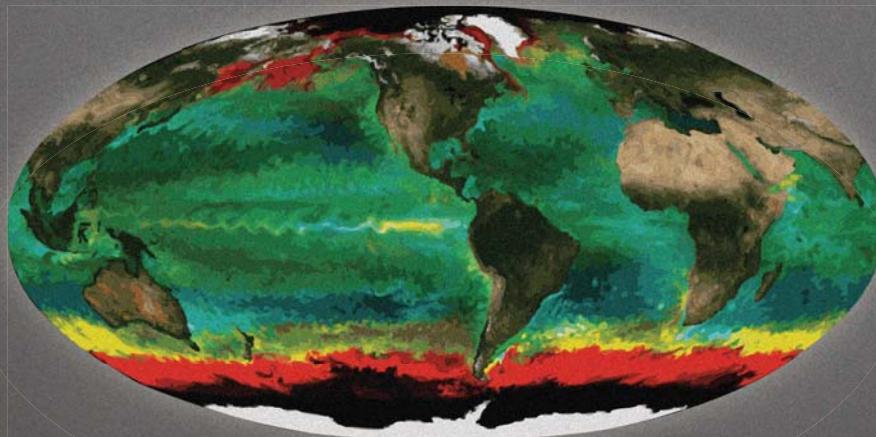
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growth and predation rates by relocating to habitats with the greatest difference between the two rates: they maximise the difference between growth and death rates.

#### COLLABORATIVE ECOSYSTEM RESEARCH

The Theoretical Ecology Group is not alone in realising the potential of the trait-based approach. The team collaborates with Mick Follow's group and The Darwin Project at Massachusetts Institute of Technology. Fiksen elaborates on their work: "In Follow's lab they have a state-of-the-art global model where new traits and trade-offs are added regularly to phytoplankton, most recently on the role of nitrogen-fixing primary producers in the open water masses".

At the Danish Technical University, a group led by Thomas Kiørboe has established the Centre for Ocean Life to understand the trade-offs and traits of marine organisms from bacteria to fish, explains Fiksen: "Kiørboe's lab has been particularly successful in modelling the traits and trade-offs involved in zooplankton swimming and feeding patterns, and in modelling size-spectra of fish communities". In combination, these groups cover a wide spectrum of research topics, from global biogeography of phytoplankton to fisheries-induced effects of harvesting with overlapping philosophy and methodology. Fiksen has been encouraged by what he has seen so far and foresees more interaction and collaboration to come.



A simulation of the global ocean showing biogeographical provinces – some areas (red) are occupied by diatoms, while tropical regions become dominated by small flagellates (green). © Oliver Jahn, MIT