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Freshwater bacteria under environmental global change:

*How do abiotic and biotic factors shape community
stability and assembly?*

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Abstract

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Understanding the mechanisms that shape microbial community stability and assembly is essential for predicting ecosystem responses to environmental change. In this thesis, the influence of abiotic factors (e.g., nutrients, salinity, and temperature) and biotic interactions (e.g., grazing) on freshwater bacterial communities was investigated. Using a combination of in situ and laboratory experiments, community responses were assessed through measures of growth, biomass production, and community composition. Community dissimilarity and null modelling were further used to quantify the relative roles of deterministic (predictable) and stochastic (random) assembly processes. Results showed that repeated inputs of nutrients and dissolved organic matter led to greater changes in bacterial responses than single disturbances. Furthermore, communities with a disturbance history responded less strongly to a subsequent perturbation than those without such history, while the role of stochastic processes increased, particularly when time between disturbance events was short. In addition, nutrient enrichment in larger communities promoted stochastic assembly, likely by reducing competitive exclusion under high-resource conditions, thereby allowing more species with similar fitness to coexist and increasing the role of random colonization and drift. Top-down control by grazing promoted deterministic assembly despite increased variability among communities. Overall, this thesis demonstrates that the balance between stochastic and deterministic processes can shift with environmental context, disturbance regimes, and biotic interactions. These findings highlight the importance of considering multiple interacting drivers when studying microbial community dynamics. Improving our understanding of these processes is critical for predicting how freshwater ecosystems will respond to ongoing environmental change, with implications for ecosystem functioning, water quality, and resource management.

Keywords: Bacteria, community assembly, community composition, stochasticity, disturbance, stability

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“Being brave means that knowing when you fail, you won't fail forever.”
- Lana Del Rey

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I. Bick, B., Ágreda-López, G., Berger, S. A., Charmpila, E. A., Jiao, C., Kulaš, A., Nejstgaard, J. C., Oppong, J. C., Sassenhagen, I., Sjöstedt, J., Yaqoob, M. M., Langenheder, S. (2026) Frequent runoff events cause shifts in freshwater bacterial communities. *Manuscript*
- II. Renes, S. E., Bick, B., McKie, B. G., Fried-Petersen, H. B., Langenheder, S., Angeler, D. G., Lindström, E. S. (2026) Disturbance history shapes microbial community assembly and predictability. *Submitted*
- III. Bick, B., Lumpi, T., Lindström, E. S., Langenheder, S. (2025) Linking nutrient availability and community size to stochasticity in microbial community assembly. *FEMS Microbiology Ecology*, 101:fiaf110
- IV. Bick, B., Jiao, C., Lindström, E. S., Langenheder, S. (2026) Grazing shapes bacterial community assembly under short-term environmental pulses. *Manuscript*

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Abbreviations

ANOVA	Analysis of variance
ASV	Amplicon sequencing variant
AUC	Area under the curve
cDOM	Coloured dissolved organic matter
DNA	Deoxyribonucleic acid
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
GAMM	Generalized additive mixed models
LME	Linear mixed effect models
LRR	Log response ratio
N	Nitrogen
NST	Normalized stochasticity ratio
OEV	Overall ecological vulnerability
P	Phosphorus
PCR	Polymerase chain reaction
PERMANOVA	Permutational multivariate analysis of variance

AI statement

This thesis was originally written by me as a doctoral student. Generative artificial intelligence (AI) tools have been used solely for linguistic refinement, specifically through ChatGPT (GPT-5.3). The use of these tools complies with the guidelines for generative AI outlined in the faculty's general study syllabus for doctoral education.

Introduction

Bacteria in freshwater ecosystems

Bacteria are integral to freshwater ecosystem functioning as they play a central role in biogeochemical cycling. In particular, heterotrophic bacteria are key drivers of organic matter degradation, transforming dissolved organic matter into biomass and inorganic nutrients that can be reused within the food web (Rousk and Bengtson 2014). Through these processes, bacteria contribute to carbon cycling and energy flow in lakes (Cole et al. 1988). In Scandinavia, humic lakes are widespread due to the dominance of forested catchments and peat-rich soils, which supply large amounts of terrestrial dissolved organic matter (DOM) to inland waters (Kothawala et al. 2014). This can lead to a brown coloration of lake water caused by humic substances, which are aromatic organic compounds derived from the incomplete decomposition of plant material in soils and wetlands (Kritzberg and Ekström 2012). Humic lakes are typically dominated by allochthonous organic matter from terrestrial inputs, rather than autochthonous material produced within the system (Wetzel 2001). Elevated DOM concentrations can reduce light penetration, limit phytoplankton primary production and promote heterotrophic processes (Karlsson et al. 2009; Kritzberg et al. 2020). The high availability of terrestrial carbon further enhances bacterial production, strengthening heterotrophy and the role of bacteria in processing organic matter and linking terrestrial and aquatic carbon cycles (Ask et al. 2009; Tranvik et al. 2009). These important bacterial functions are supported by the high diversity of freshwater bacterial communities, which encompass a wide range of metabolic capabilities (Zwart et al. 2002; Madigan et al. 2003). Despite this diversity, most bacterial taxa are typically present at low abundances, forming a large “rare biosphere”, which may contribute to community assembly dynamics by enabling taxa to increase in abundance when conditions become favourable (Sogin et al. 2006; Pedrós-Alió 2012). The spatial and temporal mechanisms underlying community composition and therefore diversity of bacterial communities still remain elusive (Zhou and Ning 2017; Langenheder and Lindström 2019), making this a central question in microbial ecology.

Disturbance effects and stability in bacterial communities

Disturbances can be drivers of bacterial community dynamics, altering both community composition and ecosystem functioning by disrupting environmental conditions and resource availability (Shade et al. 2012). In community ecology, the ability of a community to maintain its structure and function when subjected to environmental disturbances, is referred to as stability (Holling 1973). In bacteria, disturbances such as nutrient pulses, temperature shifts, or changes in salinity can restructure communities by modifying selection pressures and promoting shifts in dominant taxa (Allison and Martiny 2008; Shade et al. 2012). Salinity represents a particularly strong environmental filter for bacteria, as it imposes physiological constraints that can rapidly alter community composition and metabolic activity (Martiny et al. 2006). Bacterial communities in nature are generally functionally more redundant compared to other types of communities, which means that several bacterial taxa share the same function (Yin et al. 2000; Allison and Martiny 2008). High bacterial diversity and functional variability allow rapid responses to changes in environmental conditions, while functional redundancy may buffer the effects of disturbance on ecosystem functions (Allison and Martiny 2008; Lindström and Langenheder 2012). However, bacterial functioning can also be altered under persistent or repeated disturbances and may not return to pre-disturbance conditions (Santillan et al. 2020). For example, changes in salinity have been shown to reduce diversity, shift taxonomic composition, and affect processes such as respiration and organic matter degradation (Lozupone and Knight 2007; Herlemann et al. 2011). Disturbance effects may further persist over time through legacy effects, where previous environmental conditions influence the response of communities to subsequent disturbances, thereby shaping present-day community structure and function (Hawkes and Keitt 2015; Jurgburg et al. 2017; Thayne et al. 2022). Most experimental studies have focused on single environmental drivers, and we still know relatively little about how multiple abiotic factors acting simultaneously influence microbial communities (Philippot et al. 2021).

Lakes under global change

Climate change increases the magnitude and frequency of extreme weather events, such as heat waves and heavy precipitation events, which can act as strong disturbances for ecosystems (Havens et al. 2016; IPCC 2023). They can for example impact freshwater systems by increasing water temperature

and concentrations of nutrients and DOM through runoff (Beniston et al. 2007). Such changes affect planktonic communities that form the base of aquatic food webs, including both primary producers and heterotrophic microorganisms that drive carbon cycling and energy transfer (Field et al. 1998; Wetzel 2001). Increasing water temperature can decrease plankton diversity, promote blooms of cyanobacteria and lead to oxygen depletion (Paerl and Huisman 2009; Graham and Vinebrooke 2009). In addition, northern lakes are particularly sensitive to increased precipitation, through the enhanced transport of terrestrial DOM into aquatic systems which can promote browning and reduce light availability (Solomon et al. 2015; Kasprzak et al. 2017). Elevated concentrations of coloured dissolved organic carbon (cDOM) can drive major compositional and functional shifts in microbial communities (Tranvik et al. 2009). As browning limits light, communities may shift from autotrophic to heterotrophic systems, as primary production through photosynthesis is limited (Karlsson et al. 2009; Ask et al. 2009). These interconnected changes highlight how global change can simultaneously affect environmental conditions and microbial community dynamics in freshwater systems.

Community assembly processes in bacteria

To understand how bacterial communities are structured and maintained, it is necessary to consider the processes that govern their assembly. Four main community assembly processes are commonly described (Hubbell 2011; Chase and Myers 2011; Vellend 2016): Selection, dispersal, diversification, and drift. Selection refers to the process by which environmental conditions act as a filter, favouring species that are adapted to local conditions while excluding those that are not (Hubbell 2011). Dispersal is the movement of organisms across space, allowing species to colonize new communities through active motility or passive transport via physical forces (Vellend 2010). However, dispersal is often limited, referred to as dispersal limitation, where environmental gradients and physical barriers restrict the arrival of taxa, thereby influencing community composition (Hanson et al. 2012). Beyond dispersal, community composition can also change through diversification (or speciation), which generates new species or genetic variation within a community and typically occurs over larger spatial and temporal scales (Morlon 2014). Ecological drift reflects stochastic changes in community composition, where species may go extinct due to random birth and death events (Vellend 2010). Additionally, historical contingency can further influence community

assembly, as the order and timing of species arrivals may shape subsequent community structure through priority effects (Fukami 2015).

To better understand and predict patterns in community composition, these assembly processes are often grouped into deterministic and stochastic components. Deterministic processes generate predictable variation in community composition driven by abiotic and biotic factors; for example, selection is considered a purely deterministic process (Fig. 1; Vellend 2010, 2016).

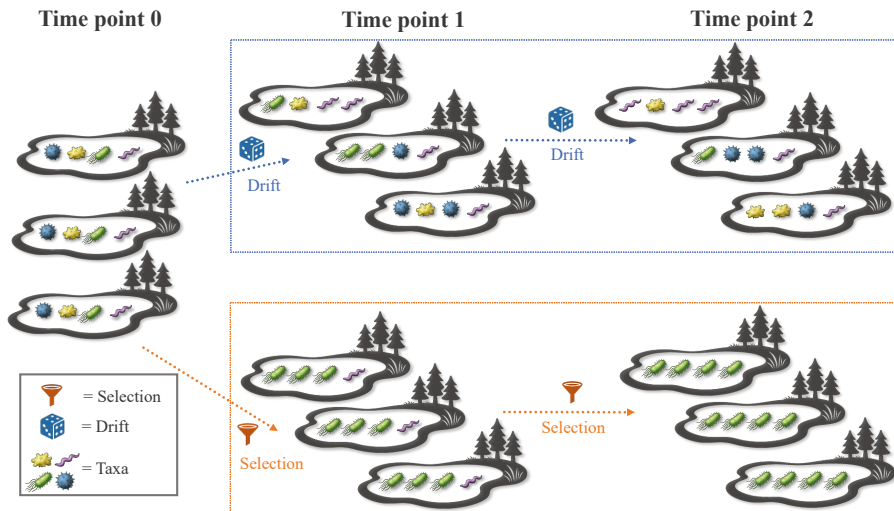


Figure 1: Conceptual figure showing stochastic (top blue box) and deterministic (bottom orange box) community assembly over three time points (0, 1 and 2). Each lake represents one community, where shapes and colours represent different taxa. Environmental conditions in all lakes are assumed to be the same. **Scenario 1 (stochasticity)**: The three lakes start with the identical community composition at time point 0, but then diverge into different communities by, e.g., ecological drift. Here one individual of a species dies out, and another one reproduces randomly and takes its spot. At time point 2 the three lakes differ completely in their community composition. **Scenario 2 (determinism)**: The three lakes start with the identical community composition at time point 0, but only the green species reproduces at time point 1 because of abiotic or biotic conditions that lead to selection pressure, whereas the yellow and blue species die out. By time point 2 all communities have the same community composition.

