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Assembly Mechanisms in Aquatic Bacterial Communities

The Role of Disturbances, Dispersal and History

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Dissertation presented at Uppsala University to be publicly examined in Friessalen, Evolutionary Biology Centre (EBC), Norbyvägen 18, Uppsala, Friday, October 25, 2013 at 10:00 for the degree of Doctor of Philosophy. The examination will be conducted in English.

Abstract
Berga Quintana, M. 2013. Assembly Mechanisms in Aquatic Bacterial Communities: The Role of Disturbances, Dispersal and History. Acta Universitatis Upsaliensis. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 1071. 56 pp. Uppsala. ISBN 978-91-554-8749-2.

Environmental conditions, biotic interactions, dispersal and history have been suggested to be important processes influencing the spatial distribution of organisms and thus to affect community assembly. Understanding how these processes influence community assembly is important, particularly because community diversity and composition are suggested to be relevant for ecosystem functioning. Moreover, bacteria are strongly contributing to nutrient and carbon cycle. Bacteria are highly abundant and ubiquitous, and thus it is relevant to study how they are assembled. This thesis aims to gain insight on the role of these processes on aquatic bacterial community assembly, diversity and functioning. The studies included in this thesis involve transplant and microcosm experiments performed in the lab as well as manipulation experiments and field surveys in a natural rock pool systems. Bacterial community composition was addressed by analysis of 16S rRNA gene and community functioning by measuring bacterial production, community respiration, and the ability to use different carbon substrates. This thesis highlights that species sorting is a very important assembly mechanism for bacterial communities, but also finds that other processes such as dispersal and history contribute to the patterns observed. Dispersal caused rescuing effects compensating for losses of diversity; at the same time it increased the similarity between communities. Moreover, bacteria have shown a high level of functional plasticity when colonizing a new locality. Interestingly, past environmental conditions explained the structure of bacterial communities better than present-day environmental conditions. Disturbances and biotic interactions are also important in the assembly of communities. Disturbance caused temporary shifts in bacterial function and changes in composition, the magnitude of which depended on the intensity and the frequency of the disturbance. However, natural aquatic bacterial communities showed quite high resilience capacities. Competition can shift the proportion of generalists and specialists species whereas predation or trophic interactions have been found to decrease diversity and to modify the importance of stochasticity. Both caused alterations of community functioning. Finally, this thesis shows that the diversity-functioning relationship is context dependent. Further research should be directed to understanding the intensity and direction of changes in composition and how this affects the functionality of bacterial communities

Keywords: diversity, community composition, metacommunity

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To my family

List of Papers

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

I   Berga, M., Székely, A.J. and Langenheder, S. (2012) Effects of disturbance intensity and frequency on bacterial community composition and function. PLOS One 7(5):e36959.

II   Berga, M., Székely, A.J. and Langenheder, S. Testing responses of bacterial communities to disturbances using whole ecosystem manipulation experiments (manuscript).

III   Székely, A., Berga, M. and Langenheder, S. (2013). Mechanisms determining the fate of dispersed bacterial communities in new environments. The ISME Journal 7: 61-71.

IV   Andersson, M., Berga, M., Lindström, E.S. and Langenheder, S The spatial structure of bacterial communities is influenced by historical environmental conditions (submitted).

V   Berga, M., Östman, Ö, Lindström, E.S. and Langenheder, S. Effects of predation and dispersal on the diversity and functioning of bacterial metacommunities (manuscript).

Contents

Abbreviations

16S rRNA	16S Ribosomal Ribonucleic Acid
DNA	Deoxyribonucleic Acid
OTU	Operational Taxonomic Unit
CSUR	Carbon Substrate Utilization Rate
NMDS	Nonmetric Multidimensional Scaling
ANOVA	Analysis of Variance

Motivation for this thesis

Each ecosystem on the planet has a specific role. From forests to the sea, from lakes to rivers; all these environments and the organisms inhabiting them are relevant to life on Earth. Some organisms fix CO_2 from the atmosphere through photosynthesis, others control plagues by predation. Others, like bacteria, are important for nutrient cycling and the degradation of organic matter while sustaining the biomass and production of other organisms. Thus, bacteria are of key importance for the functioning of ecosystems. Moreover, bacteria are highly diverse and this can also influence the functioning of ecosystems. Hence, it is of major interest to study how many different bacteria are there, "who" is there, why or when, together with whom, how they respond to changes in their environment, and how all this affects their ability to implement ecosystem functions.

Many of these questions have been answered for larger organisms, however, we are just starting to find the answers for bacteria. Several reasons exist for this lack of knowledge, the first one being that their small size makes it difficult to count and to distinguish them. This is, however, changing now due to rapid technological developments. A second aspect is their metabolic complexity since bacteria can perform many different processes as a group but also as individuals and even adapt their 'functional repertoire' depending on the environment they are in. This is as amazing as it is complex to study.

Working with bacteria offers many challenges but also provides the opportunity to gain an understanding of mechanisms governing the distribution and function of an ecologically relevant group of organisms. The main motivation behind this thesis is therefore to gain knowledge about bacterial communities, how they respond to changes in their environment and how the inter- and intra-specific relationships influence their diversity and the functions they perform at the local and broader spatial scales. The thesis starts by providing some background to ecological theory and concepts that have mostly been developed for larger organisms and relates it to what is known for bacterial communities, including e.g. disturbance-diversity and diversity-functioning relationships and the metacommunity framework.

Introduction

Bacterial communities: diversity and its drivers

Microorganisms are abundant, i.e.; more than 10^7 to 10^{10} cells can be found in 1 cm^3 of soil or 10^5-10^7 cells in 1 milliliter of water (Torsvik et al. 2002; Whitman et al. 1998).

Bacterial communities are made up of different bacterial species that occupy the same habitat at different abundances and interact with each other. Thus, community composition is described by the number of species present (species richness), their relative abundance and their identity.

Characterization of bacterial communities has however, been limited by the fact that microbial ecologists for a long time have had trouble in defining a bacterial species. None of the existing definitions of species based on either morphology, physiology or reproduction, is really appropriate for bacteria. There is still much debate about it, and nowadays one of the most commonly used species concepts in microbiology is the so called "phenetic species concept" in which the smallest units are so-called Operational Taxonomic Unit (OTUs) (Rosselló-Mora & Amann 2001). OTUs can be defined in different ways and in relation to the technique used, and thus has been influenced by new technologies (Nocker et al. 2007). Culturing independent methods are usually based on the analysis of 16S rRNA gene and typically, sequences of the 16S rRNA gene that are 97% or more similar will be grouped together and considered one OTU. Note, that to simplify the reading and avoid confusion of terms between what it is usually used in general ecology I will use the term species instead of OTU throughout this text.

In ecology, diversity is widely used as a characteristic or descriptor of communities, allowing for a comparison of communities. Diversity is related to community composition and it can be expressed as *species richness*, *evenness* (the distribution of the abundances of each of the species in the community), or as a combination of the two (*Shannon diversity index (H');* Whittaker 1972; Hamilton 2005). A community with a high number of species that are equally abundant will show high Shannon values, indicating a highly diverse community. Diversity can further be measured at different scales (Whittaker 1972); in a single sample or locality known as *local diversity (α-diversity)* or, in cases when larger spatial areas are of interest, as the total of several samples or localities known as *regional diversity (γ-diversity)*. Diversity can also be measured between communities, which is

defined as *β-diversity*. This is used to compare communities over time (*temporal community turnover*) or between locations (*spatial community turnover*) and is expressed as dissimilarity/similarity. Bray-Curtis dissimilarity is one of the most common metrics in microbial ecology (see Anderson et al. 2011 for an overview of other metrics) and also the metric used most frequently in the studies included in this thesis. Another method to calculate β-diversity is the so called "*True-beta diversity*", in which the dependence of the changes occurring in both, local and regional diversity, is excluded from the calculation (Jost 2007, 2010). A more recent concept of diversity is *phylogenetic diversity* (PD), which is based on phylogenetic relations among any set of species (Faith 1992). PD of a community is measured as the sum of the lengths of the branches in a phylogenetic tree of all the members of the community, indicating the magnitude of divergence among the members of the community (Hugenholtz et al. 1998; Lozupone et al. 2006; O'Dwyer et al. 2012).

The patterns of diversity differ among environments (Gaston 2000) and also over time and this is the result of several factors acting on the assembly of communities. Assembly mechanisms have for a long time mostly been related to niche theory (species trait – environment relationships) (Hutchinson & MacArhtur 1959), however, it has been shown that stochastic processes and processes occurring at larger spatial scales are also important. Therefore, there is still a debate about the extent to which these mechanisms are important and also how they interact with each other. While the niche theory focuses on deterministic processes such as environmental filtering and biotic interactions, the neutral theory focuses on stochastic processes such as random colonization, random extinctions and ecological drift (Hubbell 2001). The metacommunity framework (Leibold et al. 2004), integrates local and regional processes, in particular dispersal, to understand the mechanisms that determine the composition of communities in a location. It describes four scenarios that are differentiated by the degree of dispersal between the communities and the heterogeneity among localities. These scenarios are: 1) Patch dynamics, which presumes that there are no environmental differences among the localities, so that colonization-competition trade-offs determine species composition, 2) Species sorting, which presumes that dispersal among localities is not limited and that local environmental conditions cause filtering of species, 3) Mass effects where dispersal is very high and can 'override' effects of environmental filtering at different locations and finally 4) The neutral model, which presumes that all species are similar in terms of their traits and thus that communities are mainly stochastically assembled (Leibold et al. 2004).

Abiotic factors and disturbances

Many environmental parameters have been shown to define the distribution of bacteria, including salinity, pH, temperature, nutrients availability and oxygen concentration (Lozupone & Knight 2007). These parameters can be seen as 'filters' for communities because each species has its environmental requirements and range of tolerance towards changing conditions. Depending on their requirements and range of tolerance species can be distinguished as *habitat specialists* that perform well and will be abundant only under very specific environmental conditions or *habitat generalists* that are able to survive and thrive in a wide range of environments (MacArthur & Levins 1964). However, it is important to keep in mind that habitats are not defined by a single parameter, and thus defining a species' niche is not easy.

