Biological Diversity of Fish and Bacteria in Space and Time

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Abstract

Biological diversity is controlled by an array of factors and processes all active at different spatial and temporal scales. Regional factors control what species are available to occur locally, whereas the local factors determine what species are actually capable of colonizing the locality.

I have investigated how these local and regional factors affect species richness and diversity, mainly of fish in Swedish lakes and in order to assess the impact of dispersal mode one study on bacteria was also performed. In addition, potential first steps towards speciation were investigated in perch (Perca fluviatilis) from two different habitats.

Fish species richness and diversity were found to be regulated by history, dispersal limitation and the local environment. In addition, striking similarities were found in the control of community composition for fish and bacteria. Both were regulated by nearly equal parts regional and local factors. The study of morphological and genetical variation in perch (Perca fluviatilis) revealed genetic differentiation at small spatial scales, suggesting that genetic differences can evolve between groups at strikingly small spatial scales, which might have implications for speciation in a long time perspective.

Based on these findings I conclude that space and time matter. Space has the potential to isolate sites. And both dispersal and local extinctions, it seems, might take a long time, as effects of the last ice-age can still be seen on the contemporary fish community richness and composition.

Keywords: species richness, fish, lake, biogeography, glacial, colonization, metacommunity, speciation, perch, bacteria, diversity

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I will be glad when I’ve had enough of this!
Fred J. Taylor
This thesis is based on the following papers, which will be referred to by the corresponding Roman numerals

I  Ragnarsson, H., Eklöv, P. and Holmgren, K. Fish species richness in lakes: the importance of local and regional processes. Manuscript


IV Ragnarsson, H. and Eklöv, P. Connectivity vs. local environment as structuring forces in lake fish communities. Manuscript.


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Contents

Introduction ................................................................................................................................. 9
  What is diversity ........................................................................................................................ 10
  Appropriate scale of species diversity? ................................................................................ 11
  General factors driving diversity patterns ........................................................................... 12
  Specific factors driving the diversity of the study organisms ............................................. 16
  Mechanisms behind diversity – on an evolutionary scale .................................................... 17
  Summary ................................................................................................................................ 19

Aims of the thesis ....................................................................................................................... 21

Methods .................................................................................................................................. 23

Results .................................................................................................................................... 26
  Factors driving the patterns in fish species richness in Swedish lakes (I) ............................... 26
  Consequences of dispersal limitation and local processes for fish species richness and diversity (II) .................................................................................................................... 28
  Relation between local and regional processes in structuring bacterial community composition (III) .................................................................................................................. 29
  Factors explaining fish species composition (IV) ................................................................. 30
  Genetic and morphological differentiation in perch (V) ....................................................... 31

General Discussion .................................................................................................................. 33
  Fish richness/diversity in Swedish lakes ................................................................................ 33
  Differences between fish diversity and fish community composition ............................... 35
  Comparison between community composition in fish and bacteria ................................... 36
  The commonness and rarity of species ................................................................................. 38
  Small-scale genetic and morphological differentiation ....................................................... 40

Conclusions and perspectives .................................................................................................. 41

Relevance of the thesis ............................................................................................................. 42

Summary in Swedish (Sammanfattning) .................................................................................... 43

Acknowledgements .................................................................................................................. 46

References ................................................................................................................................. 48
### Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCC</td>
<td>Bacterial Community Composition</td>
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<tr>
<td>CBD</td>
<td>Convention of Biological Diversity</td>
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<td>CCA</td>
<td>Canonical Correspondence Analysis</td>
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<td>DOM</td>
<td>Dissolved organic matter</td>
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<td>FCC</td>
<td>Fish Community Composition</td>
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<tr>
<td>GIS</td>
<td>Geographic Information System</td>
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<td>HC</td>
<td>The Highest Coast-Line</td>
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<td>ME</td>
<td>Mass effect</td>
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<td>OTU</td>
<td>Operational Taxonomic Units</td>
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<td>PLS</td>
<td>Partial Least Squares</td>
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<td>SAR</td>
<td>Species Area Relationship</td>
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<td>SDD</td>
<td>Secchi disc depth</td>
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<td>SS</td>
<td>Species sorting</td>
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<td>TP</td>
<td>Total Phosphorus</td>
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<td>t-RFLP</td>
<td>Terminal Restriction Fragment Length Polymorphism</td>
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<td>SDD</td>
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Introduction

Man (and woman) has likely marveled at the diversity of animals for ages. And this diversity was vividly described: “seals, sea-hogs and innumerable other kinds of fish.” (Bacon 1623), “it is observable /…/ that there are fish, as namely the Whale, three times as big as the mighty Elephant, that is so fierce in battle”(Walton 1653) and classified (Linnaeus 1758). However, the search for the mechanisms behind this astonishing diversity started later (Darwin 1859).

