

Summary

“Mechanistic theory and modelling of complex ecological networks”

Alice Boit, Institute of Biochemistry and Biology, University of Potsdam

Coping with global environmental change through ecosystem-based management and restoration requires us to significantly improve our understanding of ecological succession. Central to ecology and ecosystem management, succession theory aims to explain and predict the assembly of ecological communities. Yet processes on lower hierarchical scales, for instance at the species and functional group level, are rarely linked to system-level indices that provide a deeper understanding of ecosystem processes and functioning and may be compared across ecosystems. The approach presented here combines established and new indices for quantifying successional progress from the functional group to the system level. These indices can be drawn from long-term empirical data and be deduced from ecosystem theory, metabolic theory, food web theory, thermodynamics and information theoretics, thus combining different bodies of theory to a comprehensive picture of successional progress in the pelagic zone of the large and deep Lake Constance. The ecological mechanisms governing diversification and changes in community composition during succession were analyzed, illuminating how successional progress leads to an increase in functional diversity, resource efficiency, and food web complexity, and to an increase in body mass which in turn leads to a decrease in metabolic activity during succession. This successional progress crucially depended on functional properties, or “traits” such as body mass and life history parameters. New aspects, such as the food quality of producers under nutrient limitation, were integrated with this trait-based approach and related to the mass-specific metabolic activity of functional groups and the entire plankton community to elucidate the impact of physiological drivers of community assembly on trophic structure during succession. Drawing on highly resolved, long-term empirical data, predictions of ecosystem development during succession which had previously been only qualitatively expressed were now quantitatively confirmed. For the first time, successional progress was mechanistically explained by reconciling different bodies of theory to reveal the mechanistic relationships between diversity patterns, energetic drivers, resource dynamics, and food web complexity during successional progress in a synergistic overview of secondary succession in a specific ecosystem: Lake Constance. This case study may therefore be used as a benchmark for quantifying successional progress across organizational scales in pelagic systems and beyond.

When moving from data analysis and interpretation to predicting the effects of changes in community composition on ecosystem structure, function, and services, it becomes critical to map ecological processes onto equations for modeling consumer-resource dynamics. Previously, the bottleneck of this endeavor had been other mechanistic models' inability to reproduce the dynamics of multiple populations interacting in the field. This limitation is overcome in this thesis by extending general consumer-resource network theory to the complex dynamics of a specific ecosystem, namely the seasonal biomass and production patterns in the pelagic food web of Lake Constance. Building on a fruitful tradition of both empirical and theoretical network analysis, the exploration of food webs has embraced network science by formalizing species or functional groups as nodes, and their interactions as the edges in a network graph. These ideas represent the foundation of ecological network theory which successfully predicts the structural properties of food webs. Here, this body of structural theory was cross-fertilized with allometric scaling rules and metabolic theory in order to enable the parameterization of a bioenergetic allometric trophic network (ATN) model of Lake Constance with realistic food web topology. Adding activity respiration, the detrital loop, minimal abiotic forcing, prey resistance, and several empirically observed rates to the ATN model substantially improved the realism of the simulated system energetics and resulted in the best ever achieved model fit to the observed seasonal dynamics and the size-abundance distribution of a complex multi-species system. The relatively high trophic resolution of 24 functional guilds and the rigorous model validation against a comprehensive data set including biomasses, production, and the slope of the mass-abundance distribution (hereafter referred to as mass-abundance slope) represent a considerable augmentation of previous work in this area.

Chapters 1-2 advance ecological theory and modeling of complex dynamics of specific ecosystems well beyond the current limitation to a small number of species interacting in the lab. The case study on Lake Constance demonstrates that successional progress observed in the field is quantifiable and reproducible by a generalizable, scalable, and efficiently parameterized network model based on metabolic theory. An ongoing extension of ATN models, through integration of ecological

stoichiometry, more sophisticated biogeochemical dynamics, and other indicators of food quality, may bring about further advances of food-web theory and its applications.