Moreover, in many systems the environment is not stable and changes either gradually or as a result of *disturbances, i.e.* stochastic events that either directly affect a community or modify the environment of a locality with possible repercussions on the community. Disturbances can occur at different spatial scales, with different intensities, at different frequencies and can differ in duration. Pulse disturbances are short-term disturbances whereas press disturbances are continuous over a long period of time. The responses of communities to one or the other are different and it has been suggested that communities are more able to adapt to pulse disturbances than to press disturbances (Bengtsson 2002). According to the insurance hypothesis (Yachi & Loreau 1999), communities with more species are supposed to be more stable because they are more likely to include species that can tolerate the disturbance. Stability can be addressed by measuring the *resistance* and the *resilience* of communities. Communities will be resistant when they can withstand the disturbance so that no compositional change occurs, whereas they will be resilient when the community is able to quickly recover and return to its original composition (Pimm et al 1984). Moreover, communities also respond functionally to disturbances, showing alterations (Figure 1). Finally, disturbances can also lead to a completely altered community or a shift to a new and *alternative stable state,* in cases where the community has neither been able to withstand nor to recover from a disturbance. Many organisms, including bacteria, have the capacity to enter in dormancy at some stage of the life usually as a response to changes in environment. *Dormancy* is found when the organisms enter a reversible state of reduced metabolic activity and is an example of *phenotypic plasticity* (Caswell 1983; Jones & Lennon 2010).

It has been suggested that disturbances at low intensities increase diversity by altering biotic interactions. In contrast, when disturbances are very strong only a few species can survive. Consequently, a hump-shaped relationship between disturbances and diversity, known as the Intermediate Disturbance Hypothesis, is expected (Connell 1978). However, it has recently

been suggested that this hypothesis should be rejected because neither empirical studies nor theoretical studies show evidence for it (Fox 2013).
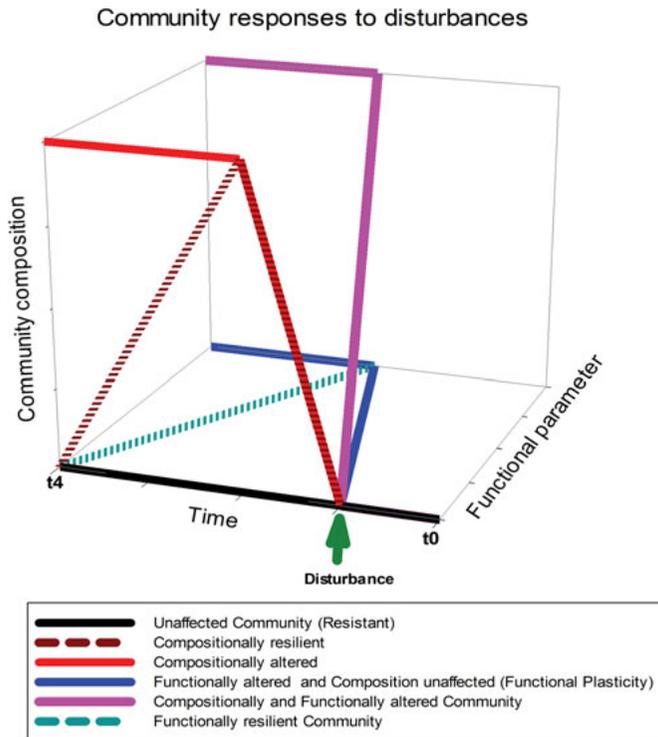
Figure 1.Possible responses of bacterial communities to disturbances, including both compositional and functional responses.

Biotic factors

Communities are associations of populations of different species and thus organisms with different trophic strategies, including predators, primary producers or heterotrophic organisms, cohabitate the same place. This leads to inter-specific interactions such as predation. *Predation* is a factor that can change community composition, reduce diversity, cause extinctions and modify competition among prey species. However, the effects of a predator on a community will depend on the type of predator and the susceptibility and traits of the prey (Shurin 2001; Leibold 1996; Chase et al. 2002). In aquatic systems, it has been shown that direct predation by heterotrophic nano-flagellates (HNF) and direct or indirect predation effects of cladocerans, such as *Daphnia magna,* can alter the abundance, cell size and the composition of bacterial communities (Langenheder & Jürgens 2001; Jürgens & Matz 2002; Pernthaler 2005; Degans & De Meester 2002).

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Moreover, each species has specific traits that result in different growth rates, nutrient efficiency or environmental tolerance, but these might overlap leading to *competition* between species. Competition implies negative effects of one species on another and it is mainly driven by resource availability. Therefore, species that can survive at low resource levels will most likely out-compete other co-existing species (Leibold 1996). Moreover, predation has the potential to modify competitive interactions by adding limiting factors, selecting a competing dominant organisms or by causing behavioral changes related to the use of specific substrates (Chase et al. 2002).

Dispersal

One of the most important regional factors is *dispersal* of organisms from surrounding communities. Dispersal is, thus, a rather stochastic factor and it involve both, the movement of organisms and their establishment at a location (Hanson et al. 2012). Dispersal can cause changes in community composition and function (Cadotte et al. 2006), but the magnitude of the change will depend on the abundance of organisms that are dispersed (dispersal rate) as well as their ability to successfully colonize the new location. Low to intermediate dispersal rates are likely to increase local community diversity because organisms from other localities can be present in more localities or because dispersal can compensate for species losses by predation or extinctions (*rescuing effects)*. On the other hand, high dispersal rates can cause mass effects, which leads to a strong homogenization of the communities (decreases in beta-diversity) as well as decreases of regional diversity. Local diversity can either increase when dispersal rates are very high because most of the empty niche space can be filled, or decrease because the most competitive species will be everywhere (Mouquet & Loreau 2003).

History

Historical and evolutionary events also influence the composition of communities at a specific time and place (Leibold et al. 2010). They include processes that occur at evolutionary time scales such as mutation, selection and genetic drift, as well as more recent processes such filtering by past environmental conditions (Martiny et al. 2006, Hanson et al. 2012). Dispersal limitation allows historical events to be reflected upon present-day community composition. Dispersal limitation can lead to *diversification* by genetic drift over time, i.e. changes in gene frequencies in a population caused only by chance (Martiny et al. 2006), but can also cause extinctions of species in a community leading to increases in beta-diversity. Moreover, spatial variation of bacterial communities could be explained by contemporary environmental conditions or historical contingencies, such as past environmental

conditions (Martiny et al. 2006), but few studies have address their relative importance.

Finally, the colonization history of a community can lead to *priority effects*. Here, the arrival sequence of colonizers affects community composition, with earlier colonizers being favored when new colonizers arrive just because they were there earlier and could adapt successfully to the environmental conditions of the colonized habitat (Drake 1991).

Rock pools: great study systems

Systems ideal for studying different processes involved in bacterial community assembly are rock pools. Rock pools are bedrock depressions filled with water. They are small in size and well-defined water entities that are easy to sample and to manipulate. The pools are primarily freshwater systems fed by rainwater but also from occasional sea spray. There is large variability among pools in terms of environmental conditions, such as salinity, pH, water color and nutrient concentrations, leading to different bacterial communities (Langenheder and Ragnarsson 2007). Rock pools also show strong temporal fluctuations in environment conditions and are therefore systems where disturbances occur naturally, e.g. in the form of drying events, changes in salinity and the presence of predators (e.g. Langenheder et al. 2012). Increases in salinity can be caused via sea spray inputs and evaporation.

Aquatic bacterial communities inhabiting these rock pools have been used in all the studies included in this thesis.

Relationships between biodiversity and ecosystem functioning

Diversity has in most cases positive effects on ecosystem functioning (Cardinale et al. 2006). One of the reasons for positive relationships between diversity and ecosystem function is complementarity, suggesting that species richness enhances a particular function, such as productivity, because the different species have different resource niches and because facilitation among species can occur (Loreau & Hector 2001; Venail et al. 2008).

Another mechanism explaining positive relationships between diversity and ecosystem functioning is that by chance, higher diversity increases the odds of including species that are particularly good or efficient in implementing the function in question, which is known as selection effects (Huston 1997). Another frequent pattern for diversity-functioning relationships is functional redundancy, which is found when many species can perform the same function at the same or similar rates, so that the positive bio-

diversity-functioning curve levels off at a certain level and adding more species does not lead to further increases in functioning (Walker et al. 1992, Johnson et al. 1996).

However, many different types of relationships and even no relationships have been observed in the literature, in particular for microorganisms (Ducklow 2008). Idiosyncrasy has often been suggested in natural communities, this is when no patterns or relationship is observed between diversity and ecosystem function (Lawton et al. 1994) and it has been pointed out that this is likely to occur because community composition, and thus, the identity of the species present is more important than species richness (Symstad et al. 1998; Petchey & Gaston 2002).

'Knowns' and unknowns

It is known that many of the processes mentioned above with regard to assembly mechanisms affect bacterial communities (Hanson et al. 2012). To summarize, it has been shown that bacterial communities are usually assembled mostly by species sorting (Jones & McMahon 2009; Logue & Lindström 2010; Van der Gucht et al. 2007; Langenheder & Ragnarsson 2007), reflecting the importance of the environmental conditions found in a location. On the contrary, mass effects have been suggested to occur only rarely in bacterial communities and could only be found at very high dispersals (Lindström & Östman 2011). Neutral effects in bacterial communities have been observed in some studies (Drakare & Liess 2010; Sloan et al. 2006). It has also been observed that assembly mechanisms can differ among habitats and bacterial groups (Barberán & Casamayor 2010), and that they can act simultaneously on communities. With regard to the latter it has, for example, been shown that both species sorting and neutral process occur during the colonization of new and sterile habitats (Langenheder & Székely 2011).

The notion that environmental conditions have effects on bacterial community assembly has lead to many studies and an increasing interest to understand how bacterial communities respond to disturbances. It has been shown that bacterial communities are in general not resistant to disturbances and that they are, in some cases, also resilient (Allison & Martiny 2008; Shade et al. 2012). Some studies have reported increased resistance or resilience to disturbances when these have occurred before (Bressan et al. 2008; Mitchell et al. 2009) suggesting that adaptation to environmental changes is important. In bacterial communities a large fraction of the adaptation mechanisms are linked to lateral gene transfer (Achtman & Wagner 2008). Moreover, communities also respond functionally to disturbances, showing alterations, recovery or functional plasticity, the latter being observed when functional changes are not accompanied by changes in composition in response to a disturbance (Comte & Del Giorgio 2011). Another strategy that bacteria can adopt is dormancy where cells enter a state of reduced metabolic activity that can be kept for long time, and helps promote the recovery of communities after disturbances (Jones & Lennon 2010).