In contrast, stochastic processes account for variation in community composition that cannot be explained by measured environmental factors, making patterns of bacterial diversity more difficult to predict (Albright et al. 2019). Ecological drift represents a purely stochastic process, arising from random fluctuations in species abundances (Fig. 1). In contrast, dispersal and

diversification can be influenced by both deterministic and stochastic mechanisms, depending on environmental context and spatial scale (Chase and Myers 2011). Additionally, depending on the underlying mechanisms, priority effects can be categorized as either deterministic or stochastic as well. Deterministic priority effects occur when differences in species traits or environmental conditions lead to consistent outcomes, whereas stochastic priority effects arise from random variation in the timing or order of species arrival, resulting in different community compositions under similar conditions (Vannette and Fukami 2014).

Drivers and importance of stochastic assembly in bacterial communities

The relative importance of different community assembly processes in bacterial communities is a widely discussed question in community ecology, and evidence supports that both deterministic and stochastic processes contribute to community structure (Stegen et al. 2012; Nemergut et al. 2013; Zhou and Ning 2017; Wang et al. 2023). While environmental selection can strongly influence bacterial community composition, particularly across environmental gradients, stochastic processes such as dispersal limitation and ecological drift often play a substantial role (Stegen et al. 2012). As most bacterial taxa are rare they can be more prone to stochastic population dynamics that cannot be explained by any abiotic or biotic factors (Fig. 1; Vellend 2010, 2016). Further, it has been found that large parts of variation in community composition in bacteria remain unexplained, suggesting a role of stochasticity (Pedrós-Alió 2012; Nemergut et al. 2013; Liu et al. 2021). Stochasticity can be especially dominant under conditions where selection pressure is weak, dispersal is limited, and environmental conditions are relatively stable (Evans et al. 2017; Albright et al. 2019). Moreover, stochasticity is important under increased productivity, e.g., enhanced nutrient availability or warming (Chase 2010; Ren et al. 2017; Cao et al. 2021). This is due to higher resource availability and enhanced metabolic rates that can weaken resource competition and promote overall population growth, in turn leading to random fluctuations in species abundances (Chase and Leibold 2002; Zhou et al. 2014). Disturbances can further lead to stochasticity, through reducing community size or biomass of a community (Siqueira et al. 2020). In smaller communities, random birth and death events have a stronger influence, because each individual represents a larger proportion of the community, making shifts in community composition more sensitive to change (Orrock and Fletcher Jr. 2005;

Orrock and Watling 2010). Grazing can produce similar effects by altering community size and structure. Experimental studies on assembly processes have so far primarily focused on bacterial communities only and excluded grazers (Lindström and Langenheder 2012; Langenheder and Lindström 2019). Selective grazers can, however, remove dominant taxa and therefore promote the occurrence of less competitive taxa which can lead to more stochasticity (Pernthaler 2005; Zhou and Ning 2017). However, the opposite effect in which determinism was promoted by grazing effects, has also been observed (Lumpi et al. 2023). Thus, the interaction between bacteria and their grazers in terms of assembly processes, especially under environmental changes, remains unknown.

Quantifying community assembly in bacteria

Quantifying community assembly processes remains challenging, as processes cannot be directly observed, but instead have to be inferred from patterns in community composition. Deterministic processes are typically associated with variation explained by environmental conditions, whereas stochastic processes are the unexplained variation after accounting for environmental and spatial factors (Stegen et al. 2012; Zhou and Ning 2017). In observational studies, variation partitioning, typically based on constrained ordination methods, is used to separate total variation into fractions explained by environmental variables, spatial variables, their shared effects, and unexplained variation (Borcard et al. 1992; Legendre et al. 2005; Peres-Neto et al. 2006). In contrast, experimental studies allow specific mechanisms to be isolated and tested directly while minimizing other factors (Jessup et al. 2005; Fukami 2010; Chase 2010). Experimental studies provide manipulation of environmental conditions and spatial processes such as dispersal or migration in controlled systems.

To quantify community assembly processes in bacteria, two complementary metrics were used in this thesis: Within-treatment community dissimilarity (beta-diversity) and null modelling. As the thesis is based on experimental work with replicated treatments, it was possible to compare replicate communities exposed to identical conditions. This within-treatment dissimilarity (beta-diversity), assessed by calculating pairwise Aitchison distances, provided a measure of how communities assembled under identical conditions (Fig. 2; Chase 2010; Chase and Myers 2011). Here, greater dissimilarity among replicates, was quantified as higher pairwise Aitchison distances and indicated a stronger influence of stochasticity (Fig. 2; Aitchison 1982; Stegen

et al. 2013). Conversely, lower dissimilarity (i.e., lower Aitchison distances) reflected more similar community composition among replicates, suggesting a greater role of deterministic processes (Fig. 2).

To assess whether observed community dissimilarity arose from stochastic or deterministic processes, null modelling was applied (Nemergut et al. 2013). Null models generate randomized community data while maintaining specific constraints (e.g., species richness or total abundance) and compare these randomized communities to observed patterns (Stegen et al. 2012, 2013). Here, stochasticity was quantified using the Normalized Stochasticity Ratio (NST; Ning et al. 2020), which estimates the relative importance of stochastic processes based on deviations in community composition from null expectations. NST values range from 0 to 1, with values > 0.5 indicating a greater influence of stochastic processes, whereas values < 0.5 suggest a stronger role of deterministic processes (Fig. 2). Phylogeny-based metrics that use relatedness as a proxy for ecological similarity (Stegen et al. 2013) may be less reliable in bacterial communities, where horizontal gene transfer can decouple phylogeny from function (Martiny et al. 2015) potentially leading to misinterpretation of deterministic assembly processes.

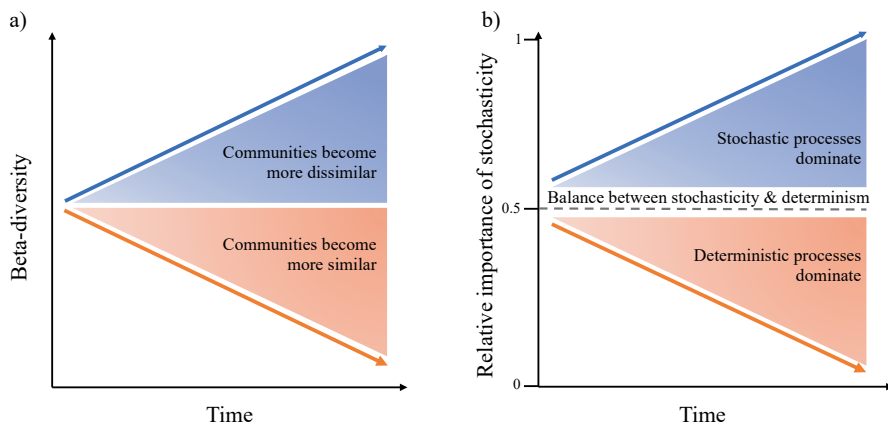


Figure 2: Conceptual figure of a) expected temporal trends for beta-diversity, based on community dissimilarity and b) the relative importance of stochasticity based on null modeling by, e.g., normalized stochasticity ratio (NST). Negative trends (orange) indicate increasing community similarity and deterministic control, whereas positive trends (blue) indicate increasing community dissimilarity and stochasticity over time. If beta-diversity and the relative importance of stochasticity decrease, results indicate **determinism**. On the contrary, increasing beta-diversity and relative importance of stochasticity were interpreted as enhanced **stochasticity**. In the case of beta-diversity increasing, but relative importance of stochasticity decreasing over time, results indicate communities becoming more dissimilar over time, due to deterministic processes.

Aims of this thesis

The overall aim of this thesis was to investigate how global environmental change influences the assembly of freshwater bacterial communities. This work focused on how key drivers associated with environmental change, such as altered nutrient concentrations, dissolved organic matter concentrations, salinity, temperature, and changes in biotic interactions (e.g., grazing), affect bacterial growth, community composition, and assembly processes. A central objective was to understand how bacterial communities respond in their growth and community composition to disturbances in for example salinity or resource availability. Furthermore, this thesis aimed to identify the mechanisms promoting stochasticity in community assembly and to assess how both disturbance regimes (e.g., frequency, magnitude, and history of disturbances) and shifts in abiotic and biotic conditions influence the balance between stochastic and deterministic processes. Ultimately, this work sought to evaluate how these factors shape the predictability of bacterial community dynamics under changing environmental conditions. This leads to four objectives studied across the four papers which comprise this thesis:

- Paper I:** How do runoff scenarios, that differ in their magnitude and frequency of nutrients and cDOM pulses, affect bacterial growth, community assembly and stability?
- Paper II:** How do repeated disturbances and disturbance history influence the relative importance of stochastic and deterministic processes in bacterial community assembly?
- Paper III:** How do bacterial communities assemble under combined nutrient enrichment and reduction in community size?
- Paper IV:** How do grazing and combined nutrient and temperature pulses shape community assembly in bacteria?

Methods

Experimental procedures

Mesocosm experiments

In **Paper I**, in situ lake mesocosm experiments were used to manipulate different magnitudes and frequencies of runoff scenarios. In general, mesocosm experiments offer the opportunity to conduct manipulations of specific environmental parameters while keeping other conditions as close to the natural system as possible (Urrutia-Cordero et al. 2021b). Here, the SITES AquaNet infrastructure was used at three field stations (Erken, Bolmen and Skogaryd) situated at Lakes Erken, Bolmen, and Erssjön respectively. From here onwards the lakes will be referred to as their station names to be consistent with other mesocosm studies (Urrutia-Cordero et al. 2021b). The experiments were replicated in time and space and carried out in summer 2022 in Erken and Bolmen and in Erken, Bolmen and Skogaryd during spring 2023. The three lakes differed in trophic status and physicochemical characteristics: Bolmen being oligotrophic with low nutrient and DOC concentrations, Erken mesotrophic to eutrophic with intermediate values, and Skogaryd a shallow humic system with high DOC and nutrient concentrations. The mesocosm set-ups at the three stations encompassed a floating platform equipped with 16 cylindrical polyethylene containers filled with 550 L water from the surrounding lake. Different runoff scenarios (extreme, intermittent and daily), were created by adding the same amount of inorganic nutrients (N in the inorganic form as NO_3^- , P as inorganic $\text{PO}_4\text{-P}$) and cDOM in form of a peat extract in different frequencies (Fig. 3; Langenheder et al. 2024). The daily treatments received daily additions with 5% of the total amount of nutrients and cDOM, whereas intermittent treatments received 7 pulses in total with variable intensity (5-30% of total nutrients and cDOM) and extreme treatments received the total amount of nutrients and cDOM in one event (Fig. 3). Each treatment and a control, that did not receive any additions, was replicated 4 times. Each experiment lasted for 37 days, of which the first 20 days encompassed additions of N, P and cDOM (Fig. 3). During the last 17 days no additions were made, and results obtained were used to assess community recovery. Samples for bacterial abundance were taken every fourth day (1, 5, 9, 13, 17, 21, 25, 29, 33, 37)

and bacterial community composition was assessed at five time points (day 1, 9, 13, 21, 37), with the exception of the Erken summer experiment where the second last sampling (day 33) was used instead due to the loss of samples.