Research has since revealed that diversity is controlled by an array of factors and processes all active at different spatial and temporal scales (e.g. Ricklefs 1987). One way of visualizing this process is to picture each individual species that form a local community, be it fish in a lake or bacteria in a rock-pool, as having passed a series of filters (Fig. 1).

That is, each process that affects the arrival or survival of an organism at a locality is represented by a filter (Tonn et al. 1990, Jackson et al. 2001, Hillebrand and Blenckner 2002). First, we have a global species pool, the size of which is determined by the balance between extinction and speciation. A history-filter (e.g. large scale migrations, glacial history, and geological history) then regulates what species from the global species pool are available to occur locally (i.e. are part of the regional species pool). Next, a dispersal-filter (e.g. connectivity of the locality to surrounding sites, distance

Figure 1. Conceptual model visualizing the assembly of local communities from the global species pool.
to some species rich area, dispersal mode of the organism) removes the species that are unable to disperse to the locality. Last, the environment-filter (e.g. adaptation to local abiotic conditions, competitive ability, predation, competition, facilitation) determines the species that are actually capable of colonizing the locality. In a way, each higher order filter is of over riding importance for species diversity and composition as species that are unable to pass through the large scale filters are limited on all lower scales (Poff 1997, Townsend 2003).

**What is diversity**

There are several ways to define the diversity of species. It can be divided into two components, namely richness and evenness (Simpson 1949). Species richness is quite simply the number of occurring species, whereas evenness describes the differences in species abundances. A community with similar number of individuals in each species is rated as even. In contrast, a large difference in the relative abundance would rate the community as uneven (Fig. 2).

![Figure 2. Example of an even and an uneven community. Both have 10 different species and 100 individuals.](image)

Both richness and evenness can be incorporated into a “diversity index”, such as the Simpson’s index (Magurran 2004). A plethora of different indices are used, for an example of fourteen different measures see Stevens and Willig (2002). Species richness is valuable for describing and comparing communities (Gaston 2000). However, as it ignores the relative abundances of species it provides limited understanding of the ways in which diversity per se responds to environmental variation (Stevens and Willig 2002). Other
questions are best answered by considering the community composition. Including both species richness and of composition can be called for (Downing and Leibold 2002).

Sampling methods that catch every single species at a locality are rare. Therefore, species richness is usually estimated through sampling until the species per sampling-effort curve levels off or by using a standardized single sample (see Magurran 2004).

Regional species richness is often calculated as the sum of all species found in the local patches, which could lead to spurious correlations. One way to solve this is to estimate regional richness from distribution maps or regional checklists (Srivastava 1999).

**Appropriate scale of species diversity?**

In nature there are no discrete scales, but rather a continuum in time and space. Still, for most organisms it is sufficient to partition the continuum into a nested hierarchy of multiple scales characterized by different patterns and processes, from a small neighbourhood to the biosphere, through the patch, “community”, landscape, regional and continental scales (Loreau 2000). Yet, in biodiversity studies the most common partition of scales is between local and regional. As the division between regional and local is so rough an estimate, correctly defining your “region” and “locality” is crucial for any study of species richness. Special caution should be used in studies of regional vs. local determinants of species richness, as diversity generally increases with increased sample area (Hillebrand and Blenckner 2002).

There is some agreement to what the “region” and “locality” should conform to. An ideal region should be different enough to have different species pools, but at the same time be similar enough to share habitat types and related species (Angermeier and Winston 1998). In addition, it should have ecologically meaningful boundaries, and all localities within it should be accessible to all species in the regional pool (Cornell and Karlson 1996, Angermeier and Winston 1998). A locality should be an environmentally homogenous spatial unit, within which organisms has the opportunity to encounter each other within ecological time, thereby forming a potentially interactive community. Hence, the size of the local region is not fixed, but rather depends on the organism in question (Cornell and Lawton 1992). Still, in aquatic systems it is relatively safe to consider each body of water as a locality, and thus some of the problems can be avoided (Leibold 1999).
General factors driving diversity patterns

