Final report of the project (GA 401/26-1, GA 401/26-2)

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

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. Funding included two post-doctoral (100%/ 24 months) and one Ph.D. position (75%/ 9 months) in the first phase and one post-doctoral (100%/ 36 months) and two Ph.D. positions (75%/ 36 months and 75%/ 24 months, respectively) in the second phase.

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 addressed the long-lasting question how to best reflect horizontal diversity in ecosystem models using a hybrid model (Wojcik et al., 2024). This study also allowed to address the question how the type of horizontal diversity (e.g. many non-adaptive or few but adaptive species or functional guilds) affects ecosystem functions and their variability. It stimulated to develop an index that enables to quantify the different facets of horizontal diversity (Wojcik et al., subm.).

2. We showed that the type (van Velzen & Gaedke 2018, van Velzen & Gaedke 2023) 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, Ehrlich et al., in prep.). 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. 2023., Adje et al. 2023). 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 and taking a trait-based food web perspective we could also 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., 2023., Adje et al. 2023). 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). The robustness to different types of perturbations depends also on the shape of the trade-off (Ehrlich et al., in prep.). In addition, we studied the impact of spatial self-organized pattern formation on the maintenance of functional diversity in bitrophic communities, showing that the interaction between dispersal and local species interactions may promote continuous trait adjustments in the trait distribution of the autotrophic community that enable a higher functional diversity at both the local and regional scale of metacommunities beyond what is expected from simple source-sink dynamics (Guill et al. 2021).
11. We also conducted comprehensive chemostat experiments ourselves to verify model predictions arising e.g. from Wojcik et al. (2021) (Blasius et al. 2020, Wojcik 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 review about different approaches that are currently used to capture biodiversity in ecosystem models (Acevedo-Trejos et al. 2022); (3) 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 (van Velzen et al. subm.); (4) 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 the projects (members of this project in bold and other DynaTrait members in italics)

1. **Wojcik, L.A., T. Klauschies, E. van Velzen**, C. Guill & **U. Gaedke** (2024) Integrating different facets of diversity into food web models: how adaptation among and within functional groups shape ecosystem functioning. Oikos (in press)
2. **Adje, G., L. Wojcik** & **U. Gaedke** (2023) Functional diversity increases the resistance of a tritrophic food web to environmental changes. Theoret. Ecol. 16, 131-150.
3. **Li, X., T. Klauschies**, W. Yang, Z. Yang & **U. Gaedke** (2023) Trait adaptation enhances species coexistence and reduces bistability in an intraguild predation module. Ecol. Evol. 13:e9749.
4. **Van Velzen, E.** & **U. Gaedke** (2023) Back to the drawing board: re-thinking growth-defense trade-offs. OIKOS e09918.
5. **Kath, N.J., U. Gaedke** & **E. van Velzen** (2022) The double-edged sword of inducible defences: costs and benefits of maladaptive switching from the individual to the community level. Scientific Reports 12:10344.

6. 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, 289: 20220178.

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.

8. *Acevedo-Trejos E*., M. Cadier, S. Chakraborty, B. Chen, S.Y. Cheung, M. Grigoratou, C. Guill, C. Hassenrück, *O. Kerimoglu*, **T. Klauschies**, C. Lindemann, A. Palacz, *A. Ryabov*, M. Scotti, S.L. Smith, S. Vage & *F. Prowe* (2022) Modelling approaches for capturing plankton diversity (MODIV), their societal applications and data needs. Frontiers in Marine Science 9: 975414.

9. **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.

10. *Flöder S.*, J. Yong, **T. Klauschies, U. Gaedke**, T. Brinkhoff, T. Poprick & *S. Moorthi* (2021) Intraspecific Trait Variation Alters the Outcome of Competition in Freshwater Ciliates. Ecol. Evol. 11: 10225–10243.

11. **Ceulemans, R.**, C. Guill & **U. Gaedke** (2021) Top predators govern multitrophic diversity effects in tritrophic food webs. Ecology 00(00):e03379.

12. Guill, C., J. Hülsemann & **T. Klauschies** (2021) Self-organized pattern formation increases local diversity in metacommunities. Ecology Letters 24: 2535-2811.

13. **Ehrlich, E.** & **U. Gaedke** (2020) Coupled changes in traits and biomasses cascading through a tritrophic plankton food web. Limnology and Oceanography 65: 2502-2514.

14. **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.

15. *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.

16. **Klauschies, T.** & **U. Gaedke** (2020) Nutrient retention by predators undermines predator coexistence on one prey. Theoret Ecol. 13, 183-208.

17. **Van Velzen, E.** (2020) Predator coexistence through emergent fitness equalization. Ecology 101: e02995.

18. 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.

19. **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.

20. **Raatz, M., E. van Velzen** & **U. Gaedke** (2019) Co-adaptation impacts robustness of predator-prey dynamics against perturbations. Ecol. Evol. 9: 3823-3836.

21. Rosenbaum, B., **M. Raatz**, G. F. Fussmann, G. Weithoff & **U. Gaedke** (2019) Estimating parameters from multiple time series of population dynamics using Bayesian inference. Frontiers in Ecology and Evolution 6: 234.

22. **Raatz, M.**, *S. Schälicke*, M. Sieber, *A. Wacker* & **U. Gaedke** (2018) One man's trash is another man's treasure - The effect of bacteria on phytoplankton-zooplankton interactions in chemostat systems. Limnol. & Oceanogr.: Methods 16: 629-639.

23. **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.

24. **Van Velzen, E.** & **U. Gaedke** (2018) Reversed predator-prey cycles are driven by the amplitude of prey oscillations. Ecology and Evolution 8: 6317–6329.

25. **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.

26. **Klauschies, T.**, R. M. Coutinho & **U. Gaedke** (2018) A beta distribution-based moment closure enhances the reliability of trait-based aggregate models for natural communities Ecol. Modelling 381: 46-77.

27. *Seiler, C.*, **E. van 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).

28. **Gaedke, U.** & **T. Klauschies** (2017) Analysing the shape of observed trait distributions enables a data-based moment closure of aggregate models. Limnology and Oceanography: Methods.

29. **Ehrlich, E.**, *L. Becks* & **U. Gaedke** (2017) Trait-fitness relationships determine how trade-off shapes affect species coexistence. Ecology 98: 3188-3198.

30. **Van Velzen, E.** & **U. Gaedke** (2017) Disentangling eco-evolutionary dynamics of predator-prey coevolution: the case of antiphase cycles. Scientific Reports, 7: 17125.

31. *Bengfort, M.*, **E. van Velzen** & **U. Gaedke** (2017) Slight phenotypic variation in predators and prey causes complex predator-prey oscillations. Ecol. Complexity 31: 115–124.

32. **Raatz, M., U. Gaedke** & *A. Wacker* (2017) High food quality of prey lowers its risk of extinction. Oikos 000: 001–010.

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

34. 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.

35. **Klauschies, T.**, D.A. Vasseur & **U. Gaedke** (2016) Trait adaptation promotes species coexistence in diverse predator and prey communities. Ecology and Evolution 6: 4141–4159.

36. 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. For example:

37. M. de la Cruz Barron, **E. van Velzen**, U. Klümper, *M. Weitere*, *T.U. Berendonk* & D. Kneis (2023) Shifts from cooperative to individual-based predation defense determine microbial predator-prey dynamics. The ISME Journal 17:775-785.