Bound to the past: Historical contingency in aquatic microbial metacommunities

MÁTÉ VASS
Abstract


The composition of ecological communities differs due to a combination of different processes, which includes selection by local environmental conditions, dispersal from the regional species pool and random events. Additionally, historical processes such as past dispersal events may leave their imprint on communities as well, resulting in historically contingent communities. However, in most ecological studies the existence and the effect of historical processes remained hidden, even though they could be important predictors of contemporary variations in ecological communities.

This thesis focuses on how historical processes could influence aquatic microbial metacommunities by investigating when and where history matters, and which factors may regulate historical contingency.

Using null model approaches, evidence for historical contingency was found in natural ecosystems, more specifically rock pool metacommunities, and appeared to be more likely to influence bacterial than microeukaryotic communities.

The thesis further used an outdoor mesocosm experiment to test how ecosystem-sized induced differences in environmental fluctuations influenced community assembly processes along a disturbance gradient. This study did, however, not provide strong and clear evidence for the importance of historical contingency.

In the face of climate change, results from a laboratory experiment showed that historical contingencies might be strengthened with warming. Specifically, warming increased the resistance of local communities against invasion by decreasing the establishment success of migrant species. Hence, temperature-dependent historical contingency was found in aquatic bacterial communities, although its persistence differed between local communities and the degree of invasion they were exposed to.

Taken together, this thesis suggests that historical processes can leave their imprint on aquatic microbial communities, even though their importance is highly context dependent. Future studies, should therefore consider historical contingency, or in other words, the legacy of the past as a potentially important mechanism that can contribute to the spatial diversity of microbial communities.

Keywords: metacommunity, historical processes, priority effects, community assembly.

Máté Vass, Department of Ecology and Genetics, Limnology, Norbyvägen 18 D, Uppsala University, SE-75236 Uppsala, Sweden.

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ISSN 1651-6214
ISBN 978-91-513-0834-0
urn:nbn:se:uu:diva-397174 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-397174)
„Chance doesn’t mean meaningless randomness, but historical contingency. This happens rather than that, and that’s the way that novelty, new things, come about.”

John Polkinghorne

To the memories of my grandmothers
List of Papers

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


Reprints were made with permission from the respective publishers.
In addition to the papers included in this thesis, the author has contributed to the following papers:

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## Abbreviations

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<tr>
<td>16S rRNA</td>
<td>16S Ribosomal Ribonucleic Acid</td>
</tr>
<tr>
<td>βMNTD</td>
<td>β-Mean-Nearest Taxon Distance</td>
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<tr>
<td>βNTI</td>
<td>β-Nearest Taxon Index</td>
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<tr>
<td>βRC</td>
<td>Incidence-based Raup-Crick dissimilarity indices</td>
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<td>βRCbray</td>
<td>Abundance-based Raup-Crick dissimilarity indices</td>
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<td>ASV</td>
<td>Amplicon Sequence Variant</td>
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<td>DESeq2</td>
<td>Differential Abundance Analysis</td>
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<td>EMS</td>
<td>Elements of Metacommunity Structure</td>
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<tr>
<td>OTU</td>
<td>Operational Taxonomic Unit</td>
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<tr>
<td>PCR</td>
<td>Polymerase Chain Reaction</td>
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<td>PERMANOVA</td>
<td>Permutational Multivariate Analysis of Variance</td>
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<td>QPE</td>
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<td>SD</td>
<td>Standard Deviation</td>
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Ecological communities and assembly processes

One primary aim in community ecology is to investigate the structure and function of ecological communities inhabiting different ecosystems at different scales of space and time. The processes (e.g. assembly processes) that shape compositional patterns and their dynamics represent the cornerstones of modern community ecology (Cottenie 2005).

In previous decades, ecologists focused mostly on local processes within a community, driven by local factors such as abiotic factors and biotic interactions (e.g. competition between species) (Leibold et al. 2004). However, the dynamics within and the variation among local communities cannot be entirely explained by local factors (i.e. Connor & Simberloff 1979). Consequently, more recently, it has been established that also regional factors linked to dispersal and certain drift processes, play significant roles (Hanson et al. 2012). The recognition that processes at different spatial scales influence community assembly has shifted the whole field away from the primarily local perspective and led to the development of integrative conceptual frameworks (Leibold et al. 2004; Holyoak et al. 2005; Vellend 2010). These frameworks integrate the assembly of local communities into their regional context and encourage scientists to take a deeper look at why species vary across spatial and temporal scales, and how community assembly dynamics influence biodiversity and ecosystem functioning (Leibold & Chase 2017).

The concept from Vellend (2010) assumes that spatial differences in community structures (= beta-diversity) can be attributed to a combination of different processes. For example, beta-diversity can be the consequence of processes that involve selection induced by the environment (causing species sorting), dispersal, random (drift) events and speciation. Although speciation, inducing genetic variation, can be a key component in driving community dynamics, it is beyond the scope of this thesis. Selection means that patches with similar environmental conditions have similarly composed communities, which is termed homogeneous selection. In contrast, spatial variation in the environment can put distinct selective pressures on local communities (variable selection), causing dissimilar community structures in space (Chesson 2000). Dispersal between patches or, in general, from the regional species pool (Holyoak et al. 2005) can diminish compositional differences among communities if it high enough to homogenize communities (mass effect). On the other
hand, dispersal can also be limited, for example, when there are physical barriers, resulting in dissimilarly composed communities (dispersal limitation) (Leibold et al. 2004). Lastly, ecological drift can further influence community assembly via random species loss and immigration (Hubbell 2001). The challenge is to link beta-diversity to different community assembly processes and to connect them to the factors that regulate them both in space and time.

Community assembly of microorganisms

Community assembly processes in microorganisms (microbes) have been studied using the above-mentioned theoretical concepts (Lindström & Langenheder 2012; Nemergut et al. 2013). Microorganisms play fundamental roles in ecosystems so that knowledge about microbial community assembly is essential to understand ecosystem functioning (Martiny et al. 2006). Moreover, targeting microorganisms in ecological studies allows us to capture temporal dynamics of assembly processes much better compared to in larger organisms due to their shorter generation times.

Numerous studies have shown that geographic distribution patterns of microorganisms are influenced by either local or regional processes, or a combination of both (Martiny et al. 2006; Hanson et al. 2012). However, the importance of regional processes related to dispersal might have been underestimated in previous studies due to the difficulties to measure dispersal and infer its importance from statistical analyses (Lindström & Langenheder 2012). Growing evidence also supports that often more than one assembly process plays a role in shaping ecological communities (Dumbrell et al. 2010; Östman et al. 2010; Langenheder & Székely 2011). Furthermore, within one community, different groups of microbes with different traits can be assembled by different mechanisms (Martiny et al. 2013). Hence, the importance of local and regional processes should be evaluated separately for organisms with different traits (Lindström & Langenheder 2012). Taken together, microbes provide an opportunity to deconstruct the complexity of natural communities into its components and to explore the role of each component forming patterns of biodiversity in nature (Jessup et al. 2004).

Does history matter?

As mentioned above, the composition of communities differs due to a combination of different processes, which include selection by local environmental conditions, dispersal from the regional species pool and random events. In
addition, historical events, such as past environmental conditions and past dispersal events, may leave their imprint on communities as well. These effects can cause historical contingency that may have a long-lasting effect on the structure and function of communities (Fukami 2015). Thus, species composition and coexistence patterns in present-day communities may to a great extent reflect selection by past environmental conditions or past dispersal events (i.e. the immigration history of a community), which are summarized as historical processes (Ricklefs 1987). However, microbial ecological studies usually present 'snap-shot' results (i.e., analyses at a single time or space) that cannot properly disentangle whether contemporary (e.g. current environmental conditions) or historical processes shape communities (Armitage 2015; Wojciechowski et al. 2017). For example, a study conducted on aquatic bacterial communities suggested that past environmental conditions can be better predictors of contemporary spatial differences in community compositions than the contemporary environmental conditions (Andersson et al. 2014). The authors also highlighted that processes related to selection by present and past environmental condition may both be important, so that some taxa are selected by the present whereas others are selected by past environmental conditions.

Priority effects can cause historical contingency

The immigration history of a community, i.e., the sequence and timing in which species or their propagules reach a new locality, can profoundly affect community composition through the so-called priority effects (Fukami 2015). Thus, priority effects can cause historical contingency and are community assembly processes that can lead to spatially dissimilar communities under identical conditions (Chase 2003, 2007). Priority effects rely on the principle of “first come, first served” and presume that early colonization offers an advantage for an early-arriving species in its interactions with late-arriving species, simply because it has arrived first (Lockwood et al. 1997). The early-arriving species may have the ability to rapidly adapt to any environmental change or disturbance and can thereby continue to be abundant or dominate the local community (Urban et al. 2008). These early-arriving species modify niches or preempt resources so that late-arriving species will not be able to successfully establish within a community (Fukami 2015). The duration of priority effects can either be temporary if early colonists are eventually replaced by better-adapted late-arriving species, or persistent if late-arriving species cannot establish successfully at all.
Factors that can influence priority effects

Disturbances and environmental fluctuations can lead to randomly assembled communities (Dini-Andreote et al. 2015), for example, by continuously disrupting species sorting processes during community formation. If dispersal is low under disturbances, early colonists will have the chance to monopolize communities, which results in priority effects (Loeuille & Leibold 2008). On the other hand, highly fluctuating conditions have been shown to promote coexistence-promoting mechanisms and with this, counteracted priority effects (Jiang & Morin 2007; Tucker & Fukami 2014; Letten et al. 2018). Clearly, there are conflicting findings, and in general, the importance of priority effects in fluctuating environments remains poorly understood.

