

**Further information on the intended vision, scope and approaches of the priority programme:**

The understanding of the consequences of anthropogenically induced biodiversity loss on the sensitivity of ecological systems to further environmental changes can only fully be attained with interdisciplinary coordinated research. While the negative effects of environmental change on biodiversity are well documented, it has rarely been studied how biodiversity and its loss impacts the ecological dynamics and response to further changes in environmental conditions. The inherent biodiversity of ecological systems, however, may promote adjustments at lower hierarchical levels that may buffer the response to environmental changes at a higher hierarchical level (Verschoor et al. 2004; Tirok & Gaedke 2010). Depending on the different facets of biodiversity (e.g. phenotypic, genetic and species diversity) individuals, populations and communities may change their properties to 'adjust' to the current conditions to improve their fitness. This should influence their temporal dynamics and those of the entire food web (Norberg 2004, Tirok & Gaedke 2010, Tirok et al. 2011). Such ongoing feedbacks are based on the biodiversity and functional characteristics of the interacting communities (e.g. mean edibility of algae and selectivity of the herbivore), given by the properties of individual species (e.g. formation of spines and other defences against predation, altered behaviour in the presence of predators, prey switching, etc.). This biodiversity-dependent potential for adjustment leads to complex, multi-way feedbacks and potential simultaneous changes at different levels of ecological organisation (Fig.1).

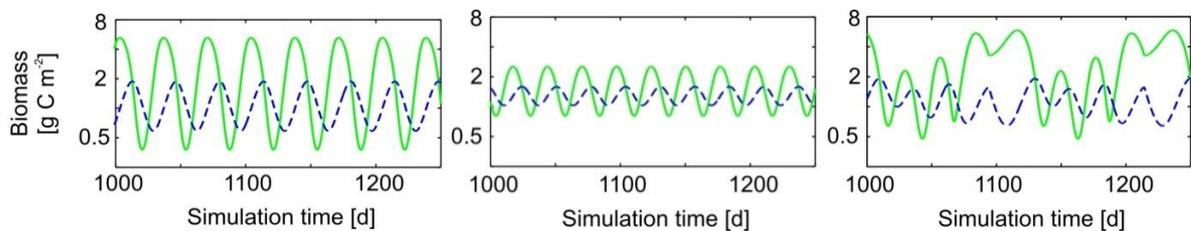


Fig. 1. Simulations of a predator (blue) – prey (green) system in a constant environment without flexibility to adjust to altered conditions (left), with potential for adjustment only for the prey (middle), and with potential for adjustment in both, predator and prey (right). The latter results in more complex dynamic patterns than classical predator-prey cycles (modified after Tirok et al.\*, 2011). For the sake of simplicity and brevity, the examples given here concern trophic interactions (e.g. predation and competition), but in principal, this holds true for all other kinds of interactions such as parasite-host interactions, mutualism, facilitation and syntrophy.

For example, a diverse group of predators (species level) may adjust its diet composition to altered prey availability (environmental change), which, in turn, reduces the consequences of the environmental change for the overall energy flow in the food web (system level). As a consequence, the responses of complex and highly interconnected networks such as food webs to altered conditions are currently very difficult to understand and predict (Duffy et al. 2007), but of exceptional importance for fundamental and applied ecology.

A recent approach to address this issue is to move from a species- to a trait-based perspective (Fig. 2A). Differences in functional trait values (e.g. in growth rates, edibility of prey, or selectivity of predators) may arise among individuals, populations, and/or communities, i.e. at different hierarchical levels, by different mechanisms such as:

- evolution by mutation, recombination and selection changing genetic composition
- shifts in clonal or species composition within a population or community or inherited up/down regulation of genes implying changes in genotype frequencies
- phenotypic plasticity of individual organisms, e.g. by reversible changes in morphology, life history, behaviour or physiological acclimation which can be much faster than the above mentioned mechanisms.