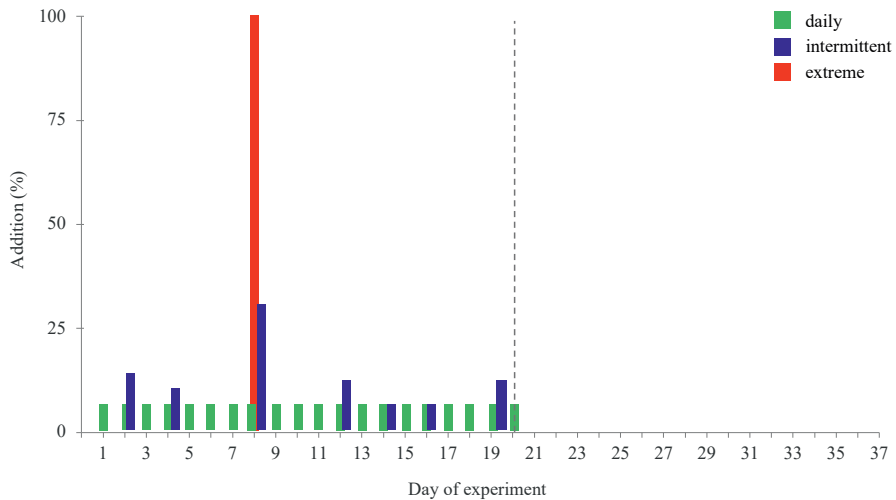


Figure 3: Schematic set-up of the mesocosm experiments (**Paper I**). Three runoff scenarios (daily, intermittent, extreme) were applied over a 37-day experimental period, including 20 days of cDOM and nutrient additions, followed by a 17-day recovery phase. The grey dashed line indicates the end of the runoff period during which nutrients were added. The y-axis shows the fraction of total added cDOM, and nutrients added in percentage (see Langenheder et al. 2024), and the x-axis represents the day of the experiment.

Laboratory experiment with continuous cultures

Paper II investigated the response of bacterial communities to salinity disturbances and whether these responses were influenced by prior disturbance history. For that, a laboratory experiment with a continuous culture set-up was used. A 3 x 2 factorial design, with three recovery treatments (background, long, short) and two pulse treatments (pulse and no pulse) was applied, with 4 replicates each, resulting in 24 vessels in total. In the first 27 days of the experiment different exposure histories were created (Fig. 4): (1) Long recovery treatments received 3 minor salinity disturbances (5 ppt NaCl each) at the start of the experiment and had a two-week recovery phase; (2) short recovery treatments received the same minor salinity disturbances and a one-week recovery period thereafter and (3) control treatments did not receive any salinity disturbances. At day 27, some of the treatments were exposed to an additional stronger salinity pulse of 15 ppt NaCl (Fig. 4). Following, all cultures were allowed to grow without further disturbances for an additional 23 days,

resulting in a total experimental duration of 50 days. (Fig. 4). Bacterial community composition samples were taken every second day.

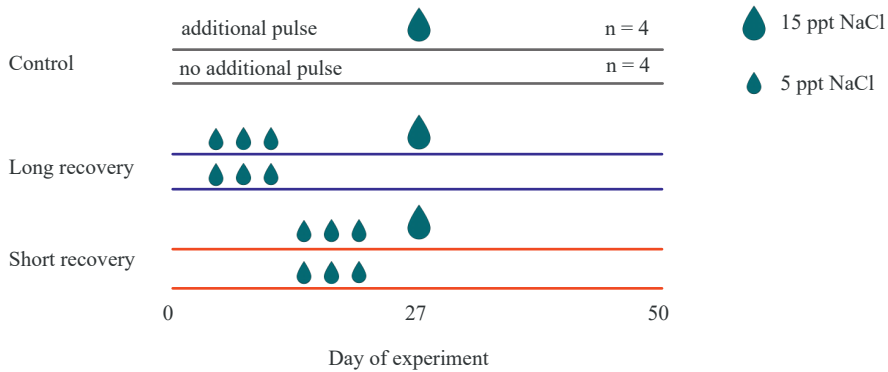


Figure 4: Set-up of the continuous culture experiment (**Paper II**), showing the 3 x 2 treatment groups, three different exposure histories (control, long and short recovery time) with additional pulse and no additional pulse conditions. Each treatment was replicated 4 times. Exposure histories are indicated by small water drop symbols and the additional pulse on day 27 with a large water drop symbol.

Laboratory experiments with semi-continuous cultures

Both **Papers III** and **IV** used semi-continuous laboratory experiments. For this, microcosms were set-up in 1 L Borosilicate glass bottles with 500 mL of a mixture of bacterial inoculum (20%) and sterile medium (80%). Water was collected from Lake Erken for **Paper III** and from Lake Siggeforasjön for **Paper IV**. The water was filtered through GF/F filters (0.7 μm) to remove grazers and used as an inoculum, which was pre-incubated under laboratory conditions to allow acclimatization prior to the start of the experiment. For the sterile medium, water was filtered (0.1 μm) and autoclaved (at 121°C for 20 min.). To ensure nutrient exchange and to compensate for volume loss during sampling, water in the microcosms was regularly exchanged. Sampling of microcosms was carried out under sterile conditions, and all bottles were shaken for homogenization before taking samples. In **Paper III**, I investigated effects of community size and nutrient pulse effects on bacterial communities. For that three different nutrient regimes (low, intermediate and high) were created by adding Na_2HPO_4 to the growth medium, NH_4Cl was further added accordingly to the Redfield ratio to avoid nitrogen depletion (Fig. 5; Redfield 1934). To manipulate community size, different volume ratios of inoculate and medium were prepared, to create small (2% of inoculum) and large communities (20% of inoculum; Fig. 5).

Therefore, the experiment resulted in a 2 x 3 factorial design, with 6 replicates per treatment, resulting in 36 experimental units.

		Community size	
		small (~40 000 cells)	large (~400 000 cells)
Nutrient concentration	high (~25 µg/L TP)	n = 6	n = 6
	intermediate (~15 µg/L TP)	n = 6	n = 6
	low (~5 µg/L TP)	n = 6	n = 6

Figure 5: Set-up of microcosm experiment (**Paper III**), based on a 2×3 factorial design with two community sizes (small, and large) and three nutrient concentrations (low, intermediate, and high). Each treatment consisted of six replicate microcosms. Small community size microcosms contained 10 mL and large community sizes 100 mL of bacterial inoculum and 490 mL and 400 mL of sterile lake water medium, respectively. Low nutrient concentrations encompassed 5 µg/L, intermediate 15 µg/L, and high 25 µg/L of total phosphorus (TP).

In **Paper IV** effects of grazing and environmental (temperature and nutrient) pulses were tested. For that, microcosms received nutrient pulses for which medium was exchanged at four time points with enhanced N and P concentrations (Fig. 6). Na_2HPO_4 and NH_4Cl were added to the medium in the same way as in **Paper III**. Additionally, temperature pulses were induced at four time points by moving microcosms from a from 15°C to a 25°C temperature-controlled chamber for 15 h for each pulse (Fig. 6). Additionally, we manipulated predator presence by establishing treatments with either bacteria alone or bacteria in combination with heterotrophic nanoflagellates. To achieve this, lake water was first filtered (5 µm) and pre-incubated under laboratory conditions, after which it was divided into two inocula; for which one inoculum was further filtered through 0.7 µm to remove grazers for the treatments without predation.

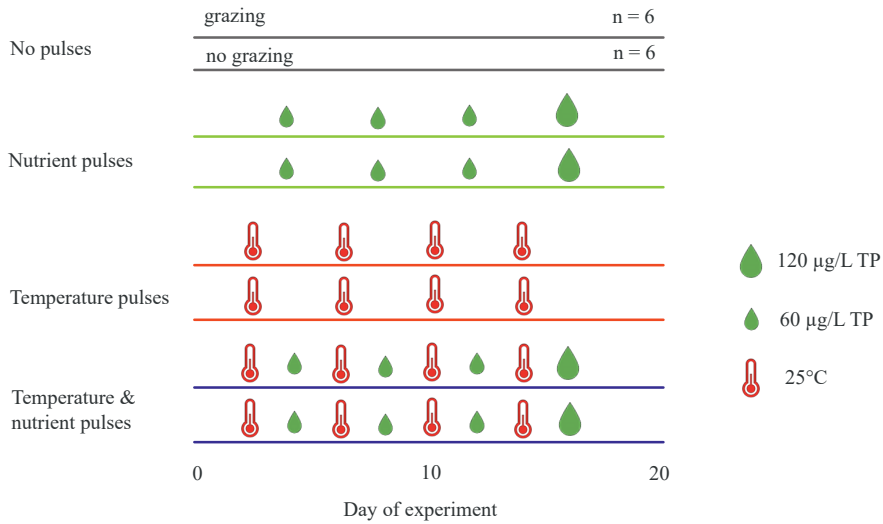


Figure 6: Experimental set-up of **Paper IV**. The x-axis represents time (in days), and the y-axis shows different treatments: Treatments included communities with and without grazers and nutrient (green droplet), temperature (red thermometer symbol), and combined nutrient and temperature pulses. Each microcosm was replicated six times.

Measurement of bacterial abundance & biomass production

In **Papers I-IV** bacterial growth was estimated as cell abundance over time, measured with Flow Cytometry. For that, samples were preserved with formaldehyde (1.85 % in sample), stained with 1.25 µM fluorescent nucleic acid stain SYTO13 (Invitrogen) and measured with a CytoFLEX flow cytometer (Beckman Coulter; Giorgio et al. 1996). Bacterial biomass production was estimated in paper III-IV by incubating samples with radioactively labelled L-(4,5-³H) Leucine (Perkin Elmer), measuring disintegrations per minute by a liquid scintillation and recalculating values into biomass production rates (Kemp et al. 2018).

Bacterial community composition

In **Papers I-IV** bacterial community composition was determined by 16S rRNA amplicon sequencing. For that, 100-200 mL of water samples were filtered onto 0.2 µm SUPOR membrane filters, DNA was extracted with the DNeasy PowerSoil Pro Kit (Qiagen) and amplifications carried out in a 2-step protocol after Vass et al. 2021. Thereafter, amplicons were purified, pooled in equimolar volumes and sent to SciLifeLab Uppsala or Stockholm for Illumina Miseq v3 sequencing of the 16S rRNA region. Removal of primers, quality

filtering and trimming was carried out in cutadapt using resources hosted by the Uppsala Multidisciplinary Center for Advanced Computational Science (UPPMAX). Further, Taxonomic classification of Amplicon Sequencing Variants (ASVs) was conducted against the SILVA reference database.

Data analysis

Community composition and assembly processes

Differences in bacterial community composition were assessed using ordination analyses. Principal Coordinates Analysis (PCoA) was performed based on a robust Aitchison distance matrix calculated from the full dataset to visualize overall patterns in community dissimilarity among treatments and time. In addition, Canonical Correspondence Analysis (CCA) was applied to Hellinger-transformed community data in **Paper I** to assess the relationship between community composition and environmental variables. The Hellinger transformation was used to reduce the influence of highly abundant taxa and to make the data suitable for ordination based on Euclidean distances. Additionally, community composition was summarized as the relative abundances of major taxonomic groups (e.g., phyla) to describe broad shifts in community structure.

To quantify the relative importance of stochastic and deterministic assembly processes, two complementary approaches were used. First, within-treatment community dissimilarity was calculated as the pairwise Aitchison distance between replicate samples within the same treatment. Aitchison distance is a measure of dissimilarity for compositional data, such as bacterial community data obtained from high-throughput sequencing, where abundances are expressed as relative proportions rather than absolute counts. It is calculated as the Euclidean distance after applying a centred log-ratio (CLR) transformation, which converts relative abundances into log ratios between taxa (Aitchison 1982; Aitchison et al. 2000). This transformation accounts for the compositional nature of the data, where only relative, not absolute, abundances are known and avoids misleading results that can arise when standard distance measures are applied directly to proportional data (Gloor et al. 2017). Higher within-treatment dissimilarity indicates a stronger influence of stochasticity, whereas lower dissimilarity suggests more deterministic assembly leading to similar community composition among replicates (Chase 2010; Chase and Myers 2011).

Second, a null modelling approach was applied to further disentangle stochastic and deterministic processes. Specifically, the normalized stochasticity ratio (NST) following Ning et al. (2020), which compares observed community

dissimilarity to null expectations while maintaining key constraints such as species richness. NST values range from 0 to 1, where values < 0.5 indicate predominantly deterministic assembly and values > 0.5 indicate predominantly stochastic assembly.

Stability metrics

To quantify stability to disturbances, we used different metrics in **Paper I** following the approach of Urrutia-Cordero et al. 2021a; 2022. For that, we estimated differences in responses in bacterial abundance and community composition of treatments compared to controls at each sampling point. For bacterial abundance we computed log response ratios (LRR), which is the logarithm of bacterial abundance in each treatment divided by the mean bacterial abundance in the controls for each time point. Values close to 0 indicate that abundances are similar to controls, and higher stability whereas larger, positive or negative values indicate stronger deviation from controls, and higher instability. To estimate differences in community composition, we calculated community dissimilarity indices between each experimental and control unit for each time point. Here, higher community dissimilarity indices represent larger compositional instability and lower values larger compositional stability.

To estimate stability over the whole experimental duration, we used the overall ecological vulnerability (OEV; Urrutia-Cordero et al. 2022). OEV is a metric which integrates abundance LRR and community dissimilarity index over time. For this, the total accumulated value (of abundance LRR / community dissimilarity index) is divided by the length of time of the experiment. Here, higher OEV values mean higher instability, and lower values higher stability.

Statistical tests

To test for treatment effects on response variables measured during experiments, a range of statistical approaches were applied depending on the data type and structure. Generalized additive mixed models (GAMMs) were used to analyse non-linear temporal dynamics, while linear mixed-effects models (LMEs) were applied to test for treatment effects on response variables with hierarchical or repeated-measures structure. Differences in community composition among treatments were assessed using permutational multivariate analysis of variance (PERMANOVA).

Main results

Runoff effects on bacterial stability and assembly

In **Paper I** the effects of runoff scenarios that differed in their magnitude and frequency of nutrients and cDOM additions on bacterial abundance and community composition were studied. Results showed that runoff treatments affected the log response ratios of abundance and the community dissimilarity index of bacteria over time compared to control conditions. Moreover, OEV (overall ecological vulnerability) a metric for overall stability in both abundance and community composition showed clear treatment effects, with stronger deviations in daily and intermittent compared to extreme treatments from controls (Fig. 7). However, treatments explained only a small part of the variation in bacterial community composition and showed no effects on assembly processes. On the contrary, factors such as lake type, season, and time shaped community variation and assembly to a larger extent. Environmental variables explained up to 14% in bacterial community composition, with dissolved organic carbon (DOC) emerging as a key driver during spring and nutrients during summer. Within-treatment dissimilarity increased over time during all experiments, except for Skogaryd (Fig. 8). Determinism was the main process shaping bacterial communities, though stochastic assembly was observed in Bolmen (Fig. 8). Assembly was more stochastic during summer than spring, and more deterministic in the humic lake (Skogaryd; Fig. 8). For community composition, differences in relative abundances were observed in Cyanobacteria being more dominant in daily and intermittent treatments compared to controls in Erken during summer.

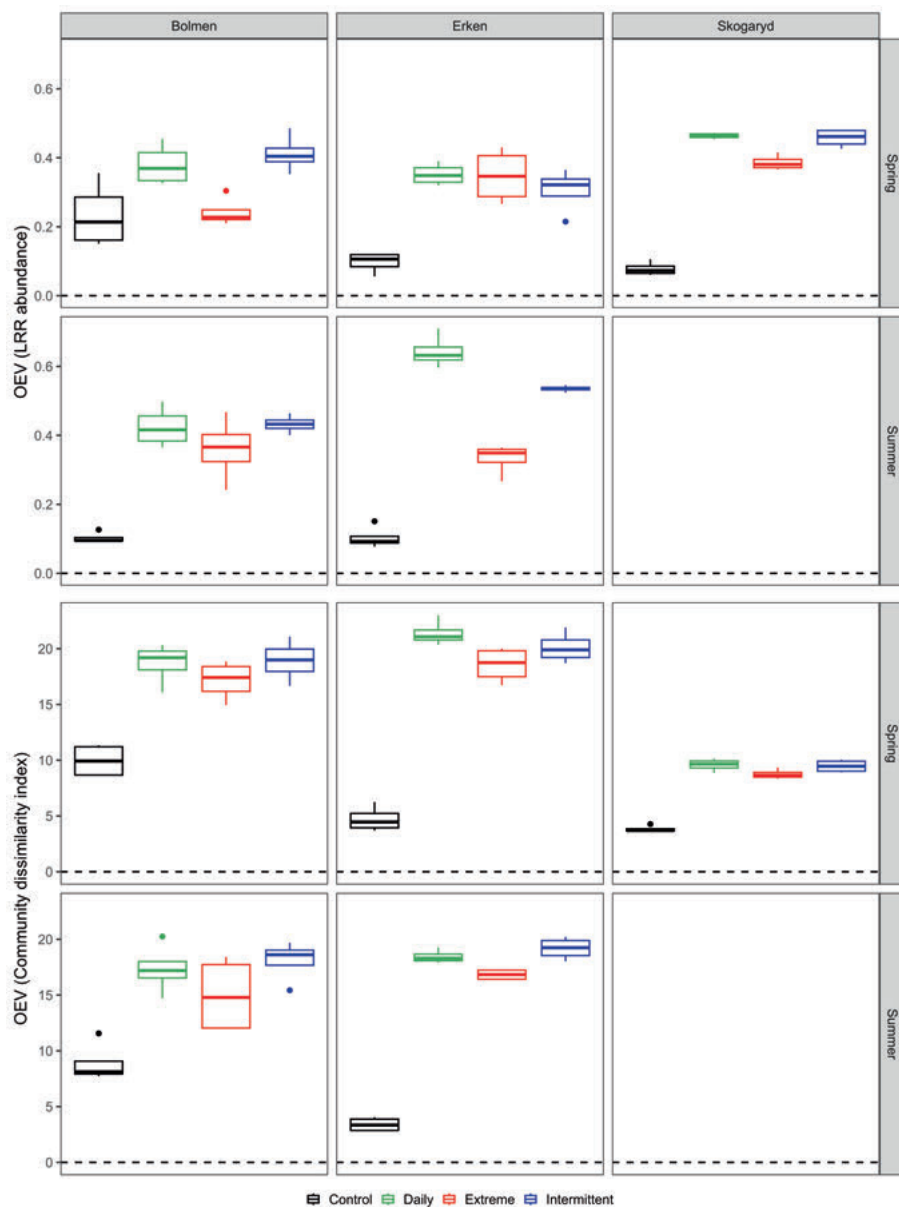


Figure 7: Results of OEV (Overall ecological vulnerability) of abundance log response ratio (LRR; top two rows) and community dissimilarity index (bottom two rows) for the different treatments (control = black, daily = green, extreme = red, intermittent = blue) across lakes (Bolmen, Erken, Skogaryd) and seasons (spring and summer; **Paper I**). The horizontal dashed line indicates 0, which means null variation from control conditions.

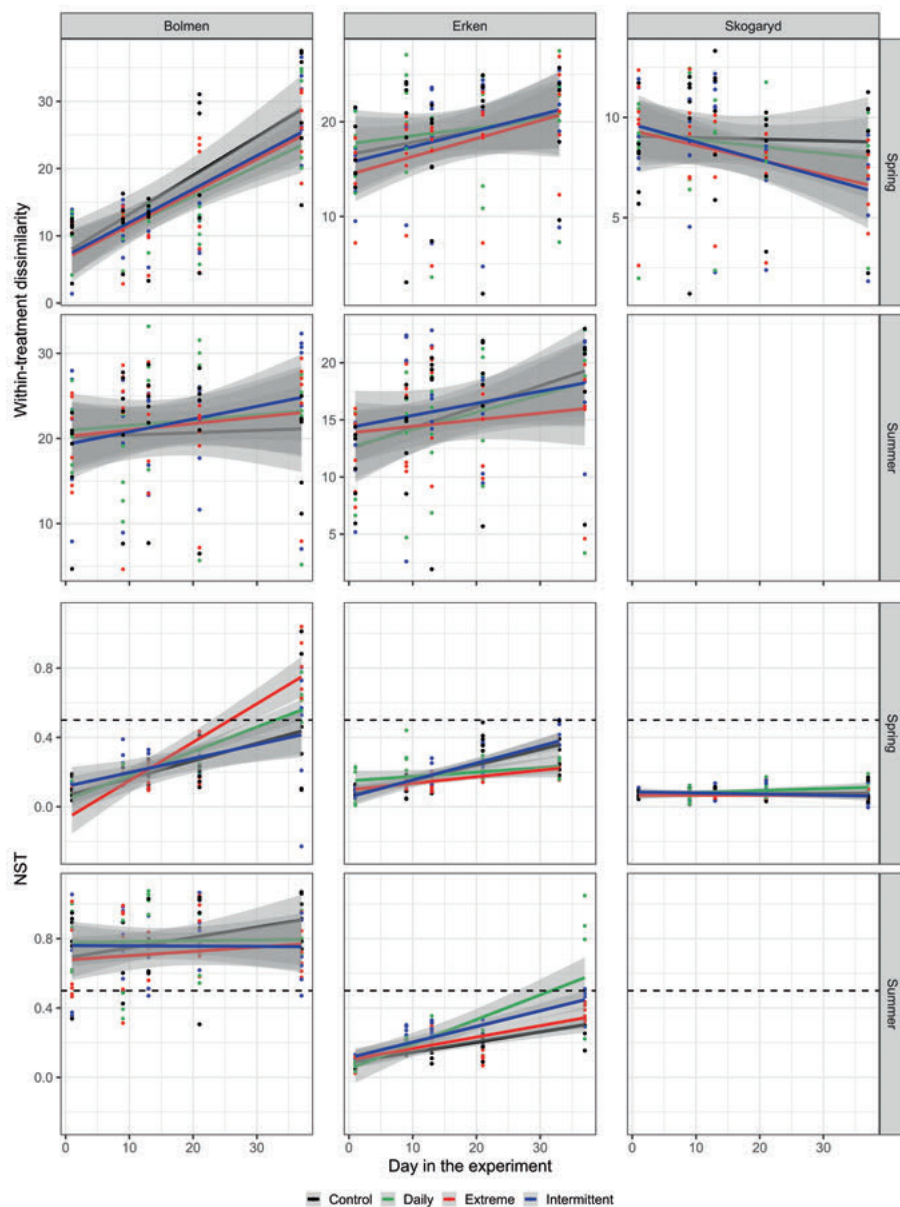


Figure 8: Temporal changes in within-treatment community dissimilarity and normalized stochasticity ratio (NST) across lakes, seasons, and treatments (**Paper I**). Points represent replicate-level pairwise distances at each sampling day, and lines with shaded bands indicate fitted trends \pm 95% CI.

Effects of repeated disturbances and disturbance history influence on bacterial community assembly

In **Paper II**, effects of repeated disturbances and disturbance history were tested on bacterial community composition and assembly. Bacterial communities with a disturbance history showed higher richness and more within-treatment dissimilarity in response to an additional major pulse. Richness in treatments without disturbance history decreased after experiencing the additional major pulse. Both within-treatment dissimilarity and NST indicated that community assembly was predominantly stochastic across treatments, particularly prior to the major pulse and in communities exposed to the major pulse (Fig. 9). The short recovery treatment showed stronger responses to disturbance, with higher increases in ASV richness and greater within-treatment dissimilarity, while the long recovery treatment exhibited more moderate changes (Fig. 9).

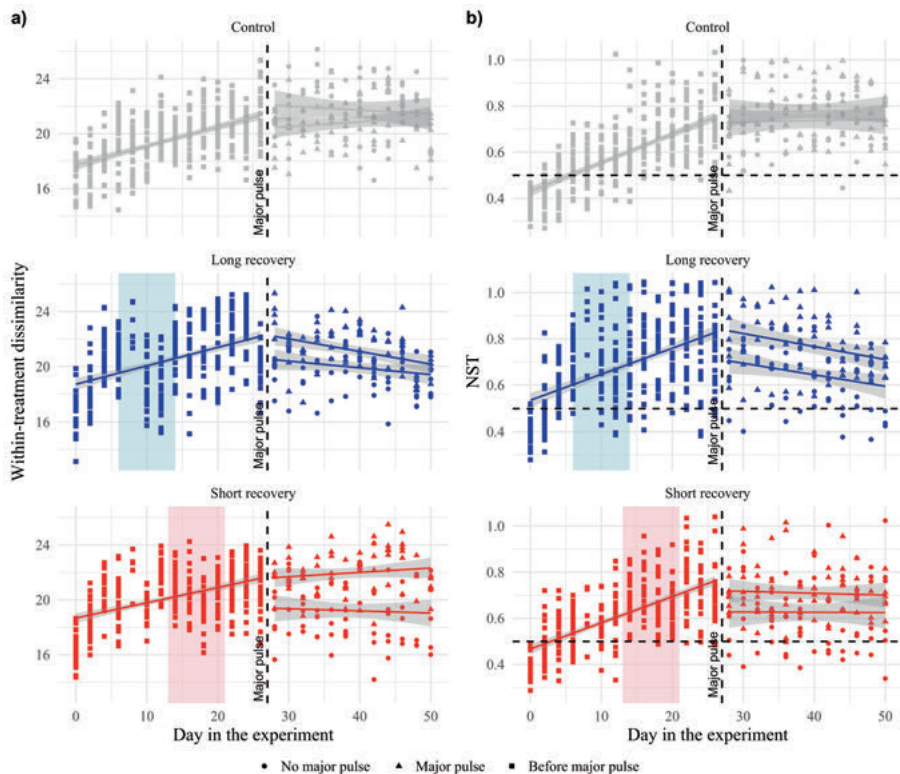


Figure 9: Temporal trends of a) within-treatment dissimilarity (measured as pairwise Aitchison distance) and b) normalized stochasticity ratio (NST) in **Paper II**. The top figures show control treatments without a recovery history, the middle figures treatment with a long recovery history and the bottom figure treatment with short recovery history. Squares indicate treatments before the major pulse on day 27, triangles treat-

ments that did and circles that did not experience the major pulse. The blue shaded area shows the timing of the minor salinity pulses for the long recovery history and red for the short recovery history. Lines with shaded bands indicate fitted trends \pm 95% CI.

Combined nutrient enrichment and community size effects on bacterial communities

Paper III studied effects of a nutrient concentration gradient and community size on assembly processes, biomass production and growth in bacterial communities. The results show that nutrient concentration and community size strongly influenced bacterial community composition, biomass production, and abundance over time. Both bacterial production and abundance increased with higher nutrient concentrations, with the strongest responses observed under intermediate and high nutrient concentrations and in large communities. Community composition diverged among treatments, with clear clustering by nutrient levels and community size, and greater variability in larger communities. Within-treatment community dissimilarity increased under intermediate and high nutrient concentrations, particularly in large communities, whereas it decreased under low nutrient concentrations (Fig. 10). NST showed deterministic assembly, especially in small communities and at the beginning of the experiment (Fig. 10). In large communities, the role of stochasticity increased among high nutrient concentration treatments over time (Fig. 10). Overall, both high nutrient concentration and larger community size promoted greater within-treatment dissimilarity and increased the importance of stochastic assembly processes over time.

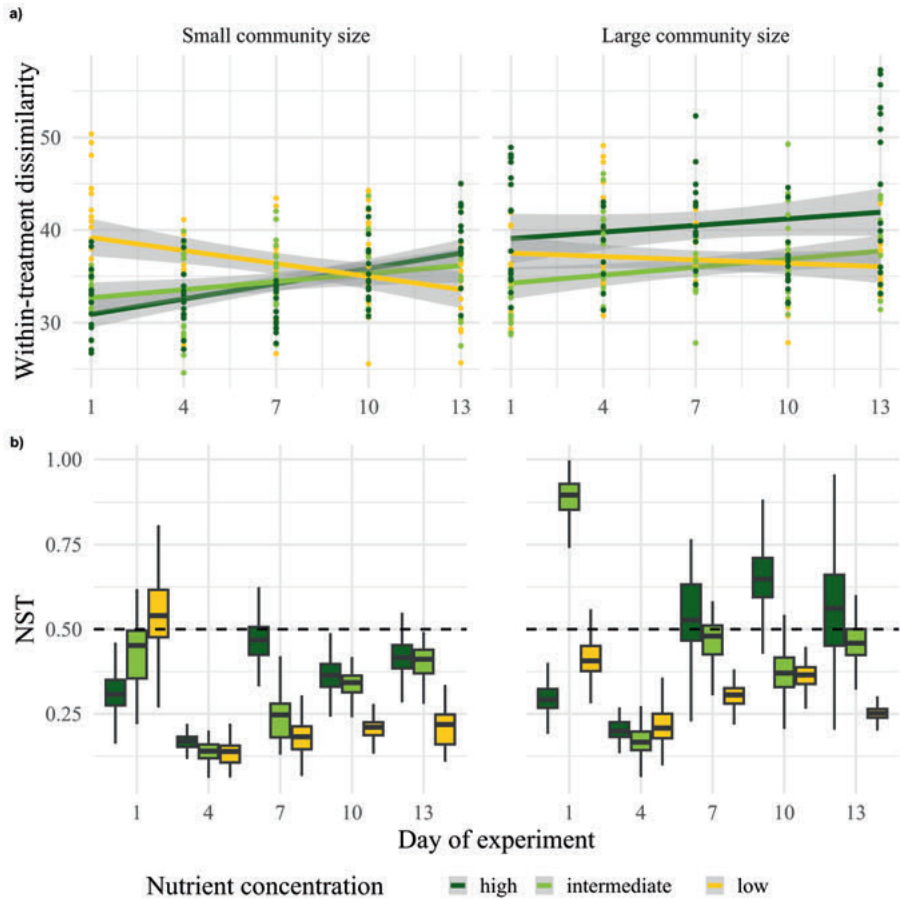


Figure 10: Trends of a) within-treatment dissimilarity (pairwise Aitchison distance; top figure) and b) NST (normalized stochasticity ratio; bottom figure) over time in **Paper III**. Treatments with different nutrient concentrations are indicated by colour (yellow = low, light green = intermediate, dark green = high) and small community size treatments are shown on the left and large community size treatment on the right side. Dots show pairwise Aitchison distances; lines represent linear regression with 95% confidence interval (grey area).

Effects of environmental pulses and grazing on community assembly in bacteria

Paper IV studied the effects of combined environmental pulses (warming and nutrient concentration) and grazing on community assembly in bacteria. Results of the paper show that bacterial growth was strongly influenced by grazing and time, with bacterial abundance increasing rapidly and reaching higher levels in the absence of grazers, while remaining lower and more variable

under grazing. Bacterial biomass production also differed between treatments, peaking earlier under grazing and later in no-grazing conditions, with higher per-cell production observed in grazing treatments. Bacterial alpha diversity responded differently depending on grazer presence, with richness and evenness declining in no-grazing treatments but increasing and remaining higher in grazing treatments. Community composition was significantly structured by grazing and time, with clear temporal trajectories but no consistent clustering by environmental pulse treatments. Within-treatment dissimilarity increased over time, particularly in the presence of grazers, indicating stronger divergence among replicate communities (Fig. 11). NST showed that community assembly differed between treatments, with higher stochasticity in no-grazing treatments and lower, more stable values under grazing (Fig. 11).

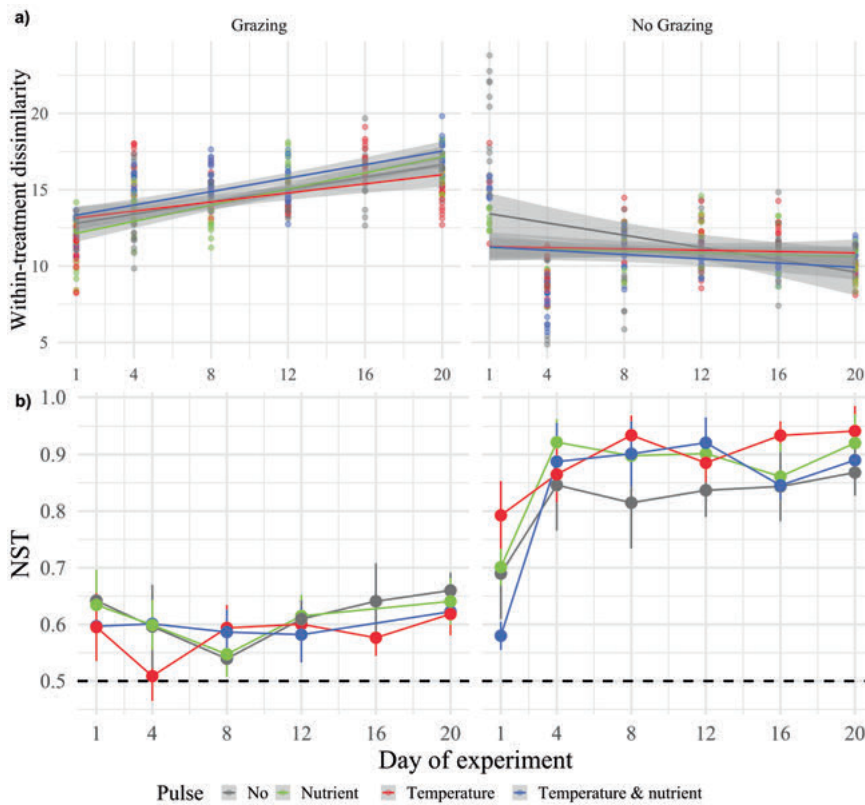


Figure 11: Within-treatment community dissimilarity a) and normalized stochasticity ratios (NST); b) in **Paper IV**. Symbol colours indicate pulse treatments (grey = no pulse, green = nutrient pulse, red = temperature pulse, blue = combined temperature and nutrient pulse). Values are means \pm SE and lines with shaded bands indicate fitted trends \pm 95% CI.

Discussion

How are runoff scenarios, that differ in their magnitude and frequency of nutrients and cDOM, affecting bacterial growth, community assembly and stability?

In **Paper I**, effects of runoff scenarios on bacterial abundance and community composition were studied and the overall responses were primarily driven by lake-specific conditions, seasonal dynamics, and temporal changes rather than by differences in runoff magnitude and frequency. However, daily and intermittent additions of cDOM and nutrients led to stronger and more persistent shifts in community composition, consistent with previous studies showing cumulative effects of perturbations (Berga et al. 2012; Urrutia-Cordero et al. 2021a). This pattern was also observed in differences of relative abundances of different Phyla, where Cyanobacteria were promoted in daily and intermittent treatments in Erken during summer. Moreover, both bacterial abundance and community composition deviated from control conditions among treatments until the end of the experiment. This could indicate nutrients and cDOM additions persistently shaped bacterial abundance and composition (Allison and Martiny 2008; Shade et al. 2012) or that the duration of the experiment was not long enough for bacteria to return to control conditions. Lake-specific characteristics further shaped bacterial community responses, with the humic system Skogaryd showing the weakest compositional changes and strong deterministic assembly, likely due to persistent environmental filtering under high DOC concentration and light limitation (Karlsson et al. 2009; Logue et al. 2016). Further, seasonal differences revealed a shift in carbon structuring variation in bacterial community composition in spring and nutrients during summer. This likely reflects seasonal differences in resource limitation: in spring, low primary production led to carbon limitation of bacteria (Cotner and Biddanda 2002), whereas in summer, primary production was nutrient-limited, making carbon supply dependent on nutrient availability and thereby indirectly shaping bacterial communities (Sommer et al. 1986).

Despite statistically significant treatment effects on community composition, assembly processes were only shaped by variables Lake, Season, and Time.

Mainly, within-treatment dissimilarity increased during the duration of the experiment, making replicate communities more dissimilar to each other over time (Vellend et al. 2014; Zhou and Ning 2017). Thus, communities became more similar to each other by deterministic assembly in the humic system, Skogaryd. This was likely driven by light limitation and high humic concentrations exerting selection pressure on bacterial communities in this lake (Stegen et al. 2012). Differences during seasons showed that stochasticity was more dominant in summer compared to spring, indicating stronger environmental filtering by, e.g., lower primary production and therefore lower quality in carbon for bacteria to utilize during the early season (Sommer et al. 1986; Kritzberg et al. 2004; Stegen et al. 2012). Overall, these findings highlight that the effects of runoff depend on both lake characteristics and seasonal dynamics that regulate bacterial community assembly and stability. This is particularly important for predicting microbial responses to increasing heavy rainfall under climate change, especially in the context of drinking water management, as elevated humic substances and the presence of toxic cyanobacteria can complicate water treatment.

How do repeated disturbances and disturbance history influence the relative importance of stochastic and deterministic processes in bacterial community assembly?

Paper II demonstrates that both disturbance history and timing of disturbance influence bacterial community responses to a subsequent, major disturbance. The results showed that bacterial communities with prior disturbance exposure showed increased richness following the additional disturbance. Whereas richness declined in communities without disturbance history, indicating that legacy effects can buffer communities against further stress, likely through prior selection for tolerant taxa (Hawkes and Keitt 2015; Jurburg et al. 2017). Dissimilarity among replicates increased over time, accompanied by higher stochasticity ratios, suggesting a growing influence of stochastic processes under dispersal limitation (Vellend et al. 2014). Contrary to expectations that disturbances strengthen deterministic assembly, communities with prior disturbance history showed weaker responses to the additional disturbance. This could indicate that disturbance history pre-filtered taxa, and that with repeated disturbance, selection played a reduced role in shaping communities, while increasing the relative importance of stochastic processes (Chase and Myers 2011; Nemergut et al. 2013). Thus, the effect of this disturbance history likely

depended on the time interval between disturbances, as effects were stronger at shorter intervals, due to limited recovery time that constrained community reassembly and maintained the influence of the prior disturbances.

How do bacterial communities assemble under combined nutrient enrichment and reduction in community size?

Effects of combined productivity and community size on bacterial assembly processes were tested in **Paper III**. The results of the paper demonstrate that nutrient availability and community size jointly regulated bacterial community assembly. Deterministic assembly dominated under low nutrient conditions, where strong resource limitation increased environmental filtering and reduced diversity, leading to more similar communities (Chase and Leibold 2002; Stegen et al. 2012). In contrast, higher nutrient availability promoted increased bacterial abundance, diversity, and biomass production, which in turn enhanced stochasticity and divergence among communities. This likely occurred because high resource availability reduced the strength of environmental filtering and competition, allowing a larger number of taxa with similar fitness to coexist, thereby increasing the influence of stochastic processes such as ecological drift and random colonization (Chase 2010; Huang et al. 2023).

Contrary to expectations, stochasticity was higher in larger communities under high nutrient conditions, contrary to theoretical predictions that smaller communities should be more strongly influenced by stochastic processes (Siqueira et al. 2020). This pattern is likely driven by stochastic variation during early population growth, where high resource availability enables multiple taxa to proliferate rapidly, increasing the chance that different taxa dominate across replicate communities (Svoboda et al. 2018; Hayashi et al. 2024). Overall, the paper showed that productivity and changes in community size can shift microbial communities towards more stochastic assembly, with important implications for predicting community dynamics and ecosystem functioning under environmental change.

Are grazing and combined nutrient and temperature pulses promoting stochasticity or determinism in bacteria?

In **Paper IV** combined effects of environmental pulses and grazing on bacterial community assembly was observed. Grazing had a strong top-down control on bacterial communities, shaping bacterial abundance, diversity, and assembly processes. While bacterial abundance remained lower under grazing, biomass production was higher, indicating compensatory growth and metabolic adaptation to predation pressure (Maloufi et al. 2016; Hu et al. 2021). Grazing further increased bacterial richness and evenness likely by reducing the dominance of fast-growing taxa and promoting the persistence of less competitive species (Winter et al. 2010; Kurm et al. 2019), whereas communities without grazers were dominated by a few abundant taxa (Burian et al. 2022), although this was not directly measured.

Grazing further altered bacterial community assembly by increasing divergence among replicate communities while at the same time strengthening deterministic processes, as indicated by lower NST values. The determinism was likely due to selective grazing that acted as an environmental filter, favouring grazing-resistant and slower-growing bacterial taxa (Salcher et al. 2015; Hu et al. 2021). While at the same time, replicate communities became more dissimilar to each other, which could have been due to small initial differences in community composition between replicates (Gralka et al. 2020). Here, patterns were primarily driven by abundant taxa, which could have been more prone to grazing (Pernthaler 2005), and rare taxa were more shaped by stochastic processes, though this was not directly measured (Jousset 2012; Pedrós-Alió 2012). In contrast, communities without grazers showed higher stochasticity, indicating a stronger role of ecological drift in the absence of top-down control. Compared to grazing, environmental pulses had relatively weak effects on community composition and assembly and were mainly observed in combination with grazing. Overall, these results highlight that biotic interactions can outweigh short-term abiotic disturbances in structuring bacterial communities and determining the balance between deterministic and stochastic assembly processes.

Conclusion & outlook

In this thesis, I aimed to investigate, which factors shape the stability (**Papers I-II**) and assembly (**Papers I-IV**) of freshwater bacterial communities under environmental change. To do this, I conducted a series of in-situ and laboratory experiments in which bacterial communities were exposed to various abiotic and biotic manipulations mimicking environmental change. I assessed patterns of bacterial community stability and assembly using multiple analytical approaches based on bacterial growth, biomass production, and community composition. Overall, I found that repeated nutrient and cDOM inputs led to greater changes in bacterial responses than single events (**Paper I**). Bacterial responses depended on season, and lake properties, indicating the importance to study global change effects on microbial communities within seasonal and spatial context. Further, disturbance history increased community resilience and shifted assembly towards stochasticity, especially when disturbances occurred close in time (**Paper II**). This indicates, that repeated disturbance can shift communities in a more unpredictable matter, when time between events is short. Moreover, higher nutrient availability and larger community size promoted stochastic assembly, whereas low nutrients led to stronger determinism (**Paper III**). Contrary to our expectations, larger communities showed higher stochastic assembly compared to smaller ones, which was likely due to initial random growth between communities. Lastly, grazing exerted strong top-down control, promoting deterministic assembly despite increased community divergence, while abiotic pulses had comparatively weak effects (**Paper IV**), indicating the importance of biotic factors when studying assembly processes.

In more detail, **Paper I**, in which runoff scenarios were tested on bacterial stability and assembly, showed that more frequent and low-intensity cDOM and nutrient inputs can lead to larger changes in both growth and community composition. Compared to one-time high-intensity inputs which showed smaller effects. Furthermore, bacterial growth and community composition differed between seasons and lakes, and variation in community composition was primarily driven by carbon-related factors during spring and nutrients during summer. Additionally, bacterial community

composition in the humic lake was less impacted by the inputs and assembly was highly deterministic. In contrast, stochastic assembly was more pronounced during summer than spring.

Further, **Paper II** showed that disturbance history mattered in bacterial communities when exposed to further disturbances. Communities with disturbance history showed higher diversity and within-treatment dissimilarity. Thus, the strength of this effect depended on the time between disturbances, with shorter intervals leading to stronger effects. Stochastic processes dominated more in communities with than in those without a disturbance history.

In **Paper III**, I examined interactive effects of nutrient levels and community size on bacterial community assembly. The results supported nutrient enrichment increasing stochasticity in bacterial communities, likely due to increased growth and reduced competition. Contrary to expectations, stochasticity was more important in the assembly of large compared to small communities, which might have been due to stochastic initial growth.

Grazing further shaped assembly processes and outweighed abiotic effects as shown in **Paper IV**. Here, grazing increased bacterial diversity, dissimilarity between replicate communities and promoted deterministic assembly, especially among abundant taxa. Replicate communities becoming more dissimilar under determinism was likely due to small initial differences in their community composition. In contrast, in the absence of grazers, stochastic processes played a greater role, primarily in rare taxa. Despite grazing reducing bacterial abundance, biomass production was less impacted, indicating metabolic adaptation to top-down control. Effects of environmental pulses of nutrients and temperature were neglectable compared to grazing effects on bacterial assembly.

When interpreting the findings of the papers of this thesis, it is important to acknowledge potential methodological limitations. In general, all laboratory experiments (**Papers II-IV**) were conducted in enclosed systems that excluded dispersal, which can be an important ecological process in the balance between deterministic and stochastic assembly (Evans et al. 2017; Le Moigne et al. 2023). As a result, the relative importance of stochasticity observed in these experiments may be overestimated compared to natural, open systems where dispersal can buffer community divergence (Zhou and Ning 2017). Moreover, **Papers I-IV** did not directly assess ecosystem functioning, so that conclusions were limited to patterns in biomass production and growth, which may not fully capture functional responses. Although grazing was identified

as an important driver of bacterial community assembly (**Paper IV**; see also Pernthaler 2005 & Lumpi et al. 2023), **Papers II and III** focused on bacteria in isolation, potentially overlooking how trophic interactions could modify assembly processes in more complex communities. Finally, in **Paper IV** only bacterial community composition was analysed, and the lack of data on grazer community dynamics limited the ability to fully resolve the mechanisms underlying observed top-down effects. Together, these limitations highlight the need for future studies that incorporate dispersal, trophic complexity, and functional measurements, like respiration or decomposition rates, to better understand bacterial community responses in natural ecosystems.

All in all, this thesis shows that bacterial community stability and especially assembly can be shaped by a complex interplay of environmental conditions, disturbance regimes, and biotic interactions, with outcomes varying across systems and contexts. These context-dependent responses highlight that no single mechanism can universally explain bacterial community dynamics, emphasizing the need for more controlled experimental studies to disentangle the relative roles of stochastic and deterministic processes. Improving our understanding of community assembly is particularly important in the face of ongoing climate and environmental change, as freshwater microbial communities underpin key ecosystem functions such as nutrient cycling, carbon processing, and water quality. Strengthening this knowledge will be essential for predicting and managing ecosystem responses in a rapidly changing world.

Populärvetenskaplig Sammanfattning

Klimatförändringar kan leda till högre temperaturer och mer nederbörd, vilket kan påverka sjöar och deras ekosystem. Små organismer som lever i sjöar, plankton, är särskilt viktiga eftersom de utgör grunden i näringsväven. Vissa plankton använder solljus för att producera organiskt material genom en process som kallas fotosyntes, precis som växter på land. Dessa organismer fungerar som föda för större plankton, så kallade djurplankton, som i sin tur äts av fisk. På så vis förs energi vidare genom hela ekosystemet. Mer nederbörd kan påverka sjöar genom att föra med sig näringsämnen från omgivande mark, särskilt från jordbruk där gödsel används. Detta kan leda till att vissa organismer växer snabbare än andra och stör balansen i ekosystemet. Regn kan även föra med sig järn och organiskt material som gör vattnet brunare, ett fenomen som ibland kallas "förbruning".

Bakterier spelar viktiga roller i sjöekosystem. De bryter ner organiskt material och återför näringsämnen, som fosfor och kväve, till vattnet. Dessa näringsämnen fungerar som byggstenar som andra organismer behöver för att växa. Bakteriesamhällen är mycket mångfaldiga, och vi känner fortfarande inte till alla arter eller hur de fungerar i olika miljöer. Vi vet att faktorer som temperatur och näringsämnen påverkar deras tillväxt, men många processer är fortfarande inte klarlagda. Detta gör det svårt att förutsäga exakt hur bakteriesamhällen skulle kunna reagera, till exempel, på klimatförändringar. För att bättre förstå detta undersökte jag i denna avhandling, genom flera experiment, hur bakterier påverkas av olika miljöfaktorer. Bakteriesamhällen i sjöar formas av både miljön och slumpen. Ibland styrs vilka bakterier som finns av förutsägbara faktorer som näring, temperatur eller ljus. Ofta spelar också slumpen en stor roll, till exempel på grund av vilka bakterier som råkar finnas på en viss plats vid en viss tidpunkt. Till exempel, när miljön är rik på resurser kan många olika bakterier växa samtidigt, och då blir det mer slumpmässigt vilka arter som kommer att dominera. Därför kan två till synes identiska miljöer ändå innehålla olika bakteriesamhällen.

I artikel I genomfördes flera experiment i tre olika sjöar, både under vår och sommar. I experimenten undersökte jag effekten av intensiteten och

magnituden av avrinning (runoff), alltså när nederbörd sköljer ner näringsämnen och brunt organiskt material från land till sjöar. I experimentet varierade jag hur mycket och hur ofta dessa ämnen tillfördes, för att efterlikna olika scenarier av regn och avrinning. Stora behållare (så kallade mesokosmer), som placerades direkt i sjöar och fylldes med sjövattnet, användes för experimenten. Resultaten visade att mer frekvent och lågintensiv avrinning kan leda till större förändringar i både tillväxt och samhällssammansättning jämfört med enstaka högintensiv avrinning. Dessutom påverkades bakteriesamhällen i brunfärgade sjöar mindre av avrinning än i andra sjöar. Slumpmässigt bakteriell sammansättning var större under sommarn än under våren, när det finns mindre organiskt material för bakterier.

I artikel II undersökte jag hur bakteriesamhällen reagerar på upprepade störningar i form av förändrad salthalt. Jag ville ta reda på om tidigare störningar påverkar hur bakterier klarar en ny, större störning. Därför utsatte jag bakteriesamhällena för flera mindre saltstörningar och lät dem sedan återhämta sig under olika lång tid, innan jag gav en sista, kraftigare saltstörning. På så sätt kunde jag jämföra hur bakterier reagerar beroende på hur lång tid de haft för återhämtning. Resultatet visade att bakterier kan anpassa sig till störningar, till exempel förändringar i salthalt. Om samma störning inträffar igen påverkas bakterierna mindre än första gången och slumpmässigt bakteriell sammansättning större, men effekten var större när tiden mellan störningarna var kortare.

I artikel III undersökte jag hur tillgången på näring och storleken på bakteriesamhället påverkar hur samhällen förändras över tid. Jag varierade mängden näring som tillsattes och hur stora bakteriesamhällena var i början av experimentet. På så sätt kunde jag ta reda på om bakterier betar sig mer förutsägbart eller mer slumpmässigt under olika förhållanden. Målet var att förstå hur resurser och samhällsstorlek tillsammans påverkar hur bakteriesamhällen byggs upp och förändras. Resultaten visade att mängden näring och storleken på bakteriesamhället påverkar hur förutsägbart samhället utvecklas. Vid låga näringsnivåer i mindre samhällen fanns färre bakterier och färre arter, vilket ledde till mer lika samhällen och mer förutsägbara resultat. Vid högre näringsnivåer i större samhällen fanns fler bakterier och större mångfald, vilket gjorde att utvecklingen blev mindre förutsägbar och mer beroende av slumpen.

Slutligen undersökte jag i artikel IV hur bakterier påverkas av predation från så kallade nanoflagellater. Jag jämförde bakteriesamhällen med och utan predation och utsatte dem även för kortvariga störningar i form av förändringar i temperatur och näring. Målet var att förstå hur samspelet mellan biologiska

faktorer (som predation) och miljöförändringar påverkar hur bakteriesamhällen utvecklas och förändras över tid. Resultaten visade att bakterier påverkas starkt av predation men i mindre utsträckning av förändringar i näring och temperatur. Predation gjorde att bakteriesamhällena blev mindre förutsägbara, eftersom olika arter kunde påverkas olika mycket. Detta tyder på att predatorer spelar en viktig roll i att styra vilka bakterier som finns i en sjö och hur de reagerar på förändringarna i miljön.

Sammanfattningsvis visar detta arbete att bakteriesamhällen i sjöar påverkas av både miljöfaktorer och biologiska interaktioner. Faktorer som temperatur, näringsämnen och predation kan förändra hur bakterier växer och vilka arter som dominerar. Samtidigt spelar även slumpmässiga processer en viktig roll, särskilt under högre näringshalter och i närvaro av predatorer. På grund av klimatförändringar kan sjöar bli varmare och innehålla mer näringsämnen i framtiden. Detta kan leda till att bakteriesamhällen blir oförutsägbara och kan påverka både vattenkvaliteten och ekosystemens funktion. Att bättre förstå dessa processer är därför viktigt för att kunna skydda och förvalta våra sjöar i framtiden.

Popular summary

Climate change is expected to increase temperature and rainfall, which can strongly affect lake ecosystems. In lakes, organisms called plankton form the foundation of the food web and are essential for ecosystem functioning. Phytoplankton are small, plant-like organisms that use sunlight to produce oxygen, much like plants on land. They are fed on by zooplankton, slightly larger organisms, which are in turn consumed by fish, transferring energy through the food web. Even smaller organisms, such as bacteria, play a crucial role in lake ecosystems by breaking down and recycling nutrients and by that supporting the growth of other organisms. Increased rainfall can flush nutrients and organic material from the surrounding land into lakes. This can in turn promote cyanobacteria growth, which can produce toxins and affect the whole ecosystem. Moreover, organic material can turn the water colour darker, a process called “brownification”, which can reduce the sunlight needed by phytoplankton.

Bacteria are very diverse, and we still do not know all species or how they behave in different environments. This makes it hard to predict how they will respond to environmental changes by, e.g., climate change. To better understand these processes, this thesis focused on the influence of different environmental changes on bacteria. Bacterial communities are shaped over time and space by different processes called community assembly. These processes can be driven by environmental factors, such as nutrients or temperature, but also by random events, known as stochasticity. Stochasticity means that communities can have different individuals of a species to die or reproduce by chance. Especially under resource rich conditions, where many bacteria can grow at the same time, these random processes can become more important. This means that even in similar environments, bacterial communities can develop in different ways, making them harder to predict.

In paper I, I wanted to understand how different intensities and magnitudes of runoff, meaning the rainwater flushing nutrients and organic material into lakes, influence bacteria. For that I conducted experiments in large containers placed in lakes, so-called mesocosms, filled with natural lake water. In the experiment different runoff scenarios were simulated by adding nutrients and organic matter in varying amounts and frequencies. The results showed that smaller but more frequent additions had stronger effects on bacterial growth

and community composition than a large one-time addition, additionally promoting the abundance of cyanobacteria. Moreover, the most humic lake in the experiment showed the lowest effects of runoff in community composition, indicating adaptation of bacteria to low light conditions and high humic concentrations in this system. Runoff did not show any effects on assembly processes, but stochasticity was higher during summer compared to spring. This could have been due to less organic material being available for bacteria during spring compared to summer, leading to more predictable outcomes of bacterial assembly.

In Paper II, I explored whether bacteria have a “disturbance memory”. I wanted to know how bacterial communities are affected by a disturbance if they have previously experienced disturbances of the same kind. For that, an experiment was done with bacterial communities that were repeatedly exposed to increased salt levels and then after each a long and a short recovery time exposed to another salt pulse, while other communities had no prior salt exposure. This allowed me to compare how previous disturbance exposure affected their response to an additional disturbance. I found that bacteria can become less sensitive to disturbances if they have experienced them before, and additionally their assembly becomes more stochastic. This effect depended on how much time was between the disturbances, as this “memory” faded over time. This shows, that bacterial communities can become more resistant to disturbances, but that this effect depended on the time between disturbance events.

Paper III examined how nutrient availability and community size influence how bacterial communities assemble over time. The goal was to study if bacterial communities become more influenced by stochastic or deterministic assembly under different nutrient concentrations and different initial community sizes. For that, I carried out an experiment with bacterial cultures and manipulated both the nutrient concentration and the initial size of the bacterial community. I found that the smaller communities that were exposed to low nutrients behaved more deterministic, therefore more predictable. While larger communities in nutrient rich conditions were more influenced by random processes and were less predictable.

Finally, in paper IV, I studied how bacterial communities behave under the combined effects of predation, here grazing and environmental changes. I wanted to know if grazing and environmental changes, in temperature and nutrient availability, drive assembly processes in bacteria to more determinism or stochasticity. For that I conducted an experiment with cultures of bacterial communities without and with predators, known as heterotrophic nanoflagellates, and short pulses in increased temperature and nutrients. The results showed that grazing had a stronger effect on bacterial communities

than the short-term changes in temperature and nutrients. Bacteria were more diverse and more predictable when exposed to grazers. While the bacterial communities without grazers behaved more stochastic. This shows the great importance of biological factors, like predation, when studying community assembly in bacteria.

Overall, this work shows that bacterial communities in lakes are influenced by both environmental changes and biological interactions. Factors like predation, smaller community size and low nutrient concentration showed stronger deterministic processes in bacterial communities. Contrary, higher nutrient concentrations, larger communities, and the absence of grazers led to more stochasticity. Additionally, the response of bacterial communities to disturbances depended on time between disturbance events, on environmental conditions and seasonality. The study shows that predictability of bacterial communities is driven by a complex combination of factors and that both biological and environmental conditions play a role. As climate change continues, lakes are likely to experience warmer temperatures and more nutrient inputs, which can make it harder to predict how bacterial communities behave. Understanding these processes is important, as bacteria affect water quality and the functioning of lake ecosystems.

Populärwissenschaftliche Zusammenfassung

Der Klimawandel kann das Auftreten von Extremwetterereignissen wie Hitzewellen und Starkregen erhöhen und dabei Lebensräume wie beispielsweise Seen stark beeinflussen. Seen bilden wichtige Lebensräume, auch genannt Ökosysteme, die wir zum Beispiel zur Trinkwassergewinnung oder für Freizeitaktivitäten nutzen. Erhöhte Wassertemperaturen können jedoch diese Ökosysteme beeinflussen und das Wachstum von giftigen Blaualgen, auch Cyanobakterien genannt, begünstigen und dadurch die Aufbereitung für Trinkwasser stark erschweren. Zudem können Nährstoffe wie Phosphor und Stickstoff bei Starkregen aus umliegenden, landwirtschaftlich genutzten Flächen in Seen eingetragen werden, und zusätzlich das Ökosystem beeinflussen. In borealen Seen, wie beispielsweise in Schweden, kann Starkregen huminhaltiges, organisches Material in Seen eintragen. Dieses Material setzt sich aus Stoffen zusammen, die beim Abbau von Pflanzenresten entstehen, chemisch sehr komplex und für viele Bakterien nur schwer abbaubar sind. Gleichzeitig geben sie dem Wasser eine dunkelbraune Färbung, sodass weniger Sonnenlicht in tiefere Wasserschichten eindringen kann. Dadurch werden lichtabhängige Prozesse wie die Photosynthese von Algen eingeschränkt, während bakterielle Abbauprozesse an Bedeutung gewinnen. In der Folge kann der Sauerstoffgehalt sinken und es kommt zu Veränderungen in den Stoffkreisläufen und der Zusammensetzung der Lebensgemeinschaft.

Bakterien sind wichtige Organismen in Seen, da sie Nährstoffe abbauen und somit für andere Organismen verfügbar machen. Sie weisen eine sehr hohe Artenvielfalt auf, von der bislang nur ein kleiner Teil erfasst ist. Während bekannt ist, dass Umweltfaktoren wie Temperatur und Nährstoffverfügbarkeit die Zusammensetzung bakterieller Gemeinschaften beeinflussen, sind viele der zugrundeliegenden Prozesse noch unzureichend erforscht. Dies erschwert Vorhersagen darüber, wie bakterielle Gemeinschaften auf Umweltveränderungen reagieren. Die Struktur und Dynamik bakterieller Gemeinschaften werden durch das Zusammenwirken verschiedener Prozesse bestimmt. Dazu zählen sowohl deterministische als auch stochastische Prozesse. Deterministische Prozesse führen zu besser vorhersagbaren Mustern in der Zusammensetzung bakterieller Gemeinschaften, da sie durch messbare Umweltfaktoren gesteuert werden. Im Gegensatz dazu umfassen stochastische Prozesse zufällige Ereignisse, etwa die Vermehrung oder das Aussterben einzelner

Individuen einer Art und führen zu einer geringeren Vorhersagbarkeit. Da stochastische Prozesse nicht direkt aus Umweltbedingungen ableitbar sind, können sich bakterielle Gemeinschaften selbst unter gleichen Bedingungen unterschiedlich entwickeln. Dies stellt eine zentrale Herausforderung für das Verständnis und die Vorhersage von Veränderungen in bakteriellen Gemeinschaften dar.

In dieser Arbeit wurden verschiedene Umwelteinflüsse auf Bakterien vor allem im Hinblick auf stochastische Prozesse mithilfe von Experimenten untersucht: In Fachartikel I wurde analysiert, wie unterschiedliche Niederschlagsereignisse, mit ihrem Eintrag von Nährstoffen und huminhaltigem, organischen Material bakterielle Gemeinschaften in Seen beeinflussen. Dabei lag der Fokus auf dem Vergleich verschiedener Niederschlagsszenarien mit unterschiedlicher Intensität und Häufigkeit. Es wurden Experimente in drei schwedischen Seen jeweils im Frühling und Sommer durchgeführt. Behälter, sogenannte Mesokosmen, wurden in Seen platziert und mit Seewasser gefüllt. Anschließend, wurden Nährstoffe und huminhaltiges, organisches Material in unterschiedlichen Mengen und zu unterschiedlichen Zeitpunkten den Mesokosmen zugefügt um verschiedene Niederschlagsszenarien zu simulieren. Die Ergebnisse zeigten, dass kleine, regelmäßig auftretende Niederschlagsereignisse stärkere Auswirkungen auf das Wachstum und die Veränderung der Bakteriengemeinschaften hatten als ein einmaliges, intensives Niederschlagsereignis. Unter diesen Bedingungen konnte auch eine erhöhte Anzahl an Cyanobakterien festgestellt werden. In dem See mit der höchsten Konzentration an Huminstoffen waren die Effekte auf die Gemeinschaften am geringsten. Dies könnte auf eine Anpassung der dortigen Bakteriengemeinschaft an die Wasserfärbung hindeuten. Zudem wurde die Zusammensetzung der bakteriellen Gemeinschaften im Sommer vor allem durch Nährstoffe beeinflusst, während im Frühling der Einfluss des organischen Materials stärker war. Zusammenfassend zeigen die Ergebnisse, dass Niederschlagsszenarien unterschiedliche Auswirkungen auf bakterielle Gemeinschaften haben können und stark von Umweltbedingungen sowie Jahreszeiten abhängen.

Fachartikel II untersuchte die Anpassungsfähigkeit von Bakteriengemeinschaften in Bezug auf wiederholte Störungen mit dem Ziel eine mögliche Widerstandsfähigkeit zu erforschen. Ziel war hierbei zu verstehen, ob Bakteriengemeinschaften sich durch vorangegangene Störungen anpassen und somit weniger stark von einer weiteren Störung beeinflusst werden. Hierfür wurden Bakteriengemeinschaften in einem Experiment wiederholt höherem Salzgehalt ausgesetzt und erhielten anschließend nach unterschiedlich langen Erholungsphasen eine stärkere, einmalige Salzstörung. Dabei lassen die Ergebnisse darauf deuten, dass sich zunehmend Arten durchgesetzt haben, die an die veränderten Bedingungen angepasst waren, während weniger angepasste Arten verdrängt wurden. Infolgedessen fiel der Effekt einer erneuten Störung geringer aus, wenn

die Gemeinschaft zuvor bereits ähnlichen Störungen ausgesetzt wurde. Dieser Effekt hing jedoch von der Dauer der Erholungsphase ab, da die Widerstandsfähigkeit an frühere Störungen mit der Zeit abnehmen kann. Insgesamt weisen die Ergebnisse darauf hin, dass bakterielle Gemeinschaften durch wiederholte Störungen eine erhöhte Widerstandsfähigkeit gegenüber weiteren Störungen entwickeln können, diese jedoch zeitlich begrenzt ist.

In Fachartikel III wurde der Einfluss von Nährstoffverfügbarkeit und Größe der Bakteriengemeinschaften auf deren Entwicklung und Zusammensetzung untersucht. Ziel war es zu verstehen, unter welchen Bedingungen die Zusammensetzung bakterieller Gemeinschaften eher deterministisch oder stärker durch stochastische Prozesse bestimmt wird. Dazu wurden sowohl die Nährstoffkonzentrationen als auch die Ausgangsgröße der Bakteriengemeinschaften experimentell manipuliert. Die Ergebnisse zeigten, dass unter niedrigeren Nährstoffkonzentrationen in kleineren Gemeinschaften die Diversität der Bakterien geringer war und die Prozesse eher deterministisch geprägt waren. Bei höheren Nährstoffmengen in größeren Gemeinschaften gab es dagegen eine höhere Artenvielfalt. Außerdem war hier die Zusammensetzung der Gemeinschaften primär von zufälligen Prozessen beeinflusst und ließ sich schlechter vorausbestimmen. Insgesamt zeigen die Ergebnisse, dass die Bedeutung deterministischer und stochastischer Prozesse von den Umweltbedingungen und der Größe der Gemeinschaft abhängen kann.

Schließlich wurde in Paper IV erforscht, wie bakterielle Gemeinschaften durch biologische Faktoren und Umweltveränderungen beeinflusst werden. Biologische Faktoren wurden durch Fressfeinde, sogenannte Prädatoren repräsentiert. Um Umweltveränderungen darzustellen wurden die Gemeinschaften kurzzeitigen Erhöhungen von Temperatur und Nährstoffen ausgesetzt. Ziel war es zu verstehen, wie stark biologische Faktoren wie Prädation im Vergleich zu Umwelteinflüssen auf deterministische und stochastische Prozesse in Bakteriengemeinschaften wirken. Dazu wurden Bakteriengemeinschaften entweder mit oder ohne Prädation von sogenannte Nanoflagellaten kultiviert und zusätzlich kurzfristigen Veränderungen in Temperatur und Nährstoffverfügbarkeit ausgesetzt. Es zeigte sich, dass Bakterien stärker durch Prädation als durch die Veränderungen in Umwelteinflüssen geprägt wurden. Zudem zeigte sich, dass die Zusammensetzung bakterieller Gemeinschaften unter Prädation stärker deterministisch und besser vorhersagbar war. Dies deutet darauf hin, dass Fressfeinde einen signifikanten Einfluss auf die Entwicklung und Vorhersehbarkeit der Bakteriengemeinschaften haben.

Insgesamt zeigt diese Arbeit, dass stochastische Prozesse von Bakteriengemeinschaften in Seen sowohl durch Umweltveränderungen als auch durch biologische Wechselwirkungen beeinflusst werden. Prädation und niedrige Nährstoffkonzentrationen haben deterministische Prozesse verstärkt und ihre

Vorhersehbarkeit erhöht. Während die Bedeutung stochastischer Prozesse unter höherer Nährstoffverfügbarkeit, in größeren Gemeinschaften und in der Abwesenheit von Prädatoren höher war. Gleichzeitig zeigte sich, dass Anpassungseffekte der Gemeinschaften auf Störungen zeitlich begrenzt waren und stark vom jeweiligen Umweltkontext abhingen. Diese Ergebnisse verdeutlichen, dass Vorhersagen über bakterielle Gemeinschaften nur unter Berücksichtigung mehrerer gleichzeitig wirkender Faktoren möglich sind und dabei biologische Faktoren sowie Umwelteinflüsse eine wichtige Rolle spielen. Mit fortschreitendem Klimawandel werden Seen wahrscheinlich wärmer und stärker mit Nährstoffen belastet, was zu einer schlechteren Prognose von Bakteriengemeinschaften führen kann. Ein besseres Verständnis dieser Prozesse ist wichtig, da Bakterien die Wasserqualität und die Funktion von Seeökosystemen maßgeblich beeinflussen.

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