Several studies have demonstrated that organisms with high growth rates have the capability to facilitate strong priority effects by hindering the establishment of late-arriving competitors (Peay et al. 2012; Tucker & Fukami 2014). This is found because a high biomass of early-arriving species can modify niches or preempt resources so that late-arriving species will not have the chance to successfully establish populations. In other words, early-arriving species can be resistant to immigration of late-arriving species. Hence, any possible environmental factor that increases growth rates of early-arriving species could possibly enhance priority effects. Accordingly, recent studies have shown that priority effects are temperature-dependent, and that warming increases the importance of early-arriving species by increasing the probability of competitive exclusion of the late-arriving species (Tucker & Fukami 2014; Grainger et al. 2018). However, it remains unknown if warmer climate conditions can strengthen priority effects in microbial communities in aquatic ecosystems.
Aims of the Thesis

The overall aim of this thesis is to investigate from multiple angles how aquatic microbial metacommunities are influenced by historical contingency (i.e. due to priority effects). More specifically, I aim to (1) provide a comprehensive overview of historical contingencies in metacommunities based on current knowledge, (2) evaluate the presence of historical contingency in a natural rock pool metacommunity, (3) examine how ecosystem size-induced environmental fluctuations may affect the importance of historical processes, and lastly, (4) investigate how warming impacts historical contingency.

The main focus for each paper includes the following:

**Paper I** is a conceptual paper that summarizes processes that can lead to historical contingencies in microbial metacommunities, and discusses potential scenarios where and when historical contingencies may matter and which factors determine their importance.

**Paper II** aims to estimate the relative importance of assembly processes, at spatio–temporal scale, in bacterial and microeukaryotic metacommunities under shifting environmental conditions in natural rock pool metacommunities. Here, I also aimed to evaluate a suite of null model approaches that could potentially reveal the existence of historical contingency.

**Paper III** aims to investigate how and to what extent ecosystem size-induced environmental fluctuations influence community assembly processes (including priority effects) over time in a natural experimental landscape consisting of artificial ponds (mesocosms) of different sizes.

**Paper IV** investigates how warming impacts assembly processes of aquatic bacterial communities with a special focus on potential temperature dependency of priority effects at both community and population levels in a laboratory experiment.
Methods

Field studies and laboratory experiment

**Paper II** was based on a field study conducted on the island of Gräsö, Sweden. Water samples were taken from 20 neighboring rock pools located at the Baltic Sea coast that were assumed to function as a metacommunity. The rock pools were sampled ten times, starting on 14 August 2015 and ending on 19 September 2015 in four-day intervals. Besides the monitoring of bacterial and microeukaryotic metacommunities, numerous abiotic and biotic variables were measured at each sampling occasion. Intensive rain events in the middle of our sampling campaign separated the study period into distinct dry and wet periods, allowing to specifically investigate the environmental dependency of assembly mechanisms of microbial communities over time.

In **Paper III**, a pond mesocosm experiment was conducted where uncovered hard-shell mesocosm units of three different sizes (24.5, 70 or 200 L) were arranged in an open field beside Lake Erken. The mesocosms were filled with water and sediment from Lake Erken. A salinity gradient (0–6 ‰) was created by addition of natural sea salt to induce species sorting (selection processes) in response to a salinity press disturbance of different strengths. Following the setup, mesocosms were monitored for 64 days. Samples for bacterial cell abundances and community composition were collected at day 1, 2, 4, 8 and every 8th day thereafter for 64 days, while for measuring physical and chemical parameters, samples were taken every 4th day after day 4.

In **Paper IV**, a full-factorial laboratory experiment was implemented where both temperature (15, 20 and 25 °C) and dispersal rates (0, 5 and 20 % cell exchange from an external dispersal source) were manipulated. Bacteria from three Swedish lakes (Lötsjön, Erken and Grytsjön) were inoculated and grown in cell-free Baltic Sea medium as early-arriving bacteria. These lake communities served as ‘recipient communities’ and were exposed to “foreign” (Baltic Sea) medium to which they were not a priori adapted to. The recipient communities differed in their proximity to the Baltic Sea, as this might alter the potential of priority effects to occur. After initial growth and establishment of the recipient communities, bacteria from the Baltic Sea (late-arriving bacteria) that were presumably better adapted to the incubation medium were dispersed into the recipient communities and then incubated for additional 15 days. At the end of the experiment bacterial community composition was analyzed and potential priority effects were investigated.
Microbial community composition analyses

To determine bacterial community composition, the 16S rRNA gene of DNA extracted directly from collected cells was amplified by a two-step PCR preparation in Paper II, III and IV with sample-specific barcodes. Note that Paper III was based on a rRNA based analysis aiming to monitor the active bacterial community composition (see details in Methods of the corresponding manuscripts).

For the microeukaryotic community composition in Paper II, 18S rRNA genes were amplified.

For all studies amplicon paired-end sequencing was performed on an Illumina MiSeq platform at the SciLifeLab SNP&SEQ Technology Platform hosted by Uppsala University.

The sequencing data was analyzed using different pipelines. In Paper II and III, the sequences were clustered at 97 % sequence similarity into operational taxonomic units (OTUs) as an estimator for ‘species’ (Rosselló-Mora & Amann 2001). In Paper IV, the sequences were processed differently, whereas amplicon sequence variants (ASVs) were used as the unit of ‘species’ instead in order to detect micro-diversity patterns (García-García et al. 2019). In all cases, the taxonomical classification of OTUs and ASVs were done using reference databases.

Statistical ‘toolbox’

A common way of investigating assembly processes is to search for patterns in similarities or differences in composition among communities (Harvey et al. 1983). Numerous statistical tools (e.g. uni- and multivariate statistics) and approaches (e.g. null models) were used in my PhD thesis work. Each method is described in detail in each paper. Nevertheless, in this chapter I would like to primarily introduce a suite of null model approaches that represents the core statistical analyses of my study in Paper II (Fig. 1A-B-C).

In general, null model approaches use ecological data to generate (through randomization) the so-called ‘null community’ or ‘null expectation’ which is expected to appear in the absence of certain assembly processes (Gotelli 2001). In other words, null model approaches are able to show us how a community would look like if it is assembled by only random processes. Then, we can statistically evaluate if the observed patterns (e.g. in beta-diversity) deviate from the null expectation, and if so, how much (Chase et al. 2011). This approach can show the importance of certain assembly processes, e.g., the balance between deterministic (i.e. selection) and stochastic (i.e. ecological drift) processes.

Null model-based analysis of community dissimilarities has led to the development of the incidence-based Raup-Crick beta-diversity metric ($\beta_{RC}$)
(Raup & Crick 1979) to estimate the balance between stochastic vs. deterministic assembly of communities (Fig. 1B).

Species co-occurrence or coexisting patterns can mirror species interactions and therefore indicate the existence of certain processes that lead to distinct structures in the communities. The Element of Metacommunity Structure (EMS) is an incidence-based null model approach that in a series of tests assesses co-occurrence patterns (Leibold & Mikkelsen 2002; Presley et al. 2010) (Fig. 1A). EMS can detect patterns that indicate competitive exclusion of species, or species sorting that causes specific patterns in species distributions along an environmental gradient.

However, neither of these incidence-based approaches can distinguish regional processes and estimate the importance of dispersal-related processes. Hence, a third null model approach was also applied (Fig. 1C), which not only use species occurrence and frequency data, but integrates abundance data and phylogenetic information (Stegen et al. 2013). Therefore, special focus is given in the following sections on the quantitative process estimate (QPE) approach (Stegen et al. 2013). QPE was used in Paper II and III to estimate the relative importance of different assembly processes in space and time, respectively. In Paper II, I focused on how communities assembled similarly in space, and how it varies over time. While in Paper III, we aimed to know how individual communities at different sampling times diverged from their initial communities.

This approach was supplemented with additional tests (Fig. 1D) in Paper II, to make further evaluations on the estimated assembly processes.

Besides null models, in the end of this section, I also introduce the so-called differential abundance analysis (DESeq2) (Love et al. 2014). This method was applied in Paper IV in order to detect and define the role that bacterial species (more precisely, amplicon sequence variants, ASVs) and groups played in either maintaining or eliminating priority effects.

Quantitative Process Estimate (QPE) and complementary tests

Stegen et al. (2013) developed an analytical framework that allows to quantitatively estimate the relative influences of different community assembly processes. Using this framework, the importance of selection processes (e.g. variable and homogeneous selection), dispersal-related processes (e.g. dispersal limitation and homogenizing dispersal) and drift can be estimated in a two-step procedure (Fig. 1C).