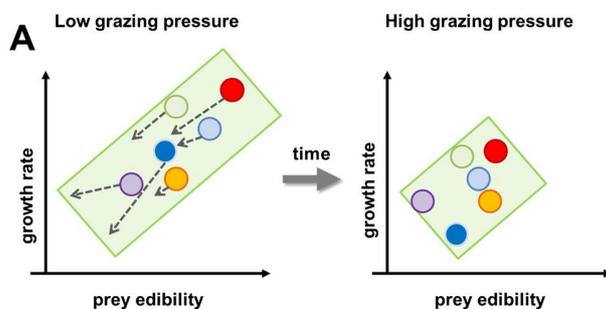


Fig. 2. Individuals are not entirely alike, but differ - to varying degrees - in their trait values. A) Example displaying the location of six individuals (or populations) in a two-dimensional trait space with the two functional traits "growth rate" and "prey edibility" under low grazing pressure (left). The trait values are correlated with each other due to a trade-off between the growth rate and

edibility. In the upper right corner of the trait space, growth but also vulnerability to grazing are maximal (and minimal in the lower left corner). Under high grazing pressure, the individuals (or populations) move in the trait space (dashed arrows) to re-adjust their trade-off between growth and grazing losses depending on their specific flexibility (right).

Importantly, trade-offs among the different functional traits of organisms are probably ubiquitous and model simulations suggest that the trade-offs among traits and their shape are decisive for system dynamics and for the maintenance of trait variation and thus functional diversity (Yoshida et al. 2003, Tirok et al. 2011, Becks et al. 2010). Given the general, multifaceted and potentially large ecological effects of trait variation,

we need to revisit classical ecological models and ask how the magnitude and heritability of trait variation alters previous conclusions (Bolnick et al. 2011).

To overcome previous limitations, we want to broaden our very limited quantitative knowledge and predictive power on how biodiversity affects ecological dynamics and responses to environmental changes (Fig. 3). We aim to study the consequences of trait variation for the dynamic properties of complex ecological systems including their non-linear feedbacks on trait variation determining whether trait variation (biodiversity) is maintained or whether the system gets locked in a „monoculture“ without further potential for adjustment (Becks et al. 2010). Additionally, a larger variation in trait values may imply a larger potential of the ecological system to adjust to perturbations (defined as external forcing on which the ecological system does not strike back), which is even less studied. The trait-based approach accounts for the fact that natural food webs continuously alter the properties of their components, which may translate into complex system dynamics (Fig. 1). Our goal is to overcome a too rigid view on ecological systems now prevailing in theoretical and empirical ecology by accounting for the inherent flexibility of individuals, populations and communities, which allows them to adjust to altered abiotic and biotic conditions. We postulate that this flexibility is related to the available trait variation (functional diversity) and influences the dynamic behaviour and response to environmental change, which, in turn, influences the maintenance of trait variation in concert with the trade-off(s) among traits.

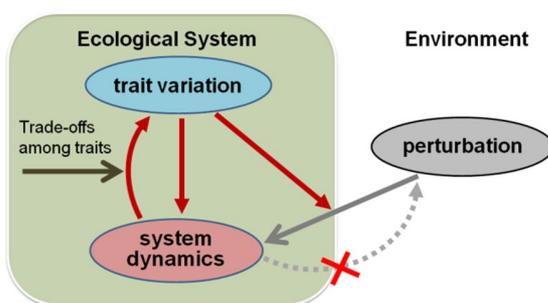


Fig. 3. **Complex causalities and feedback loops:** **Trait variation**, arising from evolution, clonal/species shifts and/or phenotypic plasticity, represents the biodiversity present and influences the dynamics of the ecological system (e.g. the dynamics of biomasses, trait values and trait variation) and the impact of perturbations on system dynamics. The latter has a feedback on the maintenance of trait variation, which depends on the trade-off(s) among traits and their shape. The type of system dynamics (e.g. strongly oscillating or rather static) influences extinction risks, frequency of pest outbreaks and the reliability of ecosystem functions and services.