There are a number of factors that are thought to be involved in the shaping of communities. Both local factors (such as species interactions and abiotic conditions) and regional factors (such as history of climate, and migration) are thought to regulate species richness and diversity in most systems (Tonn et al. 1990, Hillebrand and Blenckner 2002). Much effort is put into investigating the relative importance of local and regional processes in generating differences in diversity and composition among sites. The relative importance depends on whether species are most often excluded from sites by local conditions (Case 1990, Law and Morton 1996) or dispersal limitation (Cornell and Lawton 1992, Tilman 1994). In the former communities local processes play an important role in structuring the species assemblage. In the latter, history of colonization from the surrounding region overshadows the weak biotic interactions. At the extreme, if dispersal rates greatly exceed local extinction probabilities for many species, then sites will contain nearly all the species in the region that are capable of invading. In this case, local processes will dominate in shaping species diversity and composition within patches. If, on the other hand, dispersal events are rare, then species will often be absent from suitable local sites and community structure is under strong regional control. In this case, local species composition and richness depends on the history of colonization of the locality and local processes tend to play a minor role (Cornell and Lawton 1992).

Biogeography

The importance of biogeography and history at a geological timescale for the distribution of species has been recognized well over a century (Darwin 1859, Lundberg 1899, Ekman 1922). Especially the distribution of organisms with low dispersal potential are likely to be governed by biogeography factors (Hillebrand and Blenckner 2002). However, as historical patterns are superimposed on the geographic patterns, these two patterns can be hard to separate (Townsend 2003).

The core of MacArthur and Wilson’s (1967) “equilibrium theory of island biography” is very simple. It is that the number of species on an island is determined by a balance between immigration and extinction, and furthermore, that this balance is dynamic, with species becoming extinct and being replaced continually. The term “islands” need not only be restricted to islands of land in a sea of water, lakes are functionally islands in a “sea” of land. Island biogeography is a special case of metapopulation dynamics, with one-way migration (Taylor 1990).

The metapopulation is defined as several local populations interconnected through dispersal. The “population” is the unit within which most movement and interactions, such as reproduction, competition, and predation,
occur. All populations are essentially equivalent and equally affected by dispersal in a metapopulation, in contrast to the island-mainland structure, where the mainland is not affected by migration (Taylor 1990, Hanski 1999).

Using a metapopulation approach when addressing diversity issues is relevant, as species interactions dynamics often conform to metapopulation theory (Holyoak 2000). For example, predator-prey pairs with extinction-prone local populations can persist through metapopulation dynamics (Holyoak and Lawler 1996). Dispersal rates are a crucial part of metapopulation dynamics, and thus also for diversity. In order to maintain the current diversity the organisms must disperse at a sufficient rate to balance local extinction with re-colonization, but the proportion of the population dispersing cannot be too great or the fluctuations of the subpopulations will become synchronous. If dispersal among local communities is marginal, low diversity is expected as dominant competitors or predators in each patch drive other species to extinction. As dispersal increases to some intermediate level, an increase in local diversity is expected for two reasons (Loreau and Mouquet 1999, Mouquet and Loreau 2002). First, as dispersal increases, dispersal-limited species enter new patches. Second, increasing dispersal rates can maintain some rare species in local communities by a rescue effect. However, very high dispersal, by pure mathematics, effectively create one large community and allow a regionally dominant competitor to constantly invade each local community, thereby reducing local diversity in all patches (Amarasekare and Nisbet 2001, Mouquet and Loreau 2002).

The metapopulation theories have also been extended for communities, i.e. the metacommunity. The metacommunity is defined as a set of local communities, of multiple potentially interacting species, that are interconnected by dispersal (Wilson 1992). The different types of metacommunity dynamics has been summarized into four paradigms (see Leibold et al. 2004):

1. Patch-dynamics (PD): The patches are identical. Local species diversity is limited by dispersal or species interactions. The spatial dynamics are dominated by local extinction and (re)colonization.
2. Species-sorting (SS): Patch quality is of importance for local persistence. Dispersal of importance as it allows species to exploit suitable patches.
3. Mass-effect (ME): Immigration and emigration dominates local population dynamics. Species often rescued from local extinction by immigration from patches where they are more abundant.
4. Neutral model (NM): All species are identical competitors and colonizers. Community composition drifts randomly through time.
Species interactions

Interactions between species might serve as a potential filter on local community composition, given that the interactive species possess attributes suited to the abiotic habitat constraints (Poff 1997). The competitive-exclusion principle states that the number of coexisting competing species cannot exceed the number of limiting factors (Rainey et al. 2000). The limiting factors can be abiotic, like for example nitrogen, or biotic, for example each predator species might represent a different limiting factor (Chase et al. 2002). However, if a spatial dimension is applied a stable coexistence of a unlimited set of species is predicted on a single resource (Tilman 1994).