In the first step, one can estimate which phylogenetically-conserved selection processes drive community assembly (Fig. 1C). First, phylogenetic information is used to assess phylogenetic turnover, i.e. the phylogenetic distance (dissimilarity) between two communities. This can be done by using different metrics that vary depending on the resolution level at which phylogenetic information is used. Here we specifically aim to detect phylogenetic turnover at
the ‘species’ level, namely, the processes occurring at the tips of the phylogenetic tree. For this, the metric of $\beta$-Mean-Nearest Taxon Distance ($\beta$MNTD) is usually used. This metric determines to what extent the observed phylogenetic turnover between community pairs deviates from the mean of the null distribution. Then the significance of the deviation is evaluated using the $\beta$-Nearest Taxon Index ($\beta$NTI) (difference between observed $\beta$MNTD and the mean of the null distribution in units of SDs). If a pair of two communities showed significant phylogenetic dissimilarity, for example $\beta$NTI > 2 or $\beta$NTI < −2, the community pair is assumed to be assembled by variable or homogeneous selection, respectively. Altogether, these selection processes result in phylogenetically conserved selection. However, if there is no significant deviation from the null expectation (i.e. $−2 < \beta$NTI < +2) the observed dissimilarity between a pair of communities is assumed to be the result of dispersal-related processes or ecological drift.

In the second step, one can estimate which dispersal-related processes drive community assembly (Fig. 1C). Here, I used only those community pairs that were not influenced by phylogenetically conserved selection. First, another metric is used to estimate the relative importance of dispersal-related processes or drift. Specifically, the abundance-based version of the Raup-Crick beta-diversity was used to calculate pairwise Bray-Curtis dissimilarity ($\beta_{\text{RCbray}}$). If the two communities are not (dis)similar significantly from the null expectation ($−0.95 < \beta_{\text{RCbray}} < +0.95$), it presumes that random processes are acting alone (drift). If the community pair was very dissimilar ($\beta_{\text{RCbray}} > +0.95$), it presumes the importance of dispersal limitation coupled with drift. If the communities within a pair was very similar to each other ($\beta_{\text{RCbray}} < −0.95$), homogenizing dispersal (i.e. mass effect) is possibly important. Note that in Paper III where the calculation of $\beta_{\text{RCbray}}$ was performed between a community at any sampling occasion back to its initial community composition, values of $\beta_{\text{RCbray}} < −0.95$ could also be interpreted as the lack of temporal community shift.

However, the first fraction, ‘dispersal limitation’ ($\beta_{\text{RCbray}} > +0.95$), may be signatures of other processes than ‘true’ dispersal limitation. For example, dissimilar community pairs can also be the consequence of (i) historical contingency, (ii) phylogenetically non-conserved selection (since I already assessed phylogenetically conserved selection in the first step), but also be the result of (iii) the effect of unmeasured environmental factor(s). All these processes can result in more dissimilar communities than expected by chance. Therefore, to distinguish which one(s) influenced the observed communities in Paper II, I needed to apply complementary tests (Fig. 1D).

Observing a distance-decay relationship can support the idea of ‘true’ dispersal limitation if community dissimilarity correlates with the geographical distance of a community pair. This can be easily tested using partial Mantel tests. If there is no significant distance-decay relationship, the community dissimilarity can be the result of phylogenetically non-conserved selection. I
tested whether this was the case by assessing community dissimilarity between two communities in relation to their environmental dissimilarity. If there was such correlation, it meant that the measured variables did indeed select for different species in the two communities without inducing phylogenetic turnover. Note, that if they would have induced phylogenetic turnover, they would have already been detected in the first step of the QPE (Fig. 1C). If there is no correlation between community dissimilarity and either geographical or environmental distance, two possibilities remain: historical contingency or the effect of unmeasured factor(s).

How could one distinguish between these two possibilities? As I presented in Paper I, the community composition should not change markedly over time in the presence of historical contingency. If it changes, it could be the effect of unmeasured environmental factor(s) (Fig. 1D). Based on the two distinct periods (dry vs. wet) in the study of Paper II, I assumed that community dissimilarity at the level of an individual community should not change between these two periods if historical contingency was important. Therefore, I used Permutational Multivariate Analysis of Variance (PERMANOVA) to evaluate community dissimilarities between the dry and wet periods (Fig. 1D). This way I concluded that:

- the communities that showed no significant phylogenetic signal in the first step of QPE ($-2 < \beta_{NTI} < +2$) and
- fall into ‘dispersal limitation’ fraction during the second step of QPE ($\beta_{RBray} > +0.95$) but
- presented no significant correlation in partial Mantel-tests with either geographical or environmental distances and
- according to the PERMANOVA did not respond to environmental change

were indeed primarily assembled by historical processes (Fig. 1D).
Figure 1. Null model approaches (A-B-C) used in Paper II. (A) EMS identifies metacommunity properties emerging in site-by-OTUs incidence matrices (Leibold & Mikkelson 2002; Presley et al. 2010). (B) Incidence-based (Raup-Crick) beta-diversity ($\beta_{RC}$) tests stochasticity and determinism using a metric provided by Chase et al. (2011). (C) QPE quantifies assembly processes involving phylogeny and abundance-based (Raup-Crick) beta-diversity ($\beta_{RCbray}$) following the framework of Stegen et al. (2013). (D) partial Mantel tests as a complement to the QPE were performed between $\beta_{RCbray}$ and geographical and environmental distance matrices in order to make a clear distinction between historical contingencies (e.g. due to priority effects) and/or unmeasured factors, phylogenetically non-conserved selection and pure effects of dispersal limitation. Then, the distinction between historical contingency and the effects of unmeasured factors was made by assessing temporal changes in community composition at the level of individual communities using PERMANOVA.

Differential Abundance Analysis (DESeq2)

In Paper IV, I was assessing priority effects at the population level after the dispersal treatments. Therefore, I aimed to identify bacterial ASVs that were persistent as early-arriving species, or successfully established as late-arriving species (for clarification, see the experimental setup described earlier). To do this, I first needed to determine if there were any significant changes in the relative abundances of ASVs. The so-called differential abundance analysis, DESeq2 (Love et al. 2014), seemed as a good tool to assess this. Let’s go through step-by-step how I performed this analysis. First, I determined for all common (> 0.5 % relative abundance) early-arriving ASVs whether their abundances in the recipient communities changed significantly after exposed to dispersal by late-arriving ASVs. If the early-arriving ASVs’ abundances did not decrease significantly, I interpreted it as a sign of priority effects and grouped them as ‘persistent early-arriving ASVs’. On the other hand, if their abundances were significantly lower in treatments receiving dispersal, I categorized them as ‘forfeited early-arriving ASVs’ (Fig. 2A). They are the ones
that got replaced by late-arriving ASVs, thus, could not be resistant to the dis-
persal of late-arriving ASVs.

But which ones were the bacterial ASVs that could induce species replace-
ments and, therefore, eliminate priority effects? Since I measured the cell
abundances in the dispersal sources and in the recipient communities, I was
able to calculate the expected abundances of the most common late-arriving
ASVs’ (> 0.5 %) in the recipient communities at different dispersal rates.
Thereafter, the deviation of the measured abundances from the expected abun-
dances was assessed by DESeq2 (Fig. 2). A non-significant deviation or a
significantly higher relative abundance compared to the expected one provides
a sign of successful establishment, while a significantly lower abundance in-
dicates unsuccessful establishment of a late-arriving ASVs (Fig. 2B). By do-
ing this, I could gain information about which late-arriving bacterial ASVs
could have the potential to eliminate priority effects.

![Figure 2](image.png)

**Figure 2.** Conceptual evaluation of the differential abundance analyses. (A) Non-
significant and positive (adjusted \( p < 0.05 \)) \( \log_2 \) fold change values indicate similar
or higher abundance when late-arriving bacteria were introduced and, hence, ASVs
are defined as persistent, while negative values indicate ASVs with significantly
lower abundance, and, hence, are defined as forfeited. (B) Non-significant and posi-
tive (adjusted \( p < 0.05 \)) \( \log_2 \) fold change values indicate similar or higher abundance,
hence, successfully establishment of late-arriving ASVs, while negative values indi-
cate significantly lower abundance and, hence, unsuccessful establishment of late-
arriving ASVs after being dispersed.
Results and Discussion

When should we expect historical contingency? (Paper I)

Paper I aimed to provide a short, comprehensive summary of the processes that can lead to historical contingency, or in other words, to the legacy of the past.

In general, historical contingency occurs if historical processes (e.g. the effect of immigration history or past environmental conditions) can persist through time and leave their imprint on the community regardless the contemporary environmental conditions and ongoing changes. But when can a community be historically contingent? This is the core question that this review aimed to discuss.