### **Methodological approaches:**

In the long run we aim for empirical model systems ranging from fully controlled and closed to natural and open systems complementing each other in respect to, e.g. the level of control/importance of external forcing, the feasible number of repetitions, the range of trait variation, the food web complexity and the number of trophic levels. In the first funding period, basic mechanisms need to be clarified and hence one focus will likely be on microcosm studies with assembled food webs. We will have to examine different food webs to test the generality of the results and the role of system-specific and trade-off-specific properties that often play a large role in ecological systems. Ideally, different empirical systems with trait variation arising from phenotypic, evolutionary and clonal/species shifts will be studied.

To obtain the maximum possible generality of our findings and to distinguish between generic principles and system-specific processes, the priority programme intends to conduct comparative studies in two fundamentally different types of habitats: **pelagic and substrate-bound habitats**. The relevance of our topic is by no means restricted to the aquatic realm, but **plankton communities and biofilms** (i.e. a substrate-bound system often comprising a complex food web of bacteria, fungi, algae and protists grazed by higher organisms, e.g. on submerged plants or stones, also called "Aufwuchs") appear as the most suitable model systems for the planned experiments. For each empirical system, consisting e.g. of various predator and prey species, we first have to quantify the relevant traits and the trade-off relations among these. Subsequently, the dynamics of individual and aggregate biomasses and/or metabolic rates (e.g. production, respiration, nutrient uptake) and of the trait distributions have to be measured in numerous long-term experiments, which differ with respect to the initial levels of trait variation, trophic complexity and the kinds and intensities of environmental change. Essential requirements of empirical model systems (e.g. food webs) will likely be:

1. Their dynamics are quantifiable and sufficiently fast to be measurable for many generations to establish the long-term dynamic behaviour.
2. Multiple trophic levels with internal feedbacks are considered, i.e. a system consisting of at least abiotic resources, organismal prey and consumers.
3. The trait variation in at least one functional group can be measured and manipulated e.g. through experimental evolution
4. The major trade-off relations among traits can be estimated.
5. Population densities are sufficiently high to prevent stochastic effects arising from small population sizes (e.g. genetic drift, inbreeding depression, radiation, genetic bottleneck).

Further beneficial attributes include that key organisms are culturable to allow quantitative assessment of trade-offs among traits and that the mechanisms underlying the trait variation (e.g. phenotypic or inherited) and how it is maintained are sufficiently known or can be studied with reasonable effort.

Modelling is indispensable for addressing this issue, as intuition often fails in the face of feedback loops generated under mutual causality. We strongly promote a firm interaction between empirical and theoretical work within the priority program. Therefore we encourage empirical projects to directly collaborate with theoreticians or with an intended central modelling team. Theoretical projects not directly linked to distinct experiments or observations but addressing the above mentioned questions are welcome as well.

### **Literature references**

**Becks** L, Ellner SP, Jones LE, Hairston NG (2010) Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics. *Ecology Letters* 13, 989-997.

**Bolnick** DI, Amarasekare P, Araujo MS, Burger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26, 183-192.

**Duffy** JE, Cardinal BJ, France KE, McIntyre PB, Thebault E, Loreau M (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10, 522–538.

**Norberg** J (2004) Biodiversity and ecosystem functioning: A complex adaptive systems approach. *Limnology and Oceanography* 49, 1269-1277.

**Tirok** K, **Gaedke** U (2010) Internally driven alternation of functional traits in a multi-species predator-prey system. *Ecology* 91, 1748-1762.

**Tirok** K, Bauer B, Wirtz K, Gaedke U (2011) Predator-prey dynamics driven by feedback between functionally diverse trophic levels. *PLoS ONE* 6, e27357.

**Verschoor** AM, Vos M, Van der Stap I (2004) Inducible defences prevent strong population fluctuations in bi- and tritrophic food chains. *Ecology Letters* 7, 1143-1148.

**Yoshida** T, Jones LE, Ellner SP, Fussmann GF, Hairston NG (2003) Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* 424, 303-306.