Predation has the potential to both increase and decrease diversity. The main mechanism behind the positive effect of predation is that it frees space, and has the potential to alter the diversity and abundance of their prey’s resources (reviewed in Chase et al. 2002). Predators can also add more limiting resources, for example refugia, i.e. if species of prey have different preferred refuge-types, or utilize the refuges differently, then the addition of the predator generates limitation of the prey community by multiple resources, thus promoting coexistence (Eklöv and VanKooten 2001). Predators also has the potential to decrease richness by driving populations extinct (e.g. Ogutu-Ohwayo 1990)

Area

The relationship between the number of species and the sampled area is one of the best-documented patterns in community ecology. Besides the quite obvious fact that larger areas contain more species than smaller ones, there is no consensus about the exact form of the species area relationship. The relationship is most often found to be linear under a log-log transformation, following a power equation (Arrhenius 1921, Rosenzweig 1995).

Three factors are related to the spatial distribution of individuals that affect the relationship. The first is the sampling effect. Because the majority of species are rare (Preston 1948), most will not occur in all of the sampled areas and will be sampled only within larger ones, even if their distribution is random. Thus, the sampling effect in itself can produce a monotonically increasing relationship (Preston 1962).

The second factor is habitat heterogeneity (Rosenzweig 1995). Larger areas contain more habitat types, and facilitate coexistence of more species associated with particular habitats. As early as (1859) Darwin wrote: “The truth of the principle that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances”. Since then the hypothesis that habitat heterogeneity has a large positive effect on species richness has grown into a undisputed fact (Elton 1933, Ricklefs and Schluter 1993, Rosenzweig 1995, Ellner et al. 2001). The main
mechanisms are thought to be that spatial habitat variability influences diversity by providing physical niche space and refuges that modifies competitive exclusion and the effect of disturbances. Due to the rapid destruction and fragmentation of the environment, habitat loss is likely to be the most important factor causing species decline worldwide (Sih et al. 2000). Particularly in aquatic systems habitat heterogeneity has a strong effect mediating competitive and predator-prey interactions between species and thus has the potential to decrease the exclusion risk of species (Werner et al. 1983, Persson 1993, Persson and Eklöv 1995, Eklöv and VanKooten 2001). The number of species in fresh water ecosystems has been found to directly depend on the area, volume, and average depth (Persson 1997, Alimov 2001), factors which all affect the number and sizes of available habitats. Habitat heterogeneity also has the potential to affect the spatial clustering of individuals, but this is mainly affected by the third factor, namely spatial population dynamics.

Spatial dynamics include local colonization and extinction (Hanski and Gyllenberg 1997) and aggregative behaviour (Taylor et al. 1978). Metapopulation theory predicts that habitat degradation increases patch extinction rates while habitat fragmentation and reductions in connectivity can decrease recolonization rates - further increasing the risk of extinction (Hanski 1999, Sih et al. 2000).

Productivity

The relation between productivity and species richness is of long-standing interest to ecologists. In order to understand the determinants of biodiversity it is vital that the mechanisms that drive this relationship be unravelled (Leibold 1999, Waide et al. 1999, Dodson et al. 2000, Mittelbach et al. 2001). The relationship is fairly well studied (see review in Waide et al. 1999). Different studies have found the relationship to be either monotonic, where diversity increases, but may level off, as productivity increases or unimodal (“hump-shaped”), where diversity first increases with productivity, but eventually decreases at high enough productivities (Abrams 1995, Dodson et al. 2000). However, evidence for the mechanisms underlying the diversity productivity relation are as yet inconclusive (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Abrams 1995).

In aquatic systems the hump-shape is common, which might be due to the negative impact (oxygen depletion and reduced secci-depth) of an increase in productivity (eutrophication) on lakes (Abrams 1995, Mittelbach et al. 2001). The monotonic increase, found in some cases, can be explained by productive environments containing more individuals (has a higher carrying capacity) and therefore can support more species populations above some minimum size required for persistence (Allen et al. 2002). As productivity is
hard to estimate directly, most often indirect measures that correlate with productivity are used.