Ecological stoichiometry links metabolic processes in the living world to the biogeochemical dynamics of elemental and water cycles. In the terrestrial realm, the exchange of energy and nutrients between living organisms and the detritus in the soil feeds back onto the resource dynamics, which in turn exert a crucial influence on the metabolic efficiency of organisms. As in pelagic systems, the food quality in soils depends on elemental ratios (e.g. carbon (C), phosphorus (P), and nitrogen (N)) in food resources and constrains the body mass-dependent metabolic activity of organisms at the individual level. When scaled up to the population level, these effects limit the presence and abundance of species, and shape consumer–resource interactions at the community level. Finally, this has consequences for trophic organization and ecosystem processes at the ecosystem level. The functional diversity in a community delimits the spectrum of possible responses of organisms to biotic and environmental performance filters, for instance along nutrient gradients.

To mechanistically link functional diversity to processes at the ecosystem level, it is important to identify those key traits which allow us to predict diversity effects on ecosystem functioning. Body mass is one such key trait because, due to the close interplay between allometry and ecological stoichiometry, data on associated traits such as body mass and elemental ratios can be combined to explain patterns and processes influencing ecosystem functioning and services. For instance, the empirical evidence presented here on 170 Dutch soil food webs demonstrates the importance of phosphorus (P) availability for soil invertebrates whose actions in the ground contribute to soil fertility. Soil pH, which has a strong impact on nutrient mobility and adsorption, was the best predictor of the mass-abundance slope, followed by the C:P ratio of organic soil matter. The mass-abundance slope indicated that the small bacterivores and detritivores were coping better with limiting P conditions than the larger herbivorous, fungivorous, or predatory invertebrates. Such differential responses may lead to altered community composition under land use change which is likely to feed back on trophic structure and affect the functioning of the entire agro-ecosystem. As a result, changes in community composition by agricultural intensification may critically affect ecosystem functioning and, in the long term, ecosystem services such as soil fertility.

Broadening the view beyond isolated case studies allows the detection of (in)congruencies in the current theory of macroecological scaling and in the predicted effects of biodiversity (taxonomic and functional) on ecosystem functioning. In this thesis, an integrated perspective across taxocenes (vascular plants, aquatic vertebrates, terrestrial invertebrates) and disparate habitats (deserts, forests, soil systems, seagrass meadows, rivers) under varying degrees of human influence is achieved. The findings suggest that biomass spectra and abundances can be predicted from combined information on both mass-abundance scaling and ecological stoichiometry. In contrast, taxonomic diversity alone was less suitable for predicting system-level properties. The results from species deletion simulations highlighted that the topology of food webs and local node connectivity (and not simply taxonomic diversity) were decisive factors in stabilizing the food web against secondary extinctions. In fact, species-rich food webs were just as, or even more vulnerable, to secondary extinctions as species-poor food webs. This is further evidence that the link between biodiversity and ecosystem functioning across scales and habitats depends more on the interplay of functional traits, and less on species identity. To disentangle response and effect traits operating at the interfaces between the biota and their environment, a new conceptual framework was proposed for trait-based modeling of complex interaction networks in the field.

The insights gained in Chapters 3-4 suggest that the current emphasis on using biodiversity (at least taxonomic diversity) as a predictor of ecosystem functioning is probably overrated and should at least be complemented by incorporating the feedbacks between body-size related traits and ecological stoichiometry in environmental risk assessment and management of systems undergoing land use change.

In conclusion, this thesis helps to build a theoretical core for a synergy between ecosystem ecology and community ecology based on first principles. This encourages a scientifically optimistic outlook for the mechanistic understanding and the prediction of complex multi-species dynamics in natural ecosystems. In light of the approaches presented here, the goal of predicting biodiversity effects on ecosystem functioning and services by ecological modeling seems now more attainable than ever.