Figure 3 summarizes four major potential scenarios about how the spatio–temporal dynamics of changes in community compositions in relation to environmental changes may show signs of historical contingency (Fig. 3). First, if a community is not historically contingent, its composition should closely track changes in environmental conditions (for example, an intensive rain event that causes changes in salinity or nutrient concentrations of a given waterbody), simply because the new environment will select species that are best adapted to it (Fig. 3A). This selection can be rapid (Fig. 3A) or, alternatively, slow (Fig. 3B) either due to time-lags in species sorting, or due to the presence of weak priority effects. If there is historical contingency, community composition should not change markedly over time in spite of the environmental change due to strong priority effects (Fig. 3C). It is most likely that some species within a community undergo different scenarios (Fig. 3D). Hence, there may be cases when both historical processes and contemporary conditions define communities. One of the reasons behind this might be that some species could maintain priority effects to a greater extent than the rest, thus, these species will be persistent over time and not affected by environmental change or later immigration.
Figure 3. Different species sorting scenarios that include selection by both contemporary and past environmental conditions. The column on the left shows the extent to which communities track changes in environmental conditions; the two columns on the right show to which extent variation in community composition is due to species sorting by past and present environmental conditions at two hypothetical time points (t₁ and t₂). (A) Lack of historical contingency, (B) Transient historical contingency, (C) Persistent historical contingency, (D) Mixed scenario.

In addition, local communities of a metacommunity can be assembled differently, influenced by different immigration histories, or be exposed to distinct environmental changes. Altogether, thus, a mixed scenario is highly likely in natural metacommunities.

Besides the discussion about ‘when historical contingency matters’, Paper I also emphasizes that snap-shot studies have limitations because they do not allow to determine whether present-day patterns in community composition reflect contemporary (present-day) conditions or the influence of historical processes. Thus, a majority of previous studies may have overlooked the importance of historical contingency.
Can we detect historical contingency in natural metacommunities? (Paper II)

Temporal changes in community assembly processes of bacterial and microeukaryotic rock pool metacommunities were tracked during a five-week period. The study period was divided by an intensive rain into two periods with distinct environmental conditions: a dry period (with higher temperature and less precipitation) prior to the rain, and a cooler wet period (with lower temperature and more precipitation). Using three null model approaches (quantitative process estimates – QPE, elements of metacommunity structure – EMS, and incidence-based beta-diversity – $\beta_{RC}$), I assessed the processes that underlie community structures (Fig. 1A-B-C).

The incidence-based approaches, i.e. $\beta_{RC}$ and EMS (Fig. 1A-B), indicated that the observed metacommunities were assembled mainly randomly (e.g. by stochasticity or drift), while the abundance-based null model approach (i.e. QPE; Fig. 1C) revealed the importance of different selection and dispersal-related processes. This highlights that abundance-based metrics might be more suited to reveal more complex processes, while incidence-based approaches might overlook them. Therefore, in this chapter I primarily present and discuss the results of the QPE (Fig. 1C) and additional tests (see Fig. 1D) that helped me to make a distinction between ‘true’ dispersal limitation and additional processes including historical contingency.

QPE showed that both bacterial and microeukaryotic community assemblages were mainly dominated by dispersal limitation or historical contingencies at all time points (Fig. 4). The relative importance of dispersal limitation or historical contingencies in microeukaryotes was significantly higher in the dry period compared to the wet period, while in bacterial communities it increased towards the end of the dry period, but then decreased slightly during the wet period (Fig. 4). This suggests that a lack of connectivity among pools during the dry period led to a temporary enforcement of dispersal limitation or historical contingencies. Interestingly, none of the distinct periods (i.e. dry vs. wet) that occurred throughout the study induced strong selection.

The relative importance of assembly processes, and the way they changed in response to rain-induced changes in environmental conditions differed for bacterial and microeukaryotic communities (Fig. 4). For the bacterial metacommunity, the relative importance of homogeneous selection processes significantly increased, which conform with the idea that homogenization in environmental conditions among rock pools leads to more similarly composed bacterial communities (Langenheder et al. 2012).
Figure 4. Overall (A, B) and temporal (C, D) dynamics of the relative importance of different community assembly processes expressed as the proportion of community pairs assembled either by species sorting (variable or homogeneous selection), dispersal limitation or historical contingency, homogenizing dispersal or drift for bacteria (A, C) and microeukaryotic (B, D) communities. Note that the scales are not equal on the C and D facet plot. The dashed lines refer to the division between the dry and wet period, and red asterisks indicate significant differences between them (Kruskal-Wallis test, significance at $p < 0.05$ level).
On the contrary, for microeukaryotes, homogeneous selection processes remained negligible throughout the study period, while the relative influence of variable selection surprisingly appeared to increase in the wet period. One possible explanation for this result might be that the increased water depth in the wet period could have generated more gradients within each pool for environmental parameters such as light, which is crucial for photo- and mixotrophic microeukaryotes (Modenutti et al. 2008; Crane & Grover 2010), thus, promoting the establishment of distinct local microeukaryotic communities.

The ‘dispersal limitation or historical contingency’ fraction might comprise of a number of processes, including actual dispersal limitation, historical contingencies, but also additional processes, such as effects of phylogenetically non-conserved selection processes and unmeasured factors. In attempt to separate those processes, I used additional tests (i.e. partial Mantel tests) to detect spatial distance-decay relationships (Fig. 1D). These tests showed that there was no robust support for dispersal limitation, because of the lack of significant relationships between beta-diversity and the spatial distances between pairs of communities. Thus, altogether, it seems that there is no robust support for ‘true’ dispersal limitation. Likewise, there was also no indication that the ‘dispersal limitation or historical contingency’ fraction masked substantial effects of phylogenetically non-conserved selection processes related to measured environmental factors. Hence, the ‘dispersal limitation or historical contingency’ fraction points to the importance of the outcome of historical contingency and the effect of unmeasured factors (e.g. light) that are not phylogenetically conserved. Could this be a sign of priority effects as a potential cause of historical contingency? In that case there should be a low temporal turnover in community composition at the level of individual rock pools despite the strong environmental shift (Fig. 1D). I found, that bacteria in most of the individual rock pools did not experience significant compositional shifts between the two periods suggesting that most communities might have been influenced by priority effects. In contrast, microeukaryotic communities were unlikely to have experienced priority effects because almost all rock pools experienced significant compositional shift between the two periods.

Taken together, Paper II provides a more comprehensive understanding of how microbial communities respond to environmental changes on short-time scales compared to previous snapshot studies (Langenheder & Ragnarsson 2007; Székely & Langenheder 2014). Moreover, it highlights that refined statistical frameworks (i.e. QPE) should integrate additional analyses (Fig. 1D) such as those presented in Paper II to provide a clearer distinction between historical contingencies, phylogenetically non-conserved selection and the pure effects of dispersal limitation.
Do ecosystem size-induced fluctuations promote or erode historical contingency? (Paper III)

In this study, the overall aim was to test how environmental fluctuations induced by differences in ecosystem size would influence community assembly processes (estimated by using the QPE framework) in response to a press disturbance (salinity change) of different strengths.

The importance of selection processes in response to the salinity disturbance was higher in larger mesocosms. These large mesocosms featured relatively stable environmental conditions and high internal niche availability (due to e.g., stratification). Here, selection processes triggered by the salinity gradient could shape communities to a greater extent than in the small mesocosms (Fig. 5). Bacterial communities in smaller mesocosms with strong environmental fluctuations diverged over time due to e.g., dispersal limitation (Fig. 5). In general, the results of Paper III are in line with previous studies that have shown that ecosystem size influences community assembly processes (Drake 1991; Fukami 2004; Orrock & Fletcher Jr. 2005). But how may it influence historical contingency?

We expected priority effects to occur in the small mesocosms, as small habitat patches with small community size have been shown to increase priority effects through high niche overlap when populations reach carrying capacity (Orrock & Fletcher Jr. 2005; Fukami 2015). Small mesocosms had a low species richness, high abundance and high nutrient levels, all characteristics that have previously been shown to promote priority effects (Orrock & Fletcher Jr. 2005; Chase 2010; Fukami 2015). However, we found little indication for priority effects of taxa that were present at the initial stage of the experiment (i.e. day 4) and persisted through time. Instead communities diverged over time as a consequence of high temporal taxa turnover (resulting in an increasing importance of the dispersal limitation fraction in the QPE; Fig. 5). This suggests that strong environmental fluctuations can ‘override’ the characteristics that a small mesocosm size provides and eliminate priority effects that otherwise might have been found in the small ponds. Nevertheless, based on the data provided in Paper III, it is not possible to clearly support or rule out the presence of priority effects.
How can historical contingency be affected by climate change? (Paper IV)

Since warming (due to climate change) could possibly enhance priority effects by increasing growth rates of early-arriving species (Tucker & Fukami 2014; Grainger et al. 2018), I specifically investigated (i) the effect of warming on the strength of priority effects and, (ii) the identity of the bacterial groups that played a key role in the establishment and maintenance, or erosion of priority effects. I hypothesized that warming results in stronger priority effects in bacterial communities, namely, that recipient communities grown at high temperature will be more resistant to dispersal of late-arriving species from the Baltic Sea. Moreover, I assumed that recipient communities from lakes geographically closer to the Baltic Sea (Lötsjön → Erken → Grytsjön → Baltic Sea)
would be more prone to maintain priority effects than more distant lakes due to their higher ratio of species adapted to the applied Baltic Sea medium.