Altitude
Altitude has been found to have a significant effect on diversity (e.g. Andrew et al. 2003). However, no consistent pattern emerges, though there seem to be a tendency of a reduction in diversity with increased altitude. The effect of altitude is suggested to depend on local climate (Fleishman et al. 2000). In addition, high altitude sites are often also isolated and have a lower spatial extent than those at lower altitude. Furthermore, they are also generally of low productivity and there is a changing number of resource types with altitude (Stevens and Willig 2002).

Latitude
One of the most widely recognized large-scale diversity gradient is the latitudinal gradient. The common pattern is that diversity decreases with an increase in latitude, examples can be found for both terrestrial (e.g. Stevens and Willig 2002) and aquatic (e.g. Macpherson 2002) systems. A meta-analysis performed by Hillebrand (2004) indicates that there is a strong scale dependence of the latitudinal diversity gradient and, furthermore, that the size of the study organism is important, with increasing gradient strength and steeper slopes for larger organisms. Gradients in climate, productivity and glaciation history, all driven by latitude, have often been proposed as potential explanations to large-scale variation in species richness (e.g. Jackson and Harvey 1989, Ricklefs and Schluter 1993). However, distinguishing the mechanisms that are responsible for the latitudinal diversity gradient is difficult as most mechanisms lead to predictions that are not mutually exclusive, and the proposed null models give rise to latitudinal gradients in the absence of underlying environmental heterogeneity, e.g. the edge- /mid-domain effect (Colwell and Lees 2000).

Specific factors driving the diversity of the study organisms
Besides being affected by the major factors discussed above, the fish species and bacteria that are studied more closely are affected by some more specific factors.

The traditional view of bacterial diversity has been that they have unlimited dispersal, that “everything is everywhere, but the environment selects” (Baas-Becking 1934). The reasoning behind this perspective is that microor-
ganisms are abundant, proliferate rapidly, disperse with ease, and are unlikely to go extinct (Fenchel 1993, Pedrós-Alió 1993, Whitman et al. 1998), and it has been supported by several studies that has shown global distributions of certain species (Findlay and Clarke 1999, Finlay 2002). Factors of the local environment that has been shown to affect bacterial community composition (BCC) include DOM quality (Cottrell and Kirchman 2000, Covert and Moran 2001) and quantity (Eiler et al. 2003), primary productivity (e.g. Horner-Devine et al. 2003), inorganic nutrients (e.g. Fisher et al. 2000), grazing (Jürgens and Matz 2002) and pH (e.g Lindström and Leskinen 2002). However, recent studies have shown that bacteria might, indeed, have restricted dispersal and thus also exhibit biogeographical patterns (Whitaker et al. 2003, Bell et al. 2005).

In contrast to bacteria, the importance of biogeography and history for the distribution of fish species has been recognized for more than a century (Ekman 1922, Lundberg 1899). Few studies have, however, considered lakes in a metacommunity context, despite the long-standing interest for biogeography in fish and the suitability of lakes interconnected by rivers for studies of metacommunity, as well as metapopulation, dynamics (e.g. Gotelli 1999). As fish are restricted to rivers for migration between lakes they are more dispersal limited than the bacteria, and therefore isolated lakes are generally species poor (e.g. Magnuson et al. 1998). Local factors that are known to influence fish community composition and diversity in lakes include lake size, habitat diversity, depth of the photic layer, maximum depth, anoxia, low pH (Eadie and Keast 1984, Matuszek and Beggs 1988, Magnuson et al. 1998, Jackson et al. 2001, Amarasinghe and Welcomme 2002, Öhman et al. 2006).

Mechanisms behind diversity – on an evolutionary scale

“Nature abhors a vacuum in the animate world as well as in the inanimate world” (Grinnell 1924). That is, if there is room for a species then one will invade or eventually one will be evolved to fit that room, or empty niche if you will. The foundation of diversity is that in order for a “status quo” to be active speciation must balance extinction. As the speciation rate is highly dependent on area (Losos and Schluter 2000), and loss of suitable habitat is widespread, the global speciation rate is probably reduced. Rosenzweig (2001) suggests that the mechanisms behind the effect of area on speciation are as follows:

- Larger ranges offer larger targets for geographical isolating barriers. The formation of geographical isolates begins the sequence of events leading to allopatric speciation. Thus a range that is more readily subdivided by geographical barriers will spawn more isolated populations per unit time and have a higher rate of speciation.
• Widespread species have more genetic variability than narrowly distributed species, which may lead to an increased rate of speciation.
• Larger ranges produce species with a greater population size. And larger populations have higher speciation rates.