Predation has been observed to control bacterial biomass in aquatic systems (Pernthaler 2005; Jürgens & Matz 2002) and competition has been observed in microbial communities when nutrient availability declines

(Miller & terHorst 2012; Hibbing et al. 2010). With regard to regional factors, dispersal has been shown to create rescuing effects (Drake 1991) and dispersal limitation has also been observed (Declerck et al. 2013). Finally, two main approaches have been used in microbial ecology to study diversity-functioning relationship, which are either based on using culture experiments with artificially constructed communities (e.g. Bell et al. 2005) or the dilution-to-extinction approach (Szabo et al. 2007; Peter et al. 2011). Bell et al. (2005) found a significant positive and decelerating relationship between species richness and respiration rate, whereas other studies showed that rates of many functions are rather driven by the presence of certain key species (e.g. Peter et al. 2011). In general, it is currently still unclear how different facets of bacterial diversity, including richness and evenness, are related to ecosystem function.

Even though microbial ecologists have addressed many aspects of the processes that affect bacterial community assembly, we still do not know under which circumstances the different assembly mechanisms prevail, how they interact, and how they influence not only the composition but also the diversity and functioning of communities. More specifically, we lack information about the importance of historical processes, the importance of biotic factors, interactions between predation and dispersal or dispersal and environmental filtering. Finally, we also lack knowledge on how the strength of the disturbances (e.g. their intensity and frequency) affects the resistance and resilience of bacterial communities particularly in field studies.

Aims

The overall aim of this thesis is to gain insights into the factors and processes that regulate the assembly of aquatic bacterial communities focusing on the importance of environmental conditions and environmental changes, i.e. disturbances, and biotic interactions such as predation. Furthermore the aim is to identify how these factors interact with history and dispersal to modify bacterial communities.

More specifically, the aim of **Paper I** is to investigate how the strength of a salinity disturbance (its intensity and frequency) influences the compositional and functional resistance or resilience of bacterial communities. In **Paper II**, I aims to identify how natural communities, more specifically rock pool bacterial communities respond to changes in salinity and to identify the importance of dispersal and thus the influence of new colonizers for community recovery. The aim in **Paper III** is to address what mechanisms are driving a successful colonization of a new habitat and to disentangle the importance of environmental filtering and biotic interactions (competition). The main aim of **Paper IV** was to identify whether historical processes and more specifically past environmental conditions are important to explain the spatial distribution of present-day bacterial communities. Finally, the aim in **Paper V** was to investigate the effects of predation and dispersal on α-, β- and γ-diversity as well as the functioning of bacterial communities.

Methods

Experimental approaches

Disturbances

In **Paper I, II and III** salinity was used as the main disturbance. *Salinity* is known to be the most important environmental factor influencing the composition of aquatic bacteria generally (Lozupone & Knight 2007, Nold and Zwart 1998, Glöckner et al 1999, Newton et al. 2011), as well as in the rock pool systems used in this thesis (Langenheder et al. 2012). Moreover, salinity has lead to clear evolutionarily differences in the species composition of freshwater and marine systems with rare transitions (Zwart & Crump 2002; Logares et al. 2009). In **Paper IV** salinity is also an important structural force, even though the changes of salinity were not experimentally modified but occurred naturally.

In **Paper V** the introduction of a predator, more specifically *D. magna*, was considered as a biotic disturbance.

Transplant experiments with dialysis bags

Transplant experiments are useful to study effects of disturbances since they offer the possibility to move communities between different environments and they have been used in a reciprocal design to test effects of microbial community composition versus local environmental conditions on ecosystem functioning (Reed & Martiny 2007). Dialysis bags are very suitable for the implementation of such experiments (Gasol et al. 2002). They are made out of membranes of a certain pore size through which smaller particles (nutrients and salt) can cross following a concentration gradient whereas larger particles, like bacteria, remain inside the bags. Here, I have used dialysis bags to test the effect of environmental change on community composition and/or functioning in two papers.

In Paper I a transplant experiment with dialysis bags was used to test how freshwater bacterial communities respond to increases of salinity that differ in their intensity and frequency and whether or not they are able to recover once the salinity decreases. To test the effect of disturbance intensity bacterial communities were transplanted from freshwater conditions to envi-

ronments with different salinities (3, 5, 10, 15 or 20 ppm). After the incubation period, the bags were moved back to freshwater conditions to test for the recovery capacity of the communities (Figure 2A). Moreover, to test whether disturbance frequency affects community composition the bags were swopped between freshwater and 20 ppm conditions at different intervals: never (control), once, twice, three times or four times. I sampled each bag three times, at the beginning, right before moving them back to the freshwater tank and at the end of the experiment (Figure 2B).
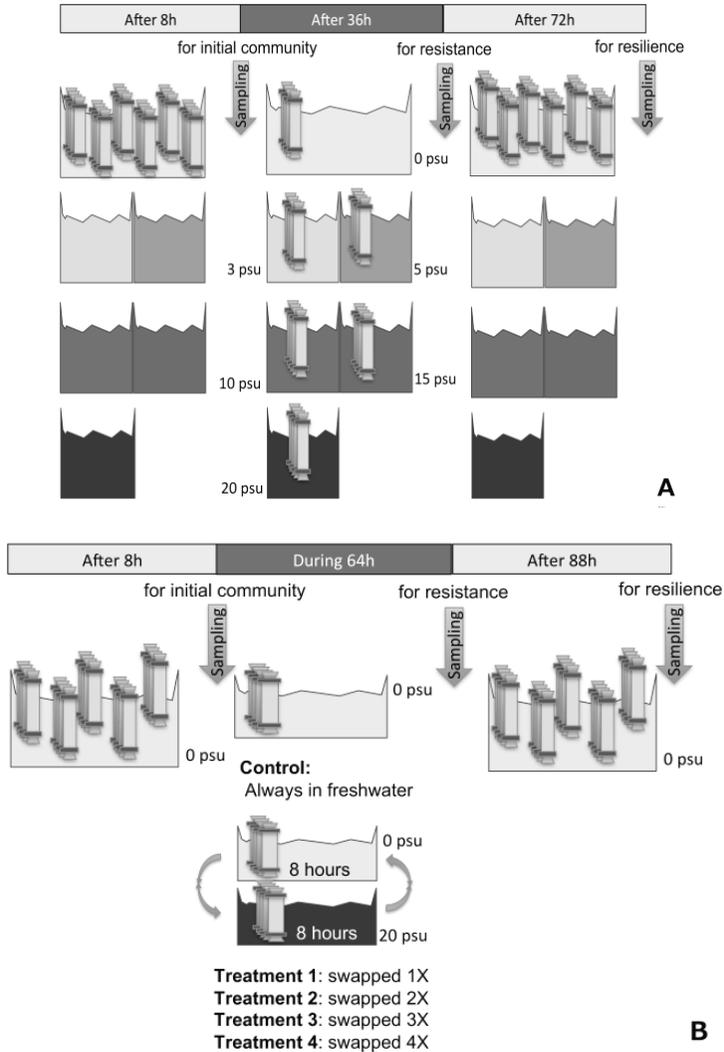

Figure 2. Experimental set-ups used to study the effect of disturbance intensity (A) or disturbance frequency (B). Psu is an equivalent to ppm, a measure of salinity.

In **Paper III** a reciprocal transplant experiment was performed to test the effect of the change in abiotic conditions for bacterial communities that enter a new environment. Both, freshwater and brackish water (termed saline) bacterial communities were incubated under freshwater and saline conditions (See Figure 1 in **Paper III** for a scheme of the experimental set-up). To test potential effects of interactions between local and dispersed communities, I also included a mixed community that contained equal proportions of both source communities. Finally, I also implemented the experiment with pre-adapted communities to test how this influences the establishment success, functional performance of dispersed communities and their interactions with local communities.

Microcosms

Microcosms are probably the most used systems for experimental studies in microbial ecology. I used such a set-up in **Paper V** to study the effects of predation and dispersal on aquatic bacterial metacommunities, in terms of community composition, diversity and functioning at all metacommunity levels. I constructed metacommunities consisting of 3 patches, which were all filled with zooplankton-free water from one of the following rock pools: freshwater, brackish water or humic water. A 2-way factorial design was performed with presence of a predator (presence or absence of *D. magna*) and dispersal (three different levels; 0, 5 or 15 %) as factors. This allowed me to test for independent effects of predation and dispersal as well as for combined effects.

Rock pools as natural "mesocosms"

Whole ecosystem manipulation experiment

The study area is located on the island of Gräsö, Sweden, at the Baltic Sea coast, and contains at least 200 pools of which some are permanent whereas others are semi-permanent. In **Paper II** freshwater pools were manipulated to test the effect of salinity increase, at different intensities, on natural bacterial community. To study the response of these communities and possible resistance, salt was added to the pools and communities were sampled before and three days after the addition. Following, the pools were re-filled by rainfall, decreasing salinity to original values and then pools were sampled again to address potential recovery of the communities. To investigate the importance of bacterial dispersal by air or rainfall in the recovery of the pools, air and rain traps were placed out in the area in order to capture cells dispersing through air and rain. Finally, to test the relationship between diversity (richness and evenness) and functioning in natural bacterial communities I

studied the effects of changes in salinity both at compositional and functional levels.

Field study

In **Paper IV** a field survey was implemented based on 16 rock pools to investigate the influence of earlier environmental conditions on present-day community composition. Environmental parameters of the pools were measured every second day during a nine-day period and community composition was sampled at the beginning and the end of this period. During the duration of the experiment there was a rainfall event, which strongly reduced salinity leading to clear changes in the composition of communities. This event allowed me to test which conditions were more important in determining differences in community composition among the pools at day 9; the salinity levels prior to the rainfall or the more recent conditions after the rainfall.

Techniques to study aquatic bacterial communities

Molecular tools: T-RFLP and 454-sequencing

In **Papers I and IV**, Terminal Restriction Fragment Length Polymorphism (T-RFLP) analysis was used to assess changes in community composition. This fingerprinting method is based on fluorescently labeled 16S rRNA amplicons that are fragmented by restriction enzymes. Each fragment of a specific size is considered a different OTU (Liu et al. 1997). In **Papers II, IV and V** barcoded 454 pyrosequencing was used, which is also based on the amplification of the 16S rRNA gene, but where the amplified gene is sequenced. This method produces a high number of reads or sequences and allows us to estimate community richness and diversity and to identify OTUs (Roesch et al. 2007).

Functional parameters and bacterial abundance

Carbon substrate utilization rate (CSUR) was measured using Biolog EcoPlates[TM] (Garland 1997). Biolog EcoPlates[TM] allow to test the ability of bacterial communities to use a set of 31 different carbon substrates representing different guilds (carbohydrates, aminoacids, carboxylic acids, amine and polymers). I used this method to calculate the number of utilized substrates (**Paper I**) and the Carbon Substrate Utilization Rate (CSUR) of all substrates (**Papers I and II**) and/or specific guilds (**Paper I**). Community respiration rates were measured as a decrease in O_2 concentrations over time and bacterial production by measuring the leucine uptake of cells (Smith &

Azam 1992). Bacterial and flagellate abundance was estimated by flow cytometry after cell staining (Del Giorgio et al. 1996; Christaki et al. 2011).

Results

Effects of disturbance intensity and frequency (**Paper I**)

The transplant experiment with dialysis bags showed that both the intensity and frequency of a salinity disturbance were important parameters affecting the response of the community and its recovery capacity.

Changes in bacterial community composition in response to increases in disturbance intensity (increase in salinity to 3, 5, 10, 15 or 20, respectively) were only observed after the bags had already been moved back from saline to freshwater conditions, and were strongest in treatments exposed to highest salinities (Figure 3 A and B). On the contrary, functional parameters and abundance were already affected directly after salinity exposure, and showed a tendency to recover to control levels after the incubation under freshwater conditions following the disturbance period. An increase in disturbance frequency led to significant changes in community composition when the salinity exposure occurred more than once and the community was not able to recover (Figure 3 C and D). Functional parameters were not or only weakly affected by differences in the frequency of salinity exposure, but when the bags were transplanted back into freshwater, the measured functions as well as bacterial abundance remained much lower compared to controls, suggesting a lack of resistance to salinity changes at any frequency. Furthermore, the different functions studied showed different response patterns, i.e.; abundance and bacterial production were mostly negatively affected by increases of disturbance intensity and frequency, whereas CSUR were less, or not at all, affected.

Finally, there was only a weak correlation between the response patterns observed at the compositional level and those observed in the functional parameters.

Responses of natural bacterial communities to disturbances (**Paper II**)

In **Paper II,** I performed a 'whole ecosystem experiment' with rock pools that were exposed to a salinity increase at 3 levels (3, 6 and 12 ppm) and went through a subsequent 'recovery period' during which salinities returned to initial levels. I studied changes in bacterial diversity, composition and
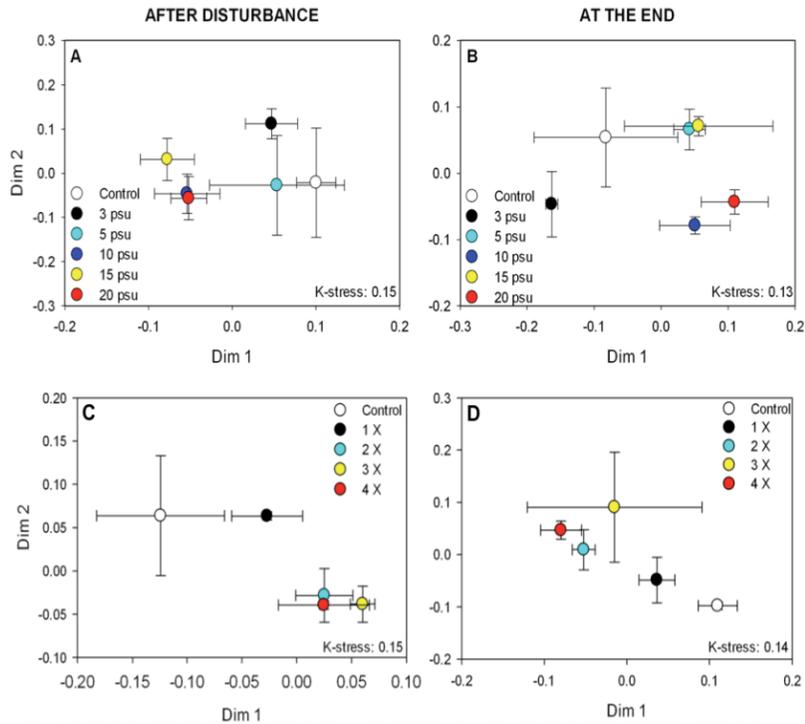
Figure 3. NMDS plots showing changes in community composition in relation to salinity disturbance intensity (A and B) and frequency (C and D) after the increases of salinity and at the end of the experiment. Psu is an equivalent to ppm, a measure of salinity.

functioning as well as potential sources that could have had an impact during the recovery period.

Despite strong initial differences among pool communities, some general patterns in their response to salinity changes could still be detected. Communities did show resistance to increases of salinity up to 3 ppm, whereas higher salinities led to stronger changes in community composition. However, these communities became more similar to the controls again by the end of the experiment, showing some degree of resilience (Figure 4A-D). External factors such as colonizers dispersing through air and rain had little influence during recovery, whereas internal sources were more important. Very similar patterns were observed for both Bray-Curtis (relative abundance approach) and Jaccard (presence-absence based approach) dissimilarities (Figure 4A and B), indicating that the observed changes in community composition were mainly a result of species replacements.
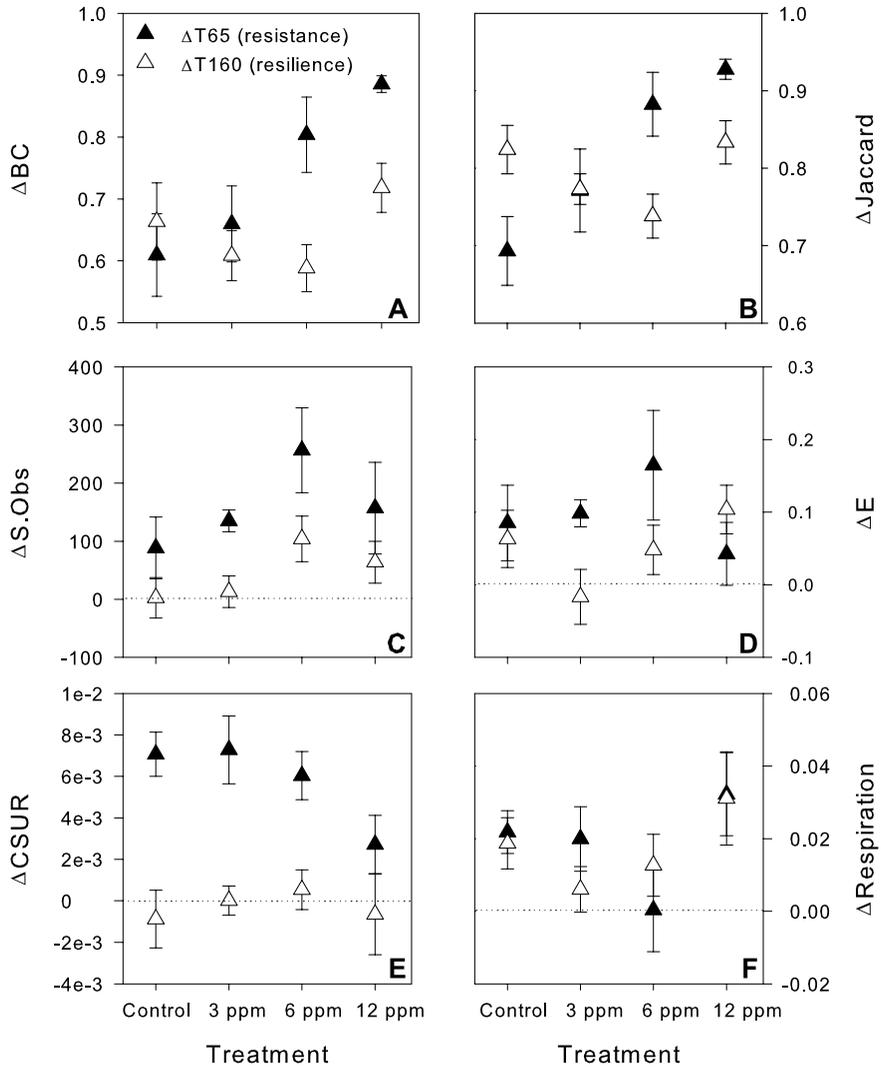
Figure 4. Rates of change in (A) community composition based on Bray-Curtis dissimilarities, (B) community composition based on Jaccard dissimilarities, (C) species richness, (D) species evenness, (E) carbon substrate utilization rate and (F) respiration rates. Filled symbols indicate changes between the communities after the salt addition and at the beginning of the experiment. Empty symbols indicate the changes between the end of the experiment and the initial communities. Dashed line indicates a zero change and thus resistance and resilience can be assess by the distance to it: The farther away the values are from the dashed line the more affected are the measured parameters.

Changes in relative abundances were observed at the bacterial class level where Betaproteobacteria decreased after salt additions, whereas Bacilli, Bacteroidia, and particularly Epsilonproteobacteria and Gammaproteobacteria increased with increasing salinity, in particular in the 6 and 12 ppm treatments.

Community diversity was not affected by additions of salinity at any time, however, there were changes over time with increases of diversity in both the control and the treatment after the manipulation and a posterior tendency to return to original values. Salinity increases did not affected beta-diversity, which did, however, decrease at the end of the experiment due to the rainfall event.

Neither CSURs nor respiration rates were affected by the salinity increase (Figure 4 E and F). However, CSURs increased in all treatments and in the controls after the manipulation. There was also a significant positive relationship between species richness and CSUR.

The fate of dispersed bacterial communities in new environments (Paper III).

In Paper III I investigated how the fate of dispersed or immigrating bacterial communities are influenced by the environmental conditions they encounter in the new environment as well as by interactions with the local resident community.

The results suggested that immigrating communities were able to adjust to new environmental conditions by different mechanisms and that they were influenced by competition interactions with the local community.

More specifically, I observed that the composition of the dispersed, i.e. transplanted, community was affected by both the source of the community and the incubation environment. Moreover, mixed communities incubated under saline conditions and both pre-adapted mixed communities, showed higher similarities to the saline communities than expected based on the ratio at which cells from the two source communities (freshwater and saline) were mixed. These changes in composition were also reflected in changes in the abundances of specialists and generalists (Figure 5). More specifically, freshwater specialists were more abundant than expected only when mixed communities were incubated under freshwater conditions, but were less abundant than expected in all the other incubations. On the other hand saline specialists were less abundant than expected in the freshwater incubations (Figure 5). Finally, general abundances of generalists, i.e. species that were found both at freshwater and saline conditions, were higher than expected when mixed communities were incubated at saline conditions or had been pre-adapted.

The incubation environment affected both bacterial biomass and production of both freshwater and saline communities, and in the case of biomass, this effect was independent of the origin of the community. Bacterial communities used different mechanisms to adapt to the new environments. Saline communities adapted to changes in environment modifying their cell size, whereas freshwater communities modified their cell numbers. Lower production than expected was found in the mixed communities incubated under freshwater conditions whereas higher rates than expected were observed when mixed communities were incubated in saline conditions.
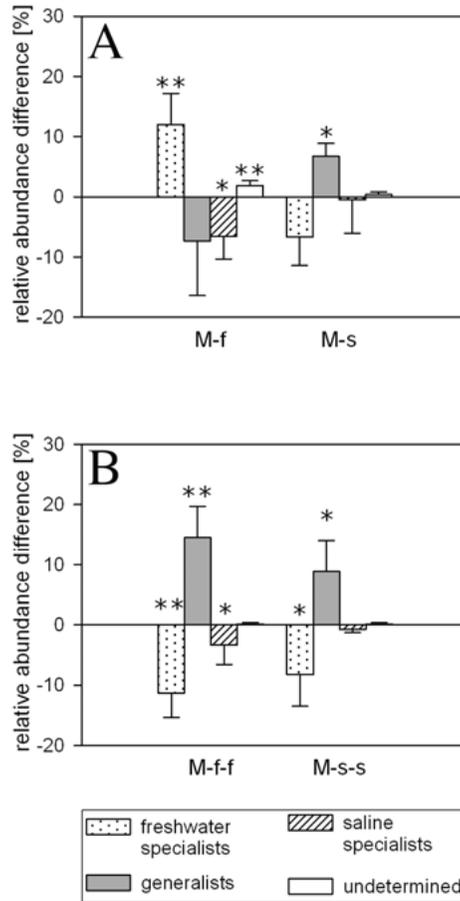
Figure 5. Differences between observed and expected relative abundances of species categories of mixed bacterial communities. Bars represent mean values of the differences between expected and measured relative abundance of habitat specialists (freshwater or saline) or habitat generalist in the mixed sample in (A)- without pre-adaptation and in (B)- with pre-adaptation. 'M' stands for mixed communities, 'f' for incubation at freshwater conditions and 's' for incubations at saline conditions. Error bars indicated standard deviations. The asterisks represent the level of significance of the corresponding t-test in the following way: *P<0.05 and **P<0.01.

Importance of historical environmental conditions (**Paper IV**)

This study showed that past environmental conditions are better predictors of present differences in community composition among localities than present environmental conditions.

Bacterial community composition changed significantly within rock pools over the nine-day period, but variability between pools remained unchanged, thus, there were no changes in beta-diversity. Rainfall events during the middle of the study period had a very strong diluting effect of the environmental parameters and reduced salinity variability among pools. Environmental conditions, especially salinity, at early sampling days (days 1 and 3) explained a larger fraction of the variability in community composition between pools at the last sampling day (day 9) than the condition at later days (days 5, 7 and 9) (Figure 6). Environmental conditions at days 1 and 3 explained more of the variation even when the environmental conditions at day 5, 7 or 9 were used as covariables, whereas the contemporary environmental conditions explained very little of the variation when the earlier days were included as covariables. Similar patterns were found using a partial redundancy analysis (pRDA) and a correlation test. Most likely this result suggests a time gap in the response in the sense that communities at the end of the study were not "at equilibrium" with the environmental conditions, however, effects of dispersal limitation and priority effects could also explain the observed pattern.
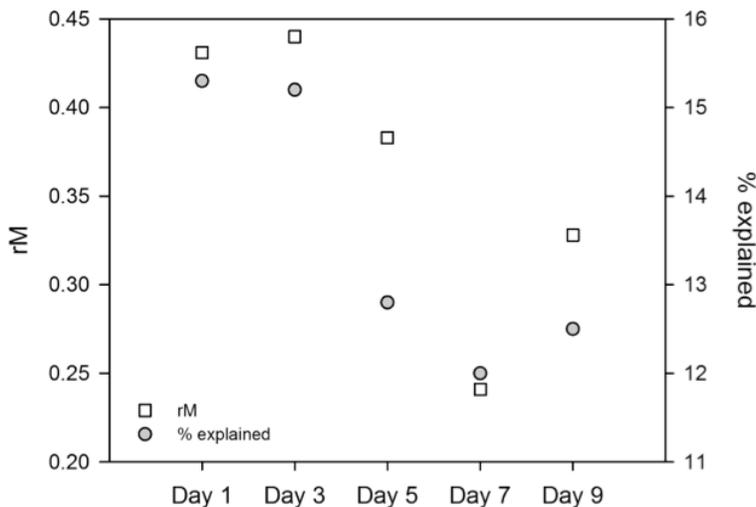

Figure 6. Relationship between bacterial community composition at Day 9 and salinities at the same and earlier sampling days. rM values from Mantel tests and the amount of variation explained by RDA are shown.

Effects of predation and dispersal on bacterial metacommunities (**Paper V**)

In **Paper V** I addressed the combined effects of predation by *D. magna* and different dispersal rates on bacterial metacommunities.

Despite the differences in diversity of each local community, *D. magna* decreased local, regional and beta-diversity and the abundance of bacteria and alternative predators (HNF), but increased concentrations of DOC, TP and chlorophyll a. Dispersal, on the other hand, increased local diversity as well as beta diversity, but had no effect on regional diversity (Figure 7).

In the absence of *D. magna,* metacommunities changed from being deterministically assembled without dispersal to being more stochastically assembled when dispersal occurred. However, when *D. magna* was present, communities became more deterministically assembled.

The presence of *D. magna* and dispersal caused significant changes in community composition as well as the relative abundance of main bacterial groups. Verrucomicrobia, Alphaproteobacteria and Betaproteobacteria decreased when *D. magna* was present, whereas Actinobacteria and Sphingobacteria were favored by its presence. Dispersal decreased the relative abundance of Betaproteobacteria and increased that of Flavobacteria.

Predation decreased bacterial production but caused an increase in community respiration, whereas dispersal did not affect any of the functional properties. The correlation between diversity and bacterial production was positive for locations where *D. magna* was present but there was no correlation when it was absent.

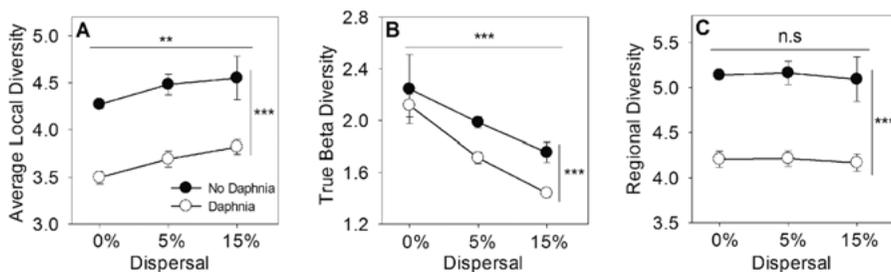*Figure 7. Average local Shannon diversity, β-diversity and regional diversity in relation to the presence or absence of D. magna and dispersal. Mean values for each metacommunity are plotted and error bars refer to standard deviations. Significance levels of ANOVA tests are shown as: *** p < 0.001, ** p < 0.01 and n.s – not significant.*

General discussion

All experimental studies included in this thesis address how different local and regional factors affect bacterial communities, focusing on the importance of disturbances and dispersal. Another aspect that this thesis addresses is how historical processes affect the spatial distribution of bacterial communities.

Bacterial community responses to disturbances

Papers II and IV showed that the environmental variability among rock pools led to differentiation of communities, i.e. high beta-diversity, thus supporting the results from previous studies about the importance of environmental characteristics and species sorting during bacterial community assembly (Van der Gucht et al. 2007; Langenheder & Ragnarsson 2007; Logue & Lindström 2010). **Paper IV** and examples from the literature (Lozupone & Knight 2007; Logares et al. 2009; Bouvier & Giorgio 2002) identified salinity to be a very important factor for determining the spatial distribution of bacteria and this thesis, in general, demonstrates the importance of salinity for community assembly and functioning.

Changes in bacterial community composition were observed as a response to changes in salinity (**Papers I-IV**). This was expected since it has been shown that bacterial communities are generally not resistant to disturbances (Shade et al. 2012) and that even small changes in salinity can cause shifts in community composition (Langenheder et al. 2003). Changes in community composition were gradual along increasing gradients of disturbance intensity and frequency, causing larger changes at the highest levels (**Papers I and II**). Similar results have also been observed along salinity gradients in estuaries (Bouvier & Giorgio 2002) and in dependence of the intensity of a disturbance (Ager et al. 2010).

In the field experiment (**Paper II**), resistance to increases of salinity from 0 to 3 ppm was observed and many of the communities exposed to stronger salinity changes (6 and 12 ppm) showed some degree of resilience, i.e. the capacity to recover and return to pre-disturbance conditions when freshwater conditions were reset. These findings are in congruence with a study along a salinity gradient in the Baltic Sea, where communities that were found in localities of salinities up to 3.2 ppm were very similar to communities found

at 0 ppm conditions (lakes), whereas communities found at higher salinities were more different, specially at salinities higher than 10 ppm (Herlemann et al. 2011). Resistance but especially resilience has been observed mostly in communities that experience disturbance frequently as it has been shown for soil bacterial communities exposed to copper additions (Girvan & Campbell 2005). Hence, the patterns observed here could be because rock pool communities were already 'pre-conditioned' to environmental fluctuations, as they regularly experience quite drastic differences in environmental conditions (Jocque et al. 2010). Both, **Papers I and II** indicated that the frequency and intensity with which disturbances occur will influence the response of communities, leading to possible adaptations. Bressan et al. (2008) showed that soil community exposed to minor perturbations, such as heat increases; copper or herbicide (atrazine) addition became more resistant to withstand another disturbance. Anticipation has been shown as a mechanism to adapt to disturbances when these have occurred earlier (Mitchell et al. 2009).

In contrast to community composition, diversity was not affected by increases of salinity (**Paper II**). This could be because increases in salinities lower than 12 ppm were not strong enough to suppress many species and is in agreement with the results from Herlemann et al. (2011), that also showed that local diversity, in terms of species richness and Shannon index, did not exhibit any clear trend in relation to changes in salinity along a gradient from 0 to 30 ppm observed in the Baltic Sea.

Functionally, there were few consistent response patterns to increases in salinity since they depended on the functional parameters addressed (**Papers I and II**), which has also been observed in other studies (Bouvier & Giorgio 2002; Mulder et al. 2001). Some functions were not affected, e.g. respiration in **Paper II** or CSUR in the frequency part of **Paper I**, while others were negatively affected (bacterial production) by increasing salinity intensity (**Paper I**). Negative effects of increases of salinity can be due to direct physiological effects on bacteria that can lead to a reduction of growth rates (Bouvier & Giorgio 2002; Gasol et al. 2004). Bacterial communities were, in general, found to be functionally able to, or had the tendency to, recover from changes in salinity (**Papers I and II**) but this recovery was limited by the strength of the disturbance, since e.g. salinities of 20 ppm did not allow for functional recovery at any frequency (**Paper I**). Differences between patterns of different functions have been related to the fact that they might reflect different levels of the community (from individual cells to the entire community) (Comte & Del Giorgio 2009) or depend on how specific the function is (Langenheder et al. 2005).

Finally, bacterial communities could respond or even adapt to changes in salinity also by changing cell abundance and/or cell morphology. **Paper III** showed that freshwater communities adapt to saline conditions by increasing

their cell numbers whereas the adaptation of saline communities to freshwater conditions was by decreasing cell size.

Biotic interactions in bacterial communities

In **Papers III and V,** the influence of biotic interactions on bacterial communities was addressed. In **Paper III** we observed that competition is likely to be an important driving force during the colonization of new habitats. We observed increases in the functional performance of communities or even 'functional overachievement' in situations where competition occurred. This was further linked to increases in the abundance of generalists, which was most likely a consequence of their higher competitive ability (Dall & Cuthill 1997) and is in agreement with studies that predict that environmental changes and exposure to new environmental conditions are likely to increase the abundance of generalists (Comte & Del Giorgio 2011).

In **Paper V**, the presence of *D. magna* led to changes in bacterial community composition and the relative abundance of bacterial groups as well as decreases of species richness and evenness. These changes could have been the results of either direct grazing effect (Langenheder & Jürgens 2001; Jürgens 1994), as well as indirect effects, such as changes in competitive interactions between bacterial species due to increases of DOC, TP and chitin when *D. magna* is present (Vrede & Vrede 2005; Beier & Bertilsson 2011). For larger organisms it has been shown that predation leads to an increase in prey species density because of the trade-offs between the ability to withstand predation and capture resources (Kneitel & Chase 2004). We did not observe such an increase but instead a decrease that could be explained by the nature of the predator since *D. magna* is an unselective grazer to which many bacteria lack effective defense mechanisms or, again, because indirect effects, such as changes in the diversity of protozoan bacterial predators, were important. *D. magna* also affected communities functionally, by increasing respiration and reducing bacterial production. This indicates that *D. magna* grazing decreased bacterial growth efficiencies, whereby a large portion of carbon is respired and less transformed into biomass. Moreover, the presence of *D. magna* in isolated communities increased stochasticity in community assembly, probably by increasing random extinctions which has been suggested to occur in response to predation (Chase et al. 2009; Chase & Myers 2011).

Dispersal alters bacterial communities

Generally this thesis supports the observation that dispersal is an important factor influencing the composition and diversity of bacterial (meta)communities (Lindström & Östman 2011; Verreydt et al. 2012; Declerck et al. 2013). **Paper V** showed that dispersal increased local richness and Shannon diversity, suggesting that the exchange of species between local communities either filled empty niches at the local scale or rescued species from local extinctions because of mass effects (Mouquet & Loreau 2003). In the same study, dispersal decreased beta-diversity, most likely due to an increase in the number of shared species among local communities (Mouquet & Loreau 2003). However, as observed previously by Cadotte et al. (2006), dispersal did not change regional diversity, probably related to the fact that the dispersal rates applied were not high enough (Mouquet & Loreau 2003; Lindström & Östman 2011). Dispersal compensated, to a certain extent, the negative effects that *D. magna* inserted on local species diversity. Moreover, dispersal increased the importance of stochastic assembly processes in metacommunities without predators, probably because dispersal as such is a rather stochastic event (De Meester et al. 2002; Chase et al. 2011).

Paper III showed that bacteria that are dispersed are able to cope and adapt functionally to environmental conditions in a new habitat, and suggested that they moreover have, through interactions with the local community, the potential to modify the taxonomic and morphological composition as well as functional performance of bacterial communities.

Paper II showed that dispersal by air and rain played only a very small role in the recovery of the rock pool communities after salinity changes, which confirms previous studies implemented with lakes, which found that atmospheric deposition is a quantitatively insignificant source of dispersal that has no influence on lake bacterial communities (Jones et al. 2008).

In summary, the results from **Paper III** suggested that "immigrant" bacteria can in principal adapt functionally to cope with the new conditions once they are dispersed and even have the potential to influence local community dynamics, but results from **Papers II and V** suggested that dispersal rates probably need to be high to see this reflected in changes of the local "autochthonous" community.

Past conditions matter for the spatial distribution of present bacterial communities

History may influence community assembly and distribution. Evolutionary processes as well as changes in the environment and dispersal or the succession of these processes in time have been suggested to be important. **Paper**

IV showed that past environmental conditions, more specifically past differences in salinities among rock pools, can be better predictors of present variability in bacterial community composition among locations compared to contemporary environmental conditions. This higher degree of correlation with past compared to present environmental conditions could be explained by: (1) adaptation of bacterial communities to more stable environmental conditions that occurred in the past, (2) a *time delay* in the compositional response of bacterial communities to the salinity change that occurred during the course of the study. This could be because of the time needed for species selected by new salinity conditions to grow to become detectable among the dominant members of the bacterial communities (**Paper I**); and finally, (3) priority effects, where early immigrants or resistant species that are already present in the community take advantage of empty niches that become available when environmental conditions change because they have the ability to adapt rapidly to them (Mergeay et al. 2011). Results from **Paper II** show that it is more likely that potential priority effects, if they occur in rock pools, are driven by species that colonize the pools from internal recruitment sources rather than from external sources, such as rain. In **Paper III,** adaptation to a different environment was addressed by incubating communities from a freshwater pool under saline conditions and vice versa and comparing pre-adapted and non-adapted communities. Pre-adapted communities showed similar response patterns in response to the transplantation than non-adapted communities. Thus, there was still a very strong source signal, indicating that the composition of the community was mainly driven by its origin and that changes in the environment caused mainly morphological and functional adaptations, which generally supports the idea that priority effects may be important in aquatic bacterial communities.

Diversity – ecosystem functioning relationships

In this thesis I investigated either relationships between community composition and functioning (**Paper I**) or between species richness, evenness or Shannon diversity and functioning (**Papers II and V**).

Correlations between community composition or richness and functions were, in most cases, rather weak. **Paper I** provided indications of functional redundancy because bacterial community composition changed with increasing disturbance frequency whereas CSUR was unaffected. Functional redundancy has also previously been observed in soils where losses of species richness did not lead to strong changes in ecosystem functions (Wertz et al. 2006).

Another pattern observed in some of the studies was functional plasticity, in particular during the colonization of a new environment, since **Paper III** showed that functions changed much stronger in response to new environ-

mental conditions than community composition. **Paper I** suggested that the weak correlation between composition and functioning can be due to a time lag in their responses, since the changes in community composition occurred slower than in those in community functioning, which makes it difficult to study diversity-function relationships in bacterial communities.

Interestingly, when studying the patterns of diversity (mainly species richness) and ecosystem functions, positive correlations between diversity and functioning were observed indicating functional complementarity, e.g. between species richness and bacterial production in **Paper V** and between richness and CSUR in **Paper II**. It is, moreover, interesting to see positive correlations also in the case of a general function such as bacterial production, which is often not correlated to changes in community composition (Langenheder et al. 2006).

Finally, diversity/composition-functioning relationships seem to be strongly dependent on the type of functions, and especially on their specificity. The uptake of one widely available substrate such as leucine that is used to measure bacterial production follows the patterns observed in community composition better than a composite functional measurement such as CSUR, which is based on a variety of more specific substrates (**Paper I**). Moreover, a very general function such as respiration did not follow the changes observed in composition nor in species richness (**Paper II**). These results are in agreement with other studies that have found that respiration is not related to changes in community composition because there are too many organisms that respire (Langenheder et al. 2005, Peter et al. 2011 and Comte & Del Giorgio 2011). Results from **Paper V** suggested that the complexity of food webs may also affect diversity-functioning relationships, since significant positive correlations between richness and production were only found when *D. magna* was present in the community. Finally, the results from **Paper II** showed that significant positive correlations between richness and CSUR were only observed at the end of the experiment, whereas significant negative correlations between richness and respiration were only found directly after the disturbance. This demonstrates that the strength of diversity-functioning relationships can also differ depending on when they are measured in relation to a perturbation.

Conclusions and perspectives

The major conclusions of the papers in this thesis are:
- "Local" factors such as environmental conditions, biotic interactions and disturbances are all relevant for the assembly of natural bacterial communities.
- Dispersal and historical environmental conditions affect the diversity of bacterial communities and their spatial distribution.
- Freshwater bacterial communities are generally not resistant to disturbances such as salinity or the presence of *D. magna*, but are in some cases resilient.
- The abovementioned factors and processes can alter bacterial communities compositionally and functionally. Depending on the function of interest, functional plasticity, functional redundancy or functional complementarity can be found.

This thesis confirms that species sorting is important during community assembly, but also highlights that historical processes, which have rarely been integrated into microbial studies so far, are important and should be further investigated in the future. In addition, the observation of time gaps in the responses of different community properties to changes in environmental conditions suggests that time is a very important aspect that needs to be incorporated in future studies. The thesis also shows that natural bacterial communities in rock pools were resistant or resilient to increases in salinity. Future studies should now address whether this is a typical characteristic of communities that experience frequent changes in their environment. Incorporating time and history in disturbance studies could lead to the identification of the importance of evolutionary filtering not only in response to changes in salinity, but also to other disturbances that may be of importance for bacterial communities, such as changes in pH, oxygen concentrations or temperature. At shorter time scales, it would also be interesting to investigate to what extent bacterial communities can pre-adapt to a disturbance regime and whether or not this pre-adaptation depends on the intensity of a disturbance.

Another aspect that we need to investigate more is to what extent bacterial communities are resilient to biotic disturbances and to address the relative importance of different disturbances (biotic as well as abiotic) on bacterial communities over longer time periods.

Moreover, I think that it is very important to study whether a community "stability" base line exists, whether and when disturbances lead to clear deviations from it and whether and when complete recovery, i.e. resilience, is likely to occur. Comparing the baseline for composition and functions and how quickly bacteria get back to them after a disturbance, could yield important insights into functional plasticity of bacterial communities. In general it is of great interest to investigate how frequent functional plasticity occurs and to what extent it is a general bacterial capacity. Tools such as metatranscriptomics might help us in find the answer to this question.

Swedish summary (Sammanfattning)

Den rumsliga utbredningen av olika organismer, det vill säga deras biogeografi, antas ofta påverkas av miljöfaktorer, biologiska interaktioner, spridning och historiska faktorer. Dessa faktorer kan verka över korta avstånd, lokalt, eller regionalt, över större avstånd. Kunskap om hur betydelsefulla dessa faktorer är för organismers biogeografi bidrar till vår förståelse av hur samhällens biologiska mångfald och sammansättning formas, vilket i sin tur kan vara av betydelse för ekosystems funktion.

Bakterier spelar centrala roller för ekosystems funktion framförallt i biogeokemiska cykler som till exempel kolcykeln. Kunskap om vad som styr bakteriesamhällens mångfald och sammansättning, t ex hur de reagerar på förändringar i miljön och på interaktioner med andra organismer, kan därför bidra till vår förståelse av storskaliga processer. Det har ofta visats att bakteriesamhällen formas i enlighet med nisch-teorin, det vill säga att lokala miljöfaktorer och biologiska interaktioner gynnar organismer med vissa specifika egenskaper. Denna typ av processer kallas också artsortering ("species sorting") inom teorin om metasamhällen. Det har dock också visats att bakteriesamhällen kan formas slumpartat, vilket inom den så kallade neutralteorin har förklarats med en stor betydelse av slumpartade utdöenden och ekologisk drift. En förutsättning för detta är dock att spridningen av individer mellan samhällen är i någon mån begränsad. En annan faktor som kan spela roll för hur bakteriesamhällen formas är masseffekter. Dessa effekter uppstår när spridningen mellan samhällen är så hög att lokala miljöfaktorer blir av mindre betydelse.

Syftet med den här avhandlingen är att undersöka den relativa betydelsen av dessa olika processer för bakteriesamhällens mångfald och sammansättning. Syftet är också att utvärdera betydelsen av förändringar i mångfald och sammansättning för bakteriesamhällenas funktion i ekosystem. En central del av den här avhandlingen är att studera vilken effekt störningar i miljön har på bakteriers mångfald och funktion. Mätningar av bakteriers mångfald och sammansättning gjordes genom genetisk analys av 16S rRNA-genen, en vanlig markör för undersökningar av bakteriers taxonomi. Funktionella egenskaper som undersöktes var bakteriers tillväxthastighet, respiration och deras förmåga att utnyttja olika kolkällor för tillväxt.

Studierna utfördes både i form av laboratorieexperiment och som fältstudier. Laboratorieexperimenten gjordes i dialyspåsar såväl som i microkosmer. Fältstudierna utfördes i hällkar, små väl avgränsade regnvattenfyllda

håligheter. Fördelen med hällkar är att miljön lätt kan förändras i dem, på naturlig väg eller experimentellt, vilket gör dem lämpliga för att studera effekten av störningar. De störningar som samhällena utsattes för var förändringar i vattnets salthalt. Detta är en relevant störning eftersom det är känt att det är en av de mest kraftfulla miljöfaktorerna som påverkar bakteriers biogeografi. Dessutom förändras salinitet ofta på naturlig väg i de hällkar som studerades längs med Östersjökusten.

I den här avhandlingen visar jag att bakteriesamhällen inte var resistenta mot störningar i någon större utsträckning. Ju större förändring i salthalt desto mer förändrades bakteriesamhällenas sammansättning. På samma sätt hade en ökad störningsfrekvens en ökad effekt på bakterierna. Många av de studerade samhällena var dock resilienta det vill säga de kunde efter en störning och påföljande förändring återgå till ursprungstillståndet. I ett fall var bakterierna resistenta mot en ökad salthalt. I det fallet rörde det sig om bakteriesamhällen från hällkar som naturligt utsätts för stora förändringar i salinitet. Störningarna påverkade också bakteriesamhällenas funktion och då främst tillväxt och förmågan att utnyttja olika kolsubstrat. Däremot påverkades inte respirationshastigheten av störningen. Detta innebär att betydelsen av resistens och resiliens efter en störning beror på sammanhanget.

En utmaning som möter bakterier som sprids från en plats till en annan är möjligheten att etablera sig i den nya miljön. Jag undersökte om etableringen påverkas av hur stor miljöomställning bakterierna utsätts för och om interaktioner med samhället som redan finns på den nya platsen har betydelse, genom at sprida sötvattensbakterier till en marin miljö och vice versa. Jag fann att denna salinitetsförändring fungerade som ett "filter" och att artsortering troligen var en mycket viktig process. Sammansättningen av samhällena påverkades dock i mindre grad av miljöförändringen jämfört med funktionen. Detta innebär att samhällena innehöll bakterier som var funktionellt plastiska. Dessutom fann jag att andelen generalister ökade, sannolikt som en följd av konkurrens med ursprungssamhället.

En relativt ostuderad aspekt inom biogeografi är betydelsen av historiska miljöförhållanden för nutida mönster i bakteriesamhällens sammansättning och mångfald. In en studie i denna avhandling fann jag dock att miljöförhållanden som rådde omkring en vecka tidigare till en högre grad kunde förklara bakteriers sammansättning i hällkar än samtida miljöförhållanden.

I en experimentell studie fann jag att vattenloppan *Daphnia magna* kan ha effekt på bakteriesamhällens sammansättning och minska bakteriernas mångfald. Jag fann också att närvaron av *D. magna* påverkade i vilken grad slumpen har betydelse för samhällenas sammansättning. *D. magna* påverkade också bakteriernas funktion såtillvida att dess närvaro ledde till minskad tillväxt men ökad respiration. Spridning av bakterier mellan samhällen minskade den negativa effekten *D. magna* hade på mångfalden. Med andra ord hade spridningen en "räddningseffekt" (rescue effect) på bakteriearter

som var känsliga för predation av *D. magna*. Spridningen ökade också likheten mellan samhällen.

Det var inget tydligt repeterbart samband mellan samhällets sammansättning eller mångfald å ena sidan och dess funktion å andra sidan, vilket visar att huruvida det finns en koppling mellan funktion och diversitet beror till en hög grad på sammanhanget. Bland de faktorer som påverkar denna koppling beror på vilken funktion som avses, om det är en specifik funktion eller en mer allmän funktion. Vidare spelar det roll till vilken grad samhällena störs experimentellt. I experiment av den här typen är det också viktigt att ta hänsyn till att tidsförskjutningar i olika effekter kan leda till svagare samband.

Sammanfattningsvis visar jag i denna avhandling att artsortering är viktigt, men att spridning och slumpmässida processer också är av betydelse för bakteriesamhällens sammansättning. Jag visar också att störningar kan leda till förändringar i samhällen och att störningens omfattning och frekvens är av betydelse. Resultaten visar också att de bakteriesamhällen som studerats är resilienta. Mina resultat visar också att historiska faktorer bör inkluderas i studier av bakteriesamhällens ekologi. Slutligen bör framtida forskning inriktas på att utröna under vilka förhållanden som biodiversitet är av betydelse för samhällens funktion i ekosystem.

Summary in Catalan (Resum)

El fet que processos com les interaccions entre espècies i la pressió o la selecció de l'ambient influeixin en la composició de les communitats biològiques és conegut des de fa temps. Fins el moment es desconeixen encara alguns detalls sobre les comunitats, com la direcció o la magnitud d'aquests processos, la dispersió d'organismes o com el conjunt de fets que aquesta ha experimentat al llarg de la història poden afectar-ne la seva composició o bé les funcions que aquestes realitzen. La composició de les comunitats pot ser explicada per diferents casos com la selecció, de manera que l'ambient filtra les espècies que no poden viure en certes condicions. Una altra alternativa és que la composició que s'observa estigui relacionada amb la dispersió, és a dir, organismes d'altres llocs que emmigren a la localitat que s'estudia. Si la dispersió és elevada, aquesta amortiguarà els efectes selectius de l'ambient. Finalment, el tercer cas es dóna quan cap d'aquests processos explica la composició de la comunitat i siguin factors aleatòris com l'especiació o les extincions els que s'hi desenvolupen.

Les comunitats bacterianes són molt importants en l'ecosistema perquè són clau en els processos de regeneració de nutrients i en el cicle del carboni; a més, són molt abundants i es troben en tots els ecosistemes del planeta. Donada aquesta importància a gran escala és rellevant estudiar-les i, més específicament, intentar entendre com els processos que les afecten interactuen entre ells i en quines situacions podem esperar que passin canvis importants. Les comunitats poden veure's afectades per perturbacions, situacions puntuals que les alteren directament a elles o a l'ambient en el qual viuen. Fins ara se sabia que les comunitats bacterianes no resisteixen composicionalment les perturbacions i que en alguns casos poden ser resilients (tenen la capacitat de tornar a la composició que tenien abans de la perturbació). També s'ha observat que canvis petits i freqüents poden arribar a causar que les comunitats no es vegin tant afectades quan una perturbació més gran té lloc.

En aquesta tesi ens concentrem en comunitats bacterianes aquàtiques i, més en concret, en bassals en superfícies rocoses prop del mar. Els bassals estudiats en aquesta tesi estan localitzats a l'illa de Gräsö, a la costa est de Suècia del mar Bàltic. Aquests bassals són depressions de la roca que s'omplen amb l'aigua de la pluja, alguns d'ells són grans i permanents i d'altres petits i temporals. Les tempestes i el fet de rebre sal pels esquitxos del mar fa augmentar la salinitat de l'aigua dels bassals que pot arribar a ser

superior a la del mar, que en aquesta zona és d'aproximadament 4-5 ppm. La salinitat és el factor més important que explica les diferències en les comunitats bacterianes a nivell global i és degut als processos evolutius que els organismes han experimentat al llarg del temps. En un experiment al laboratori amb aigua d'un dels bassals s'ha estudiat com els canvis de salinitat afecten les comunitats bacterianes, si aquestes són capaces de recuperar-se un cop tornen a estar en aigua dolça i si la intensitat de l'augment o la freqüència en que passen impliquen canvis en les respostes de les comunitats. L'experiment ha demostrat que les comunitats bacterianes no resisteixen canvis de salinitat i que la seva composició està més afectada i canviada com més alta és la salinitat o com més freqüents són els augments de salinitat. També mostra que els canvis en la funció i en la composició no passen a la mateixa velocitat, ja sigui degut a la plasticitat funcional dels bacteris o degut a limitacions metodològiques. Per tal de saber si aquests patrons també s'observen en comunitats naturals es va realitzar un altre experiment directament als bassals. El fet que els bassalts siguin masses d'aigua petites i ben delimitades permet que es puguin manipular fàcilment. Així doncs, es va afegir sal a alguns bassals per obtenir diferentes intensitats; es va mostrejar abans i després de l'addició de sal per poder saber si les comunitats, inicialment diferents entre elles i en condicions naturals, resistien als increments de salinitat. Els resultats suggereixen que aquestes comunitats poden resistir fins a increments de salinitat de 3 ppm, però no salinitats més altes. Posteriorment els bassals es van omplir amb aigua de la pluja i es va poder estudiar què passa quan els bacteris tornen a estar en aigua dolça. Els resultats mostren que moltes de les comunitats afectades eren força resilients. Aquests resultats poden estar relacionats amb el fet que els augments de salinitat tenen lloc regularment en aquests sistemes i per tant el seu impacte pot ser menor. També s'ha observat que la dispersió i colonització per part de bacteris en l'aire o la pluja no influencia la recuperació de les comunitats, sinó que és més probable que mecanismes com la latència (entrar en estat inactiu temporalment quan les condicions ambientals no són favorables que es pot revertir quan les condicions tornen a ser favorables) o la tolerància als increments de salinitat dels organismes que ja hi ha als bassals tinguin major importància.

En aquesta direcció, en un altre estudi d'aquesta tesi s'estudien els factors que afecten a les comunitats bacterianes quan es dispersen i entren en una localitat nova, és a dir, en un ambient diferent amb una comunitat de bacteris residents o locals. L'estudi suggereix que les noves condicions ambientals tenen una gran influència en la taxa de les funcions realitzades, per exemple en la producció. D'altra banda, els canvis en la composició de les comunitats dispersades depenen de les condicions ambientals del lloc d'origen i també de les noves condicions ambientals, suggerint que tant el filtre ambiental com la "plasticitat fenotípica" són importants. A més a més, la competència

entre espècies causa un augment d'espècies generalistes i com a conseqüència un augment en les taxes de les funcions de les comunitats.

En un altre estudi s'ha centrat la mirada en si les comunitats que s'observen en un moment donat són així degut a com és l'ambient en aquell moment o si és conseqüència de com l'ambient era anteriorment.S'ha pogut observar que la composició de les comunitats bacterianes reflexen més les condicions ambientals passades que les actuals. En l'últim estudi s'ha estudiat l'efecte que un deprador com la *Daphnia magna* causa en les comunitats bacterianes, i tot i que *D. Magna* té afectes directes i indirectes sobre els bacteris, s'ha observat que quan és present redueix la diversitat de les comunitats, en canvia la composició, les fa ser més semblants entre elles i augmenta la respiració; a canvi, però, disminueix la producció de la comunitat. Al mateix temps, s'observa que la dispersió d'organismes entre les comunitats contraresta la pèrdua d'espècies degut a la presència de *D. magna*.

En resum, aquesta tesi suggereix que malgrat que l'ambient filtra gran part de les espècies d'una comunitat, les comunitats bacterianes aquàtiques també estan influenciades per la història i la dispersió d'organismes. La tesi també assenyala que les perturbacions efecten les comunitats bacterianes però que aquestes poden ser resilients i per tant recuperar-se, almenys parcialment, i tornar a tenir una composició semblant a l'original. També suggereix que hi ha canvis més importants quan les perturbacions són més fortes o més freqüents. Una altra conclusió d'aquesta tesi és que la història o el passat de les comunitats pot explicar molt de com són les comunitats en un moment donat i per tant, s'hauria de tenir present en altres futurs estudis.

Així doncs, s'han pogut identificar més detalls de com varis factors efecten a les comunitats bacterianes, però encara queda molt per aprendre especialment en els aspectes que es donen en la relació entre diversitat i funció, ja que tan els estudis aquí presentats com en d'altres, no s'ha pogut descriure cap patró general.

Acknowledgments

It is now time to thank everyone that, in one way or another, has contributed to this thesis and making the last year 4.5 years such a great and enriching experience.

First of all I want to thank my main supervisor. Silke, thanks for being there every time I needed, thanks for your wise and experienced comments about science and being so involved in all the stages during my PhD. Thanks for your support and encouragement.

I would also like to thank my co-supervisors Eva and Örjan. It has been great to have you around. You always had good advice and ideas when I needed help. I really enjoyed our hard-thinking meetings that were always filled with laughs. Lars, thank you for all your support and for help all this time.

Jürg, thanks for all the patience with my endless questions, for all the time you have spent teaching me the ins and outs of lab work and for helping me in going through "Uppmax and Ampliconnoise". Hannes, thanks for all the help in getting started in the experimental world, for all the tips on dialysis bags and help with the flow cytometer. Also many thanks for the inspiring science discussions, or not, but always sharing some nice chocolate. Ina and Jerome, many thanks for letting me learn from you, thanks for helping me move forward with the Biologs and the whole 454 "thingy". Ina, thanks for being such a dedicated co-lab-responsible. Anna S., thanks for all your valuable comments on manuscripts and for your great initiative and imagination. Yinghua, what can I say!! My right hand in the lab and the field. Thanks for the superb job you have always done. Thanks for joining and helping during the rock pools experiment and during the insane pipetting to disperse bacteria. Thanks for being so easy to work with. Anne, thanks for listening to all my boring explanations about how things went in the lab or by the computer, thanks for always coming up with the right questions and to help me sorting out all my English related doubts. Andrea, thanks for all the help in the lab, for the discussions about methods, and science in general, and for being so positive about everything and for the support. Dolly, thanks for your interest in microbiology and for all your valuable comments on my presentations and manuscripts.

I'm very thankful to everyone in Limno. To the present and earlier limnos thank you all to keep such a nice and friendly atmosphere in the department. Pia, Philipp, Lorena, Cristian, Fred, Eddie, Laura, Ramiro and Sara thanks

for all the fun during the first years. Kristin, thanks for your support, encouragement and help in getting to know and enjoy science. Janne, thousands of thanks for fixing all the "little" crises in the lab. Peter, Sebastian, Richard, Stefan, Gesa, Anna B., and Alex, thanks for being so accessible and keeping the department so lively.

Charles, thanks for drawing a smile on my face even on the darkest of grayest days in the Swedish winter. Inga, thanks for doing all the steps with me, it was nice to have another PhD student at a similar stage than I was in. Roger and Blaize, thanks for the great time and knowledge I got from you teaching GIS. Martin, Elias, Erik and Ida thanks for teaching me more about Sweden, the Swedes and all the "very important words/sentences" in Swedish. To all the present PhDs and Monica, Lucas, Jovana, Hannah, Valerie, Torsten, Yang Yang, Maria thank you very much for all the fun and for your motivation to do things. Omneya, Birgit, Francois, Xavier, Tom, Claudia, and Preet thanks for contributing to making limno such a nice place.

I also want to thank all the people that, in addition to the aforementioned, have made life in Uppsala very pleasant. Eli and Ola, thanks for letting me be part of your Swedish-Catalan life, thanks for the many dinners and fikas and for being so good in keeping my thoughts out of science for some time. Yvonne, thanks for being such a lovely person. Kathi, thanks for all your kindness and for always being ready to have me over, for a dinner, fika, baking or watching TV. Javi, it is great to have you around. Monika, thanks for all the nice weekends when you were visiting.

Finally, the last few lines in Catalan, to acknowledge all the support and help that I received from my family during all this time.
Com dic a la línea anterior les últimes ratlles són per als de casa, per agraïrvos tot el suport que m'heu donat tot aquest temps, per les numbroses visites, hores al telèfon i a l'skype que fa que sembli que només hagi passat quinze dies cada cop que torno a casa i que per tant ha ajudat a fer que tot passes ben ràpid. Hagués sigut tot molt més dificil sense tenir-vos a tots tant a prop tot i està tant lluny. Gràcies

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