In agreement with previous studies that have used similar approaches (Svoboda et al. 2017; Rummens et al. 2018), I found that dispersal by late arrivals induced some species replacement because all recipient communities converged towards the dispersal source communities to some extent (see Fig. 3 in Paper IV). In other words, dispersal shifted the communities away from their initial compositions, thus, there was no complete priority effects (Fig. 6). However, it seemed that warming had the potential to promote priority effects in aquatic bacterial communities, because some recipient communities shifted less at higher temperature levels (20 and 25 °C) than at 15 °C (Fig. 6; Lötjsjön). However, whether this happened or not depended on the rate of dispersal of the late-arriving, better adapted Baltic Sea communities and on the identity of the recipient community (Fig. 6).

![Figure 6. Dispersal-induced shifts in community composition in relation to temperature. Bray-Curtis dissimilarities between recipient communities in the 5 and 20 % dispersal treatments in relation to the 0 % dispersal treatment were calculated. The lower the community shift, the higher is the strength of potential priority effects detectable at the community level.](image)

At the population level the total relative abundance of successfully established late-arriving species (ASVs) in the recipient communities decreased at increased temperature (Fig. 7). But why? Well, one possibility is that warming stimulated high growth rates of the early-arriving bacteria which might have increased their resistance to dispersal by late-arriving bacteria. However, there were differences among recipient communities because warming did not always affect dispersal-induced shifts in community composition at the community level in the same way (Fig. 6). These differences might be the result of intrinsic differences in traits of ASVs such as in temperature optima. Nevertheless, warming had a clear negative effect on the total relative abundance of successfully established late-arriving ASVs (Fig. 7).
Taken together, the results suggest that warming may enhance the persistence of early-arriving species and reduce the establishment of late-arriving species. Altogether, warming may increase the importance of priority effects. Furthermore, the results, in agreement with those by Tucker & Fukami (2014), also highlight that the overall strength of warming-enhanced priority effects is context dependent and differ depending on the composition of early-arriving communities as well as dispersal rates of the late-arriving bacteria.

![Graph showing changes in relative abundances of successfully established late-arriving ASVs.](image)

*Figure 7.* Changes in the relative abundances of successfully established late-arriving species (ASVs, > 0.5 % relative abundance) at different dispersal rates (5 % or 20 %) and temperatures (15, 20 and 25 °C). ASVs are grouped by bacterial order and were identified by differential abundance analysis (see Methods of Paper IV).
Conclusions and Perspectives

So, what can be learned from my studies? Let’s start to summarize the main findings of my thesis together with several unanswered questions that have been raised during these years.

Microbial (meta)communities vary in space and time due to a combination of different processes, which include selection by local environmental conditions, dispersal from the regional species pool, stochastic (drift) events and, as it became evident, by the effects of historical processes (i.e. priority effects). All these community assembly processes are not static, and their relative importance can vary under different conditions and between different microbial groups (e.g. bacteria vs. microeukaryotes). This is especially true for historical contingency because its importance is greatly context dependent as I emphasized in this thesis.

My experiences of being a microbial community ecologist is that it is challenging. Doing research in this field gives one the opportunity to choose tools from the available wide selection of statistical approaches. As I found, it is many times difficult to infer assembly processes from detectable patterns (i.e., species coexistence patterns), and even if it works, the outcomes could be misleading. For example, by investigating the relative importance of assembly processes in natural microbial communities, in Paper II, I found that even the most promising statistical tool (QPE) acts merely as a guide, because the fraction expected to indicate ‘true’ dispersal limitation may in reality depict historical contingency. Or even other, unmeasured processes, depending on the organism group of interest. None of the null model approaches is able to connect compositional patterns to their regulating factors directly, or analyze the data both in space and time simultaneously. Hence, there is a clear need to develop reliable statistical approaches and frameworks, which could utilize other relevant data (e.g. environmental data) than species information, moreover, which could be flexible for both spatial and temporal datasets. Such approaches also need to go beyond existing multivariate statistical methods, such as variation partitioning that have their own limitations (Brown et al. 2017).

Are organism groups influenced by historical contingency differently? The findings in Paper II revealed that bacterial communities could have a higher chance to be impacted by historical contingency (i.e. as a result of priority effects) than microeukaryotes in natural ecosystems such as rock pools. In the future, it would therefore be interesting to investigate if this difference between bacteria and microeukaryotes can also be found at larger spatial scale.
or even at longer time scales. Moreover, it would be great to “zoom in” the
diverse group of microeukaryotes and put the focus on distinct microeukary-
ates. During my study in Paper II, I handled microeukaryotes as a single
group, a unit, although, this group is built up by several distinct organism
groups, each with possibly different sets of traits. Hence, future studies should
separately investigate the importance of historical contingency in e.g., micro-
fungi, diatoms or ciliates. Nevertheless, this paper highlights that temporal
observations with high-resolution provide a more comprehensive understand-
ing than snap-shot studies.

Later, I was curious about how differences in ecosystem size may influence
the existence of historical contingency (Paper III). We found that there was
no clear evidence that priority effects were important in any of the ponds. This
finding suggests that environmental fluctuations that often impact small eco-
systems, may promote the coexistence of species over time (Tucker & Fukami
2014; Letten et al. 2018) and, thus, dampen priority effects. This seemed quite
surprising giving that communities of similar size (rock pools) were able to
harbor priority effects under highly variable environment conditions in the
study of Paper II. However, one difference was that the freshwater commu-
nities in the mesocosms in Paper III were initially exposed to a salinity dis-
turbance that they had not experienced before, while the rock pools studied in
Paper II have a long history of exposure to fluctuating environment, includ-
ing changes in salinity. Maybe a simpler set-up or a laboratory experiment
with controlled conditions could more easily support or rule out any of the
discussed possibilities, and provide more robust evidence on how ecosystem
size-induced fluctuations impact historical contingency.

In the face of climate change, investigating how historical contingency, in
particular priority effects, can be affected by warmer climate is obviously a
relevant research question. Paper IV suggests that priority effects might be
strengthened by warming as in some occasions higher temperatures increased
the resistance of recipient communities against immigration and decreased the
relative abundance of immigrant species. However, warming-enhanced prior-
ity effects were not always found and their strength differed between recipient
communities and dispersal rates. But why do distinct lake bacterial commu-
nities respond differently to dispersal at warmer conditions? What makes some
bacterial groups to be persistent or forfeited by immigration? Surely, further
investigations are needed to determine the roles of species traits in the for-
mation of priority effects. Nevertheless, Paper IV provides further evidence
for temperature-dependent priority effects that have been previously detected
in studies targeting e.g., yeasts or aphid species (Tucker & Fukami 2014;
Grainger et al. 2018).

Taken together, this thesis provides evidence that historical processes can
lead to priority effects that can leave their imprint on aquatic bacterial com-
munities, resulting in historically contingent communities. Hence, the effect
of historical processes cannot be overlooked, even though their importance is
highly context dependent and generally difficult to detect. With this thesis, I encourage future studies to consider historical contingency, the legacy of the past, as a potentially important driving force that can contribute to the spatial diversity of ecological communities.
Summary

Microorganisms, or microbes, are tiny creatures that represent an extremely diverse organism group including all microscopic single-cells or colonies of cells. They inhabit almost every habitat on Earth, and are present as microbiota in and on all multicellular organisms. Despite their invisibility, they do a lot of work: they participate actively in nutrient flows and in the carbon cycle. They decompose all kinds of dead matter, can represent the food source for other organisms (e.g. predators), and can even modify their own habitats like a group of engineers. However, many times, they do not have enough space to live together or just do not get along in a given habitat. Therefore, it can happen that some microorganisms fight for the same resource and the outcome of the competition determines which species remain and which ones need to leave. All sorts of interactions between microbes defines ecological communities (the aggregate of groups of various species), resulting in variations in the composition of communities across space and time.

One of the biggest challenges of microbial ecologists is to understand what kind of processes shape community composition and how different factors (e.g. warming due to climate change) regulate these processes. Why? Because we have this optimistic dream that we will, eventually, be able to predict the composition of microbial communities under a given environmental condition, place or time. We want to understand how changes in the environment will influence ecological communities and their role in ecosystem functions.

But let’s start at the beginning, when habitats are not yet colonized. These new empty habitats can be created by a drastic change in the environment, for example, when a pond dries out and aquatic organisms need to wait until it gets refilled in order to recolonize it. Let’s imagine that such a new habitat has been formed. Species from the surrounding habitats will reach the new, empty habitat through dispersal pathways. The communities located in these linked habitats are called a metacommunity. Naturally, the arrival sequence of the first couple of species (colonists) to a newly-formed habitat is determined by random mechanisms such as dispersal by wind from different directions, or transport of microbes by animals from one locality to another as their microbiota, or as random splashes from the sea. From this point, on a “first come, first served” basis these early colonists can modify the habitat or preempt resources so that colonists that arrive later will not have the chance to successfully establish populations in this already occupied habitat, simply because they arrived too late. However, if the amount of colonist that arrive later to the
occupied habitat is large (a mass of late colonist), they have a higher chance to successfully replace, e.g. through competitions, the early colonists. Hence, monitoring community compositions over time and detecting changes in them can indicate such processes. There is increasing evidence that the “first come, first served” phenomenon called priority effects, are often found in ecological communities. When priority effects are important, the random arriving order of early colonists, the so-called immigration history, defines the composition of the communities. This is the reason why communities may be bound to the past.