Furthermore, as all species are “nursing grounds” for future species, a loss of diversity in itself leads to a decreased speciation rate (Rosenzweig 2001).

High rates of speciation can be found in the tropics, where high temperatures increase the standing stock of species by accelerating the biochemical reactions that control speciation rates (Allen et al. 2002). However, it can also be found where empty niches are abundant, for example in the previously glaciated parts of Europe where colonization and speciation processes of fishes are relatively young (Schluter 1996).

Not only geography governs the rate of speciation. Evolutionary consequences of species interactions may together with regional and local variability of the environment lead to adaptive radiation of species that ultimately influence species diversity (Schluter 2000a). For example, some of the most classic ecological studies regarding the Galapagos finches have used competition to explain a morphological diversification (Lack 1947). Even habitat heterogeneity has evolutionary implications, which involves the partitioning of habitat and consumable resources (McArthur and Wilson 1967, Rosenzweig 1995). For example, habitat diversity may promote speciation if traits related to different habitat utilization strengthen reproductive isolation between phenotypically divergent forms (Schluter 2000b). Ecological trade-offs, for example that between foraging and predation risk by shifting habitat, may also lead to habitat specialization in resource use that in turn may affect individuals phenotypically (Robinson et al. 1995, Eklöv and VanKooten 2001, Svanbäck and Eklöv 2003). Furthermore, there is strong empirical evidence that habitat diversity lead to trophic polymorphism that can be considered as a first step in the process of speciation (Skulason and Smith 1995, Smith and Skulason 1996, Schluter 2000b), see Fig. 3.
Increased intraspecific competition and invasion of unexploited niches.

Adaptation of morphs to discrete resources and divergent selection regimes.

Evolution of polymorphism.

Stable polymorphism with high gene flow.

Reduced gene flow.

Evolution of reproductive isolation.

Speciation.

Figure 3. Schematic view showing potential steps and mechanisms leading to resource polymorphism and eventually speciation, according to Smith and Skulason (1996). From Olsson (2006)

Summary

To sum up, it can be said that many processes influence the species richness and diversity, and that the dominating process differs between sites, and even within sites, depending on the scale of which the study is conducted. Large-scale processes, like migration history and biogeography, set the hard limit on diversity. That is, no matter how suitable the location, if a species cannot get there, it cannot populate the site. Once a species reach a site it might, if physiochemical conditions are favourable, resources are available and nothing eats them, establish a population there. If the population is large enough to avoid stochastic extinction it will remain indefinitely, but it will definitely go extinct (as all species are transient and will ultimately go extinct).

Species interactions are important for coexistence locally. All types of interactions that disfavour the superior competitors favour diversity. Predation seems to be vital for coexistence of species that normally could not coexist. Other factors that are of importance locally are productivity, and a number of physicochemical parameters.
Metapopulation dynamics can further expand the conditions for coexistence of species. As populations are interconnected and their extinctions often are asynchronous all populations have to be eradicated at once for a species to go extinct in the whole region.

We are losing diversity not only through an increase in the number of extinctions, but through a decrease in speciation as well. In order to turn the tide and reach a new steady state of species richness more suitable habitat must be returned to nature. Even if some hot spots of diversity are preserved as natural reserves stochastic extinctions will eventually remove some species, but with the currently low rate of speciation no new species will be evolved to take their place.
Aims of the thesis

The focus of this thesis is to try to explain observed patterns in species diversity, richness and composition. The majority of the work is focused on fish, but to evaluate the effect of dispersal mode, for different organism size and mobility, one investigation was done on bacteria. Furthermore, in order to shed some light on the very early stages of speciation the genetic and morphologic differentiation in perch was investigated.

The papers presented in this thesis highlight many of the processes that shape the patterns in local species richness and composition (Fig. 4).

