Interplay between trait variation, food web dynamics and maintenance of biodiversity

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What this subproject is about

Abstract

Variation in functional traits within individuals, populations and communities allows them to adjust to altering environmental conditions such as grazing pressure and resource competition, giving rise to biomass-trait feedbacks including eco-evolutionary dynamics. Using mathematical models, cooperating with experimentalists and conducting experiments ourselves, we contributed to a unifying theory that explicitly considers how such feedbacks affect the structure, diversity, dynamics and robustness against perturbations of predator-prey systems and more complex tritrophic food webs, where trait adaptation was accounted for at all trophic levels. We postulated that the standing trait variation (functional diversity) influences biomass and trait dynamics, and that this influences the maintenance of trait variation in interaction with the trade-off(s) among traits, which, in turn determines the response to future environmental changes. We considered the effects of trait changes resulting from different mechanisms such as species sorting, evolution and phenotypic plasticity that occur simultaneously in natural systems. We evaluated their impact e.g. on clonal or species coexistence and dynamics, as well as quantitative properties that are highly relevant for ecosystem functions and services such as compensatory dynamics stabilizing the trophic level biomasses, exploitation efficiencies of prey and nutrients and top yield (e.g. fish production) in multitrophic systems.

Three Ph.D. students, Laurie Wojcik, George Adje and Arne Pfennig are working along these lines until ca. 2024.

Major achievements include:

1. We used a variety of complementary model approaches to describe changes in the trait composition of natural communities: multispecies sorting models, full trait distribution models or aggregate models approximating full models by explicitly considering the dynamics of the mean and variance of the underlying trait distribution. We used additional approaches to reflect intraspecific trait variation and corresponding trait adjustments including for example clonal sorting models or the fitness-gradient approach from quantitative genetics to represent evolution. In contrast, switching functions were incorporated to describe environmentally driven trait changes within individuals through phenotypic plasticity. Finally, we considered intra- and interspecific trait variation simultaneously using a hybrid model approach that combines a multispecies model with an aggregate approach. This enabled us to investigate the intertwined biomass (i.e. ecological) and trait dynamics (e.g. evolutionary processes), and to test the robustness of our results against model assumptions.
   When required we improved existing modelling approaches, which now enable e.g. a better consideration of non-normal trait distributions (Coutinho et al. 2016, Klauschies et al. 2018), which frequently occur in nature (Gaedke & Klauschies 2017). Furthermore, we are addressing the long-lasting question how to best reflect horizontal diversity in ecosystem models using a hybrid model related to the plankton food web of Lake Constance.
2. We showed that the type (van Velzen & Gaedke 2018, van Velzen & Gaedke subm.) and shape of the trade-offs among functional traits play a decisive role for species coexistence and system

dynamics (Ehrlich et al. 2017, Ehrlich & Gaedke 2018). This also holds for other related key model assumptions (Klauschies & Gaedke 2020).

3. Mostly during the first funding period, we studied dynamic biomass-trait feedbacks in bi-trophic food web models from numerous perspectives, also enabling a synthesis of current theory of this field of research. We focused on how differences in structure, functional traits, trade-offs and sources of trait variation affect population and community dynamics, e.g. to explain unusual predator-prey dynamics such as reversed or intermittent predator-prey cycles (Klauschies et al. 2016, Raatz et al. 2017, Bengfort et al. 2017, van Velzen & Gaedke 2017, van Velzen & Gaedke 2018, van Velzen 2020, van Velzen et al. 2022). Among others, we could show that adaptation of prey defense (van Velzen 2020) or coadaptation between prey defense and predator offense (Klauschies et al. 2016) may enable supersaturated coexistence; that intermittent cycles may be surprisingly relevant for conservation as they are often linked to high extinction risk (van Velzen et al. 2022); and that unusual predator-prey dynamics mainly arise when prey adapt more rapidly than their predators (van Velzen & Gaedke 2017, van Velzen et al. 2022).

4. During the second funding period, we extended e.g. knowledge gained on biomass-trait feedbacks for bitrophic predator-prey models to tri-trophic systems including food chains and intra-guild predation modules that accounted for functional horizontal diversity at each trophic level (Ceulemans et al. 2019, Ceulemans et al. 2021, Wojcik et al. 2021, Li et al. subm., Adje et al. in prep.). This allowed us bridge between more abstract but also more tractable predator-prey models, and more realistic complex food web models, and field observations, e.g. on the seasonal plankton development in Lake Constance. Considering such more complex adaptive webs additionally enables to consider system wide ecosystem functions. For example, a higher degree of functional diversity generally enhanced the resource exploitation efficiency and production of the top trophic level and trait adaptation greatly enhanced coexistence of the three species in the IGP module along an enrichment gradient.

5. We used a comprehensive plankton data set of Lake Constance compiled by the project leader during the past decades to test key assumptions of trait-based approaches (Weithoff & Gaedke 2017) and to determine the trade-off shape in a naturally evolved phytoplankton community and its consequences for seasonal dynamics (Ehrlich et al. 2020)

6. Using the Lake Constance food web data set we could show how trait changes at one trophic level cascade through this tritrophic web, i.e. the biomass-trait feedbacks assumed in our models were well observable in a natural food web (Ehrlich & Gaedke 2020). This trait-based approach shed new insights on driving forces of the seasonal plankton development.

7. We provided empirical evidence that the evolution of grazers' resistance to cyanobacteria in Lake Constance may be due to a trade-off between gleaners and opportunists, mediated by food quality (Isanta-Navarro et al. 2022). That is, grazers with a high sterol affinity but a low maximum growth rate thrive if low food quality cyanobacteria dominate the phytoplankton community, while grazers with a lower sterol affinity but a high maximum growth rate are competitively superior when cyanobacteria are of minor importance.

8. The cooperation with four experimental partners (S. Moorthi, Oldenburg, R. Tollrian, Bochum, Th. Berendonk & M. Weitere, Dresden/UfZ and L. Becks, Konstanz) within this priority program inspired several theoretical studies, which paved the way to better understand causal relationships presumably ruling the experimental systems (de Ruiter & Gaedke 2017, van Velzen et al. 2018, Raatz et al. 2018, Rosenbaum et al. 2019).

9. We also developed and applied models tailored specifically to the data of our experimental partners (Seiler et al. 2017, Flöder et al. 2021). This helped optimizing the experimental designs, interpreting and generalizing the experimental results, and facilitating the comparison among findings derived from different experimental set-ups. In addition, this allowed to confront the

developed theory with data, to improve the realism of the mathematical models and to strengthen the validity of future forecasts based on these models.

10. Beyond the original plans stated in the project proposal we could also address the consequences of biomass-trait feedbacks for the ability of bi- and tritrophic food webs to buffer the effects of pulse and press perturbations (Raatz et al. 2019, Wojcik et al. 2021, Li et al., subm., Adje et al. in prep.). There is no simple answer to this question but systems with a larger potential to adapt at a reasonable speed often showed a higher robustness against perturbations (e.g. a higher resistance, resilience and elasticity).

11. We are also conducting chemostat experiments ourselves to verify model predictions. E.g. concerning the response of systems with different functional diversity to pulse and press perturbations (Blasius et al. 2020, Pfennig et al. in prep.).

12. We promoted synergies within the priority programme DynaTrait and also internationally, e.g. by teaching summer schools and by leading or contributing to synthesis papers. Our most important synthesis work are (1) a systematic comparison of different ways in which inducible defenses can be represented in predator-prey models, and the consequences of these modelling choices (Yamamichi et al. 2019); (2) a highly collaborative project bringing together modellers and empiricists working across various scales within DynaTrait, aiming to bridge gaps between different sub-fields of ecological research and apply many of the insights listed above to global ecosystem models (Prowe et al. subm.); (3) a conceptual framework to study the impact of intraspecific trait variation and associated trait changes in the light of modern coexistence theory (Klauschies et al. in prep).

Overall, this work stimulates to reconsider concepts in fundamental ecology that form the basis for nature conservation and helps to improve the realism of biogeochemical models tailored to specific ecosystems.

Publications arising from our DynaTrait projects [downloads at our Working Group homepage possible]

1. Li, X., T. Klauschies, W. Yang, Z. Yang & U. Gaedke (subm.) Trait adaptation facilitates species coexistence and community stability and reduces alternative states of the intraguild predation module.

2. Van Velzen, E. & U. Gaedke (subm.) Back to the drawing board: re-thinking growth-defense trade-offs

3. Kath, N.J., U. Gaedke & E. van Velzen (revised) The double-edged sword of inducible defences: costs and benefits of maladaptive switching from the individual to the community level.

4. Prowe, A.E.F., S. Wollrab, O. Kerimoglu, U. Gaedke, H.-P. Grossart, M. Kasada, H.C.L. Klip, S. Moorthi, T. Shatwell, P. Thongthaisong & E. van Velzen (subm.) Flexibility in aquatic food web structure: linking scales and approaches

5. Isanta Navarro, J., T. Klauschies, A. Wacker & D. Martin-Creuzburg (2022) A sterol-mediated gleaner-opportunist trade-off underlies the evolution of grazer resistance to cyanobacteria. Proceedings of the Royal Society B.

6. Klauschies, T. & J. Isanta-Navarro (2022) The joint effects of salt and 6PPD contamination on a freshwater herbivore. Science of the Total Environment 829: 154675.

7. Van Velzen, E., U. Gaedke & T. Klauschies (2022) Quantifying the capacity for contemporary trait changes to drive intermittent predator-prey cycles. Ecol. Monogr. e1505. https://doi.org/10.1002/ecm.1505

8. Wojcik, L. A., Ceulemans R. & U. Gaedke (2021) Functional diversity buffers the effects of a pulse perturbation on the dynamics of tritrophic food webs. Ecol. & Evol.11: 15639–15663.
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12. Ehrlich, E., N. Kath & U. Gaedke (2020) The shape of a defense-growth trade-off governs seasonal trait dynamics in natural phytoplankton. The ISME Journal 14: 1451-1462.
13. Blasius, B., L. Rudolf, G. Weithoff, U. Gaedke & G. Fussmann (2020). Long-term cyclic persistence in an experimental predator-prey system. Nature 577: 226-230.
14. Klauschies, T. & U. Gaedke (2020) Nutrient retention by predators undermines predator coexistence on one prey. Theoret Ecol. 13, 183-208.
15. Van Velzen, E. (2020) Predator coexistence through emergent fitness equalization. Ecology 101: e02995
16. Yamamichi, M., T. Klauschies, B. Miner & E. van Velzen (2019) Modelling inducible defenses in predator-prey interactions: assumptions and dynamical consequences of three distinct approaches. Ecology Letters 22: 390-404
17. Ceulemans, R., U. Gaedke, T. Klauschies & C. Guill (2019) The effects of functional diversity on biomass production, variability, and resilience of ecosystem functions in a tritrophic system. Scientific Reports 9: 7541.
18. Raatz, M., E. v. Velzen & U. Gaedke (2019) Co-adaptation impacts robustness of predator-prey dynamics against perturbations. Ecol. Evol. 9: 3823-3836.
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21. Van Velzen, E., T. Thieser, T. Berendonk, M. Weitere & U. Gaedke (2018) Inducible defense destabilizes predator-prey dynamics: the importance of multiple predators. OIKOS 127: 1551-1562.
22. Van Velzen, E. & U. Gaedke (2018) Reversed predator-prey cycles are driven by the amplitude of prey oscillations. Ecology and Evolution 8: 6317–6329.
23. Ehrlich, E. & U. Gaedke (2018) Not attackable or not crackable - How pre- and post-attack defences with different competition costs affect prey coexistence and population dynamics. Ecology and Evolution 8: 6625–6637.
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25. Seiler, C., E. v. Velzen, T. Neu, U. Gaedke, T. Berendonk & M. Weitere (2017) Grazing resistance of bacterial biofilms: A matter of predators' feeding trait. FEMS Microbiology Ecology 93 (9), doi: 10.1093/femsec/fix112

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31. Ruiter, PC. de & U. Gaedke (2017) Emergent facilitation promotes biological diversity in pelagic food webs. Food Webs, 10:15-21.

32. Weithoff, G. & U. Gaedke (2017) Mean functional traits of lake phytoplankton reflect seasonal and inter-annual changes in nutrients, climate and herbivory. J. Plankton Res. 39: 509-517.

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34. Coutinho, R., T. Klauschies & U. Gaedke (2016) Bimodal trait distributions with large variances question the reliability of trait-based aggregate models. Theoretical Ecology, 9: 389-408.

Other projects of the priority programme directly benefitted from the work done in this project. See e.g. M. de la Cruz Barron, E. van Velzen, U. Klümper, M. Weitere, T.U. Berendonk and D. Kneis (subm.) Shifts from cooperative to individual-based predation defense determine microbial predator-prey dynamics.