During my PhD study, I investigated priority effects from multiple angles by conducting a field study, a natural mesocosm experiment and a laboratory experiment. I was curious about whether bacterial and microeukaryotic (microscopic eukaryotic organisms including microfungi, algae, protozoans) communities experience priority effects in nature, for example, in rock pools (rocky pools on the sea shore). In the face of climate change, both increasing magnitudes of environmental fluctuations and warmer climate are predicted, hence, I was curious about how these factors may regulate the existence and the importance of priority effects in bacterial metacommunities.

I obtained evidence that even in small rock pool communities priority effects can occur, and that even a rain storm that induced a strong change in environmental conditions, could not erase them. However, this was only found in the case of bacterial communities, but not in microeukaryotes. The community composition of microeukaryotes proved to be less stable after the storm than their bacterial peers. Thereafter, I was interested in how strong environmental fluctuations would need to be to erode priority effects in bacterial communities. Me and my colleagues created an artificial pond metacommunity which contained mesocosms of 3 different size categories to induce different magnitude of fluctuations in their environmental conditions. We expected that the smaller the mesocosms the stronger the fluctuations will be. The results did not provide support for the existence of priority effects in any of these communities, thus, we were unable to examine whether priority effects tend to be more frequent in highly variable or in relatively stable environment. Most likely, the strong fluctuations in the small ponds continuously interrupted communities to establish priority effects over time.

And last but not least, what about the warmer climate? In a laboratory experiment, I let more than a hundred lake bacterial communities grow at different temperature levels. These communities became the early colonists of my habitats. When these early colonists successfully established populations, I tested whether they are resistant to invasion by late-arriving bacteria that the early colonists most likely have never met previously. By doing this, I could test how the importance of priority effects was modified by increasing temperatures. I found that early-arriving bacterial communities were to some extent able to resist invasion by late-arriving bacteria, thus, they maintained their original compositions that were formed initially. But this was not the end of
this study, because I also wanted to know which bacterial groups are actually responsible for priority effects. For example, my aim was to identify who are the early colonists that can persist and the ones that can be forfeited after an invasion. Further, I identified bacterial groups among the late-arriving bacteria that can eliminate priority effects and those that did not induce changes in local communities. The results showed that different lakes had different bacterial groups that maintain priority effects. Further, I found that as temperature increased, the chance for successful establishment of invading late-arriving bacteria declined. And even though some late-arriving bacteria can find space to colonize the occupied communities, they will not get huge space to increase their populations, they need to be living on a budget when climate changes drastically and aquatic ecosystems gets warmer.

But why is it so important that I spent more than 4 years on it? Investigating, and most importantly understanding priority effects in nature could help us to predict how communities assemble, how they will be assembled in the future, and how communities inhabiting aquatic habitats respond to shifts in environmental conditions, fluctuations or to climate change. Scientists in other fields can also use these findings as analogues in their research studies. For example, doctors need to consider that giving probiotics to a patient, or doing a fecal transplant therapy will not necessarily work due to the “first come, first served” phenomenon present in our gut microbiota. Or, just to mention another example, researchers in agriculture need to test when and how they should inoculate microorganisms (usually symbiotic fungal species) into the soils in order to promote the growth and fertility of plant because now we know that the immigration history does matter. Examining community assembly processes such as priority effects and for this, working with microorganisms and using small waterbodies such as ponds are extremely useful tools to rapidly gain knowledge in this field of community ecology.

But of course, this is not all. Many questions remained unanswered or were raised during my studies that could represent the basis for future studies. Generally, studies should further investigate historical processes that can shape communities, and develop statistical tools that could allow us to easily detect if a community is bound to the past.
Mikroorganismer, eller mikrober, är små varelser med extremt stor mångfald. I gruppen ingår alla mikroskopiska encelliga organismer och cellkolonier. De finns i nästan alla habitat på jorden och dessutom som mikrobiota i och på multicellulära organismer. Trots sin ringa storlek åstadkommer de mycket: de är en aktiv del av näringsflöden och i kolcykeln. De bryter ner alla former av dött material och utgör en näringskälla för andra organismer (det vill säga konsumenter) och de kan till och med agera som ingenjörer och ändra sina egna livsmiljöer. Många gånger har de dock inte tillräckligt med utrymme för att leva tillsammans, eller så kommer de inte överens i en given livsmiljö. Därför kan det ibland hända att vissa mikroorganismer kämpar om samma resurser och resultatet av konkurrenser avgör vilken art som finns kvar och vilken som måste lämna platsen. Alla former av interaktioner mellan mikrober formar de ekologiska samhällena (d.v.s. alla arter på en viss plats) vilket ger upphov till variationer i sammansättningen av samhällen över tid och rum.

En av de största utmaningarna för mikrobiella ekologer är att klarlägga vilka processer det är som formar samhällssammansättningen och hur olika faktorer (till exempel global uppvärmning) påverkar dessa processer. Varför? Det är för att vi har en optimistisk dröm om att vi till slut kommer att kunna förutsäga sammansättningen av mikrobiella samhällen i en given miljö, på en viss plats eller vid en viss tidpunkt. Vi vill också kunna förstå hur förändringar i miljön kommer att påverka ekologiska samhällen och deras roll för ekosystemens funktion.

anländer senare att framgångsrikt etablera populationer i denna redan befolkade livsmiljö, helt enkelt för att de anlände för sent. Om mängden senare kolonisatörer som anländer till livsmiljön är stor, har de en större chans att tränga ut de tidiga kolonisatörerna i livsmiljön t ex genom konkurrens. En sådan process kan påvisas genom att man observerar sammansättningen av samhällen över tid och iaktta förändringar. Det finns ett ökande vetenskapligt stöd för att "först till kvarn"-fenomenet, även kallat prioritetseffekten, är vanligt i ekologiska samhällen. Vid de tillfällen som prioritetseffekterna är viktiga, formar den slumpmässiga ordningen kolonisatörerna anländer i, kallad immigrationshistoriken, sammansättningen av samhällena. Detta är anledningen till varför samhällen kan vara kopplade till det förrutna.

I mina doktorandstudier undersökte jag prioritetseffekter från många olika synvinklar; genom fältarbete, ett mesokosmexperiment i naturen och laboratorieexperiment. Jag var nyfiken på huruvida bakteriella och mikroekologiska samhällen (mikroskopiska eukaryota organismer som mikrosvampar, alger, protozoer) utsätts för prioritetseffekter i naturen, exempelvis i hällkar (pölar i stenhällar på stranden). Då klimatförändringarna förutspås leda till ökande fluktuationer i många miljöfaktorer och ett varmare klimat var jag nyfiken på hur dessa faktorer kan påverka existensen och betydelsen av prioritetseffekter i bakteriella metasamhällen.

Mina resultat visade att prioritetseffekter kan observeras i små hällkar även efter en kraftig förändring i miljöförhållandena efter ett intensivt regnväder. Detta gällde dock bara i bakteriella samhällen och inte för mikroekologiska. Samhällssammansättningen av mikroveukaryoter visade sig också vara mindre stabil efter stormen jämfört med deras bakteriella motsvarigheter. Därnäst intresserade jag mig för hur kraftig miljöpåverkan måste vara för att undergräva prioritetseffekter i bakteriella samhällen. För att undersöka detta skapade jag och mina kolleger ett konstgjort metasamhälle som innehöll mesokosmer i tre olika storlekskategorier. Vi antog att storleken skulle avspeglas i fluktuationer i miljön så att ju mindre mesokosmerna var, desto större skulle fluktuationerna bli. Resultaten gav inget stöd för prioritetseffekter i dessa samhällen och vi kunde därför inte undersöka om prioritetseffekter är vanligare i mer varierande eller i mer stabila miljöer. Trots att orsakade de starka fluktuationerna i de små dammarna konstanta störningar i samhällena och prioriteringseffekter kunde inte etableras över tid.

allt, för jag ville också ta reda på vilka grupper av bakterier som ger upphov till prioritetseffekter. Till exempel var ett av mina mål att identifiera vilka av de tidiga kolonisatörerna som är kvar och vilka som försvinner efter en invasion. Jag identifierade grupper av bakterier bland de invaderande bakterierna som kan minska prioritetseffekter och också de som inte orsakade förändringar i samhället de invaderade. Resultaten visade att olika sjöar innehöll olika grupper av bakterier som upprätthöll prioritetseffekter. Jag observerade också att sannolikheten för en framgångsrik etablering av invaderande arter minskade när temperaturen steg. Även om vissa av de senare kolonisatörerna kan hitta utrymme att kolonisera de redan upptagna samhällena kommer de inte att få något större utrymme för att utöka sina populationer, utan de kommer att behöva leva snält när klimatet förändras drastiskt och akvatiska ekosystem blir varmare.

Men varför är detta så viktigt att jag har tillbringat mer än fyra år med att studera det? Att studera och framför allt förstå prioritetseffekter i naturen kan hjälpa oss förutsäga hur samhällen uppstår, hur de kommer att sättas samman i framtiden och hur samhällen som finns i akvatiska livsmiljöer reagerar på ändrade miljöförhållanden, fluktuationer och klimatförändringar. Forskare inom andra fält kan också använda dessa upptäckter att jämföra med i sina forskningsstudier. Till exempel behöver läkare som ger probiotika till en patient, eller gör en fekaltransplantation, inse att dessa inte alltid kommer att fungera på grund av "först till kvarn"-fenomenet i vår mag-tarmbakterieflora. Ett annat exempel är att forskare inom jordbruk behöver undersöka när och hur de bör ympa mikroorganismer (vanligtvis symbiotiska svamparter) i jorden för att främja tillväxt och bördighet, eftersom vi har kunskap om att immigrationshistoriken kan spela en roll. Att arbeta med mikroorganismer, samt att använda små vattendrag som dammar och pölar är mycket användbara verktyg för att snabbt skaffa kunskap om hur samhällen sätts ihop.

A mikroorganizmusok, azaz a mikróbák rendkívül fajgazdag élőlénycsoportjába mikroszkopikus méretű egysjejtűek vagy azok telepeit (kolóniáit) soroljuk. A mikróbák a Föld szinte bármely részén megtalálhatóak, csakúgy, mint bármely többsejtű élőlény (ilyenek vagyunk mi is, emberek) testfelületén, vagy azon belül (pl. a bélfloránkban). Annak ellenére, hogy szabad szemmel a mikróbák legtöbbször láthatatlanok, mégis rengeteg hasznos munkát végeznek: aktívan részt vesznek különböző tápanyagforgalmakban és a szén körforgásában. Lebontanak mindenmű elhalt élőlényeket és azok telepeit (kolóniáit) soroljuk. A mikróbák a Föld szinte bármely részén megtalálhatóak, csakúgy, mint bármely többsejtű élőlény (ilyenek vagyunk mi is, emberek) testfelületén, vagy azon belül (pl. a bélfloránkban). Annak ellenére, hogy szabad szemmel a mikróbák legtöbbször láthatatlanok, mégis rengeteg hasznos munkát végeznek: aktívan részt vesznek különböző tápanyagforgalmakban és a szén körforgásában. Lebontanak mindenmű elhalt szerves anyagot, de ők maguk is tápanyagként szolgálhatnak más szervezetek (fogyasztóik) számára. Nem mellesleg, saját élőhelyeik környezeti adottságait is képesek megváltoztatni, akárcsak egy szorgos mérnöksapattal. De sok esetben nem áll rendelkezésre elég élőhely, hogy jól kijöjjenek egymással, hogy együtt tudjanak élni nyugalomban. Ezért előfordulhat, hogy néhány mikróba harcban áll bizonyos tápanyagforrásokért, és emiatt a kialakult versengés (kompetíció) kimenetele fogja eldönteni végősorom, mely mikróba maradhat, és melly az, akinek mennie kell. Ilyen és ehhez hasonló interakciók sokasága alakítja ki és formálja az ún. ökológiai közösségek sokaságát, azok fajosztételében (kompozíciójában) felléphető térbeli és időbeli variációnak is.

Mikrobiális ökológusok számára az egyik legnagyobb kihívást az jelenti, hogy megértsük, feltérképezhessük, mely folyamatok, mechanizmusok és interakciók formálják a közösségek fajosztételét, valamint, hogy a különböző külső tényezők (pl. a klimaváltozás következményeként észlelhető felmelegedés) miképp befolyásolja ezeket a közösség alakító folyamatokat. Hogy miért? Egyszerűen azért, mert többek között az az optimista álom vezérel minket, hogy egyszer képesek leszünk előre jelezni, megbecsülni, mely fajok, mikróbák, képesek közösségeket kialakítani egy adott környezetben, időben vagy akár térben. Meg akarjuk ismerni, hogy a környezetben végbemenő változások miképpen befolyásolják a közösségek egészét, és az általuk biztosított ökológiai rendszerek javait és szolgáltatásait.

De kezdjük a legelején, mikor egy élőhelyet még nem népesítettek be különféle élőlények. Ilyen új élőhelyeket alakíthatnak ki a környezetben végbemenő drasztikus változások, például, mikor egy pocsolya kiszárad, és a vizi élőlényeknek várnia kell egy újabb esőzésre, hogy ismét benépesíthessék az élőhelyet. Képzeljünk el egy ilyen vagy ehhez hasonló élőhelyet a kialakulása pillanatában. Ekkor a mikroorganizmusok különböző fajai készhen...
állnak, hogy a környező élőhelyekről, különböző terjedési csatornákon át benépesíthessék az újonnan képződött, szabad élőhelyet. Ezeket az élőhelyeket, ahol a közösségek fajai képesek terjedni egyik élőhelyről a másikra, akár egész hálózatot is kialakítva, úgynevezett metaközösségeknek hívunk. Természetesen, a terjedés során az első fajok (az első „telepesek”) érkezési sorrendjét véletlenszerű, úgynevezett random folyamatok határozhatják meg, hiszen a terjedésüket elősegítő folyamatok, mint például a szél aktuális iránya, az állatok vonulása, vagy a tengervíz peremé – melyek mind szállíthatnak mikróbákat egyik helyről a másikra –, mind-mind random folyamat. Ettől a ponttól kezdve, előfordulhat, hogy az „aki kapja, marja” elv alapján az első telepesek úgy formálják újdonsült élőhelyüket, vagy akár oly mértékben, hogy a később érkező telepeseknek nem lesz esélye megtelepedni a már foglalt élőhelyen. Egész egyszerűen azért, mert túl későn érkeztek. Habár, ha késve is, de tömegesen érkeznek, akkor nagyobb esélyük van – kemény harcok, versengek – átkiszorítani az első telepeseket vagy azok egy csoportját, és elfoglalni az élőhely felszabadított területeit. Ezért aztán a közösségek fajösszetételének időbeli nyomonkövetésével, és az abban bekövetkező változások detektálásával, ilyen és ehhez hasonló közösségalakító folyamatokat igyekvünk meg. Viszont egyre több kutatás világított rá arra, hogy az „aki kapja, marja” elv, mely az első telepeseknek (fajoknak) biztosít elősbséget egy élőhelyen, gyakran megjelenik. Sikeres közösségképző folyamat az okololóiai közösségek mindennapjaiban. Ezt a folyamatot a szakirodalomban elősbségi hatásnak nevezzük. Abban az esetben, ha az elősbségi hatás érvényesülne népszerű, a fajok érkezési sorrendje (migrációs múltja) határozza meg a közösség összetételét az azt követő időszakban. Emiatt fordulhat elő tehát az, hogy a közösségek a múlt rabjai, és azok fajösszetétele múltbeli eseményekhez kötött.

A doktori képzésem alatt ezt a jelenségkört vizsgáltam különböző szemléletekkel, terepi vizsgálat, természeti élőhelyen kialakított kísérleti közösségek, valamint egy laboratóriumi kísérlet megtartásával. Kíváncsi voltam, hogy a mikróbák sokszintű csoportján belül vajon a baktériumok és a mikroeukarióták (mikroszkopikus, sejtmaggal rendelkező szervezetek, mint pl. mikrogombák, algák, állati jellegű egyszejteknél) természetes metaközösségeiben fellelhető-e az elősbségi hatás. A globális klímaváltozás küszöbén, a szélsőséges környezeti ingadozások (fluktuációk) és a melegedő klíma jelentősége miatt arra is kíváncsi voltam, hogy mindezen folyamatok miképp változtatják meg az elősbségi hatás jelenségének előfordulását és jelentőségét a baktériumok által összekapcsolt metaközösségekben.

Sikerült az elősbségi hatás jeleit feltérképezzem természetes eredetű, alkalmi vízgyűlésekhez, ún. litotelmák mikrobiális közösségében, melynek múltjhoz köthető fajösszetételeit egy intenzív, viharos időszak, illetve egyéb telepesek (fajok) sem tudtak meggyengíteni. Ugyanakkor ez a jelenség csak a baktérium közösségekben volt megfigyelhető, mivel a mikroeukarióták
metaközösségét a viharos időszak jelentősen átalakította, nagymértékű változásokat generálva azok fajosszetételeiben.

Ezt követően felmerült a kérdés, hogy mégis milyen erős környezeti fluktuációra lenne szükség ahhoz, hogy az elsőbbségi hatás érvényét veszítsék. Ennek vizsgálatához kollégáimmal mesterséges „pocsolyákból” álló metaközösséget hoztunk létre arra szándékoztunk, hogy a mérsékelt környezeti fluktuáció, ingadozás éri őket (pl. a hőmérséklet napi ingása nagyobb mértékben befolyásolja a kisebb, mintsem a nagyobb víztérfogattal bíró pocsolyákat). Sajnos azonban nem sikerült döntő erejű bizonyítékokat szerezniünk arra vonatkozóan, hogy az elsőbbségi hatásvajon a szélsőségesen ingadozó vagy inkább a mérsékelt ingadozó, stabilabb élőhelyekben fordulhat-e elő gyakrabban. Legvalószínűbb, hogy az erősen ingadozó környezeti körülmények folyamatosan meggazdagítják a közösségeket, azok kialakulását, ezzel pedig nem tud érvényesülni az elsőbbségi hatás.

És végül, de nem utolsó sorban mi is a helyzet a melegedő klímával? Egy laboratóriumi kísérlet alkalmával több mint 100 tavi baktérium közösséget „keltettem életre” és hagytam őket fejlődni különböző hőmérsékleti szinteken. Mikor ezek az első telepesek baktérium közösségeket alakítottak ki a különböző hőmérsékleteken, teszteltem, hogy vajon mennyire ellenállóak idegen, tengeri baktériumok „megszállásával”, inváziójával szemben. Ily módon megbizonyosodhatottam, hogy a növekvő hőmérséklet milyen hatással lehet a jövőben az elsőbbségi hatás jelentőségére. Nos, az eredmények azt mutatják, hogy bizonyos mértékben a tavi baktérium közösségek képesek megtartani a kísérlet elején létrejött fajosszetételeiket. De ez még nem minden, ugyanis kíváncsi voltam, mégis mely korai telepes baktériumok, pontosabban baktérium csoportok felelősök az elsőbbségi hatás kialakításáért, illetve melyek azok, amiket a megszállás, az új telepesek jelenléte kiszoríthat a tavi közösségekből. E mellett, a másik irányból, a megváltás, vagyis a tengeri baktériumok szemszögéből is érdekelhetett a helyzet, tudni akartam, kik lesznek azok a tengeri megszállók, akik sikeresen benépesíthetik a már foglalt élőhelyeket, a tavi baktérium közösségeket. Az eredmények azt mutatták, hogy a különböző tavi közösségeknél különböző baktérium csoportok lehetnek felelősek megőrizni, a múthoz kötni közösségük összetételét. Ezzel párhuzamosan pedig, a melegedő klima korlátozza a megszállók sikeres megtelepedését. És ha mégis sikerül valamely tengeri baktériumnak megtelepednie, nem számíthatnak nagyfokú populáció növekedésre, ugyanis szüksős keretei között kell fenntartaniuk magukat, mikor a klímaváltozás beüt, és a vízi ökoszisztémák elkezdődnek felmelegedni.

Persze, de miért is érdekesek ezek a kérdések annyira, hogy több mint 4 évvel töltött megválaszolásukkal? Az előbbiekben bemutatott, természetben fellelhető jelenségek, folyamatok vizsgálatai és megértése segíthet minket abban, hogy előrejelzéshessük miképp formálódnak és alakulnak ki az élőlények közösségei, továbbá, milyen módon módosulhatnak mindezen
folyamatok a jövőben, és persze, hogy fognak a vízi mikrobiális közösségek reagálni a környezetükben végbemenő változásokra, ingadozásokra vagy éppen a klimaváltozásra. Más területeken munkálkodó tudósok támaszpontokra, ötletekre lelhetnek a doktori munkám során felkutatott eredményekben. Vegyünk erre egy pár példát. Az orvosoknak például figyelembe kell venniük, hogy a probiotikumok, vagy a bélyegyulladásoknál újabban felmerülő széklet-transzplantációs terápiák során nem minden esetben érhetnek el sikeres eredményeket a pácienseiknél, hiszen bélrendszerünk baktériumflórája az elsőbbségi hatás által érintett lehet. Hasonlóképpen, az agrárterületen dolgozó szakembereknek is figyelembe kell venniük, mi a legeredményesebb módja annak, hogy a termőtalajokat különféle termést fokozó mikróbákkal (leggyakrabban a termőnövényel szimbiózist kialakító mikrogombákkal) beoltsák. Mert ugye tudjuk: a „telepesek” érkezési sorrendje nem mindegy. A közösségeket kialakító és formáló mechanizmusok kutatása, a mikroorganizmusok megfigyelése, valamint a kisvíztestek kutatása kimondottan hasznos lehet, hiszen segítségükkel viszonylag gyorsan és egyszerűen gyarapíthatjuk tudományos ismereteinket.

De persze ez még nem minden. Számos megválaszolatlan kérdés, nem mellesleg újabb kérdések láttak napvilágot kutatásaim során, melyek megalapozhatják a jövő alapkutatásait. Nem mellesleg szükség lenne olyan új, statisztikai keretmódszerek fejlesztésére is, amik segítségével a közösségeket alakító mechanizmusok pontosabban feltérképezhetőbbek lehetnének, és amikkel egyszerűen megmondhatnánk, vajon egy adott közösség a múlt rabja-e.
Acknowledgements

What do you think, will you be able to cope with the “Swedish darkness” during winters? – asked me Eva during the interview, my first visit here in Uppsala, Sweden, five years ago. For this question, I naively said: *yes, of course.*

Well, I tried to survive the winters but it was not easy. It was sometimes tougher than the data I need(ed) to deal with. What made it easier, though, was the supportive, great working environment, the Limnology Department and its kind, diverse community.

It was a long journey with ups and downs, full of numerous good memories and many challenging days. I never expected that I was learning so much during these years. Besides gaining scientific knowledge, attending several conferences and workshops, I had the chance to get to know an amazing culture, a kind of mentality, and experience enormous amount of kindness that surrounded me here every day.

I am very grateful for you, Silke, to made this journey possible and let me to work with you. Thanks for your great ideas, your patience, and your tireless faith in the legacy of the past. Thanks for supporting me and all my travels to workshops and conferences, thanks for the discussions. Many things piled up on our desks in the last month, so thank for all your hard work, especially these days, when I’m writing these lines. I’m very impressed how well you maintained your calmness all this time, and how well you handled my stubbornness. Thanks for keeping me on the right track.

Eva, thanks for the great discussions, and for your interest in my results whenever I needed to present and/or explain them. Thanks for your hard work in following my journey. I will always be amazed by your happiness, cheerfulness, and by how you always look on the bright sides of everything. Thanks for showing me this, and thanks for your time and your leadership at the department.

Having blond hair and the name Anna doesn’t necessarily mean that the person is a Swede. I learnt this quite quickly, actually just after the interview, when I realized that Anna Sz. is also a Hungarian. Your presence made my first couple of months much smoother. You were the one who showed me the way in the labs, and provided numerous practical advices during these years. Thanks for completing a pedagogic course just to be able to co-supervise me. Your workaholic attitude impressed me a lot and many times showed me how hard I should (have) work(ed). Surely, you always loved to challenge ideas.
during our meetings, discussions, and even though it caused me super busy days during my last weeks, your ideas were certainly great.

Thanks for developing my critical thinking.

Thank you all for being my supervisors.

I would like to thank a few people, in no particular order, who made my work possible, kept my motivation alive, and made me love Sweden.

To Alina, thank you for being my true friend, understanding my sarcastic humor, sharing your love in art, and having long discussions about Hungary and Russia as we burnt million cigarettes down. I miss you.

To Karólina, thank you for your friendship, your never-depleting love and help, and spreading your ever-renewed energy all over the department and beyond that. Thanks for being always honest and straightforward.

To Fernando, my soon-to-be neighbor, thanks for letting me be your office-mate, for inviting me your parties and show me how good Spanish cuisine can be. Thanks for listening my complaints and support me in difficult times.

Thank you, Theresa, for your faith in our never-finished laboratory experiment, and your overestimation of my cooperative skills :) Thanks for the great time in Berlin, and your never-depleting kindness. And, of course, thanks for letting me be your ‘annoying older brother’.

To Xavi, thanks for your wise thinking, the great chats we had. Your tenacity impressed me many times. Keep it!

To Anna N., thanks for your friendship, for the great parties we had, and for showing how cool the Swedish culture is. Thanks for the great memories of Valborg and Midsommar. Och tack för inspirationen att lära svenska.

To Bianka for giving me company and made me laugh all the time.

To Matilda for being the president of the PhD group, and for organizing Halloween party and relaxing fikas.

Raven, thank you for letting me get involved in a great experimental study. Thanks for your kindness and the inspiring discussions no matter where we were.

To Vasiliki and Omneya, thanks for your assistance and work in the experiment. It was great to work with you.

Thanks, Christoffer and Janne, for all your support in the labs and your kindness.

To Anna B., thanks for giving me numerous opportunities to teach. I really appreciated it.

For reading this thesis in draft form, for your enormous amount of comments and feedbacks, thanks to Theresa, Silke, Eva, Anna Sz. and Peter.

To Johan, thanks for helping me with the Swedish summary.

Thank you, Sándor, for all your support, your interest in my research topic, and the great discussions when you let me to drawn stupid analogues between the phenomena in sociology/politics/economy and the microbial communities
that I had observed and got obsessed with. Thanks for making my days happier!

Thanks to some of my Hungarian friends, Kálmán, Dia and Bea, who visited Uppsala during these years.


To the superb team (current and former people) of the department who maintained a great working environment: Annika, JP, Stefan, Sara, G, Charlotte, Martin, Sara, Elizabeth, Dolly, Maliheh, Don, Kristin, Sebastian, Lars, Pablo, Holger, Gesa, Vicente, Yang, Jovana, Monica, Blaize, Yinghua, Omneya, Valeria, Maria, Alex, Moritz, Heli, Súria, Birgit, Katrin, Andreea, Haiyan, Baolin, Sophia.

To all fellow PhD students – Karólína, Fernando, Xavi, Matilda, Theresa, Ana, Fabian, Marloes, Lorena, Anastasija, Stephen, Nana, Rhiannon, Simone, Karla, Bianka –, I wish you all the best and remember:

“It always seems impossible until it’s done.” (Nelson Mandela)

Thank you all!
Tack!
Köszönöm!
References


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