![A diagram showing the connections between regional species pool, local community, metacommunity dynamics, dispersal, and metapopulation dynamics.](image)

*Figure 4. A conceptual model showing where in the different steps from the regional species pool to the local community my research fits. The Roman numerals represent the papers presented in the thesis.*

More specifically, this thesis focuses on these issues and questions:

- What regional and local processes are of importance for the number of fish species in lakes? (paper I&II)

- Are local or regional factors most important for species composition for organisms with different dispersal abilities? (III&IV)
• What metacommunity dynamic type best describe the different communities? (III&IV)

• What local and regional factors are of importance in shaping the species composition patterns for fish and bacteria (papers III&IV)

• Why are some species common and others rare? (paper IV)

• Can early stages of speciation between pelagic and littoral perch be found in Lake Mälaren? (paper V)
Methods

Fish diversity
All fish data for paper I, II, IV was extracted from the Swedish Board of Fisheries database of standardized test fishing. The lakes in the data-set had been surveyed with standardized Nordic multi-sized mesh gillnets. The fishing effort was higher in larger lakes, in order to get a representative sample of the fish fauna independent of lake size. The nets were distributed randomly, within different depth zones. The fishing was carried out in late summer to avoid any spawning aggregations and because most fish species are fairly active at that time of year. The test fishing did not catch all species present in a lake, but as the procedure was conducted in a standardized manner the results from different lakes should be comparable. The method is described in detail in (Appelberg 2000). Different subsets from all the available lakes (Fig. 5) were extracted to answer different questions.

A few species are undoubtedly missed – especially in the lakes with comparatively high diversity. Some species are hard to catch in nets due to their body-form, such as eels (Anguilla anguilla), others because of their lifestyle, such as the sit-and-wait predator pike (Esox lucius). However, as all lakes are sampled in a standardized manner, comparisons between lakes are valid.

Species number was used as a measure of diversity in paper I, species number and the reciprocal Simpson’s index in paper II. In paper IV species composition was analysed using CCA.

In addition to species richness we also studied a diversity index, namely the complement of the Simpson diversity index (I). This index is less sensitive to rare species and is less dependent on sample size than species richness, and as the data contains many rare species and varying sample sizes we decided to make a comparison between the two. \( I = 1 - D, \ D = \sum n_i(n_i-1) / N(N-1) \), where \( n_i \) = the number of individuals in the \( i \):th species; and \( N \) = the total number of individuals.
Bacterial diversity

In contrast to fish, bacteria are, mostly due to their small size, difficult to separate into taxonomic units based on the morphospecies concept commonly applied to larger organisms. Isolating single species is a hard task and
the isolation approach generally underestimates the bacterial diversity in natural environments and is biased towards opportunistic taxa that readily grow in culture media. Therefore, we used a molecular approach, which is based on the isolation and amplification of 16S rRNA genes from environmental samples. More specifically a fingerprinting method, namely terminal restriction fragment length polymorphism (t-RFLP, Liu et al. 1997). In t-RFLP, 16S rDNA is amplified by polymerase chain reaction (PCR) using a fluorescently labelled primer and the amplicons are subsequently digested (i.e. cut into fragments of different length) with restriction enzymes. After the enzymatic digest the obtained mix of fluorescently labelled fragments differing in length can be separated electrophoretically to produce a pattern of peaks. Only peaks with a relative peak area larger than 0.5% to the total signal were included in the analysis. This procedure produced a list of operational taxonomic units (OTUs), which are then treated as “species” during the subsequent statistical analysis.

Fish phenotypic and genetic variation

In order to find out if the difference in populations of perch was due to environmental induction (i.e. phenotypic plasticity) or heritable genetic differences we analyzed the differences in the genetic structure of the individuals. In paper V we looked at the individual variation at a number of microsatellite loci. The microsatellite-method was chosen as it is especially useful in the studies of processes acting on ecological time scales (Selkoe and Toonen 2006). Another reason for using microsatellites as population genetic markers is that they are, assumed to be, neutral.

Morphological analyses of the perch was analyzed using landmark-based geometric morphometrics, which is a powerful, flexible and easily interpretable multivariate technique for analyzing shape variation between objects (Marcus et al. 1996). The left side of each specimen was photographed with a digital camera. 15 homologous landmarks were subsequently digitized. The shape variation in the material was then calculated by comparing the landmark configuration of all specimens. We analyzed the resulting shape variation by calculating relative warps (principal-component vectors in a multivariate-shape space). Each relative warp represents a unique multivariate-shape dimension and explains a part of the total variation in morphology. To estimate the differences in morphology between sites and sampling dates we performed a separate ANCOVA for each relative warp with site and date of capture as factors and size as a covariate. We performed linear regressions on pair-wise FST-values and pair-wise differences in relative warp scores between sites (spatial and temporal comparisons) to estimate the relationship between genetic and morphological differentiation in both space and time.
Results

Factors driving the patterns in fish species richness in Swedish lakes (I)

The major aims of this study was to investigate the large scale patterns in fish species diversity in Swedish lakes and to find out what factors were driving them. The data showed that most Swedish lakes were species poor; few lakes harboured more than five species. The diversity hot spots were found mainly close to the large lakes and the east coast, whereas the diversity cold spots were primarily found above the highest coastline (HC) and along the west coast (Fig. 6). Our analysis showed that half of the variation in species richness could be explained by the area of the lake, the altitude at which it is positioned, the straight line distance to the closest major pool of species (SLD), whether it is situated above or below the highest coastline and the mean annual temperature:

\[
\log_{10}(\text{Species richness}) = 0.650 + 0.178 \log_{10}(\text{Area}) - 0.106 \log_{10}(\text{Altitude}) - 0.006 \sqrt{\text{SLD}} - 0.028 \text{HC} + 0.009 \text{MAT}.
\]

Analysis of the residuals after explaining half of the variation showed that there were more species than expected close to the east coast and fewer species than expected in the northern and south-western parts.
Figure 6. An interpolation of the number of species caught during standardized test fishing of lakes throughout Sweden. The dashed area is situated above the highest coastline, i.e. it has not been under water since the last ice age.
Consequences of dispersal limitation and local processes for fish species richness and diversity (II)

The aim of this study was to test how fish species richness and diversity is controlled by dispersal of species from the regional species pool and by exclusion in the local environment. In addition, we wanted to test if the observed longitudinal gradient in richness (see paper I) was due to limited migration through the saline water off the west coast or due to acidification of the lakes.

We showed that more than 60% of the variation in fish species richness, and 45% of the variation in fish diversity, was explained by the combined effect of the environmental and spatial factors. Apparently the degree of explanation was higher for richness than diversity, although both results were generally concordant. Lake area and stream order of the river at the outlet of the lake was the most important variables. pH, maximum depth, water colour, altitude and the position of the lake relative to the highest coastline were other influential variables. The results were very similar for diversity and richness (Fig. 7).

The variables that were related to the size of the regional species pool and the barriers were found to be of little importance for both richness and diversity.

![Figure 7. The factors that were found to have an influence on fish species diversity and richness in Swedish lakes.](image-url)
Relation between local and regional processes in structuring bacterial community composition (III)

This study investigates the importance of local environmental vs. spatial factors on bacterial community composition in rock pools.

We found that both environmental and spatial factors influence BCC, in both cases independently of each other. Our results indicate that 14% of the variation in community composition between rock pools can be attributed to the environment, whereas 9% can be explained by spatial factors alone.

Salinity, chlorophyll a concentration, and water colour, had a significant effect on the composition of bacterial communities in the rock pools. Salinity was the most important factor, followed by chlorophyll a concentration and water colour. The environmental effect was still significant after accounting for spatial effects, explaining more than 10% of the total variation. After accounting for the environmental effect, the spatial effects were still significant and explained slightly less. However, the distance from the pools to the shore, which presumably reflects the likelihood to receive spray water inputs, was not a significant factor in explaining the variation in BCC between pools, indicating that distance from the sea per se was not important. However, the communities in pools located within the same spatial cluster were more similar than communities in different clusters (Fig. 8).

Figure 8. Map showing the sampling area along the Baltic Sea Coast, central Sweden. The rock pools are grouped into five locations (L1–L5). From Langenheder and Ragnarsson (2007).
Factors explaining fish species composition (IV)

The major aims of this study was to deduce what metacommunity dynamics type best describes the fish community composition (FCC) in Swedish lakes and investigate what specific local and spatial factors were of importance.

23 species were present in the dataset. There were a few very common species and a tail of rare species (fig. 9).

Figure 9. The fish species caught during standardized test fishing in 125 Swedish lakes.

Nearly 35% of the variation in FCC was explained by a total of 10 significant factors. Almost 10% of the variation in FCC was explained by the significant connectivity factors (figure 10). Altitude was the most important factor, when the effect of the environmental variables was taken into account, followed by dispersal barriers, stream order, dispersal barriers between the lake and the next lake downstream, and the position of the lake relative to the highest coastline. The five significant environmental variables (Fig. 10) explained more than 14% of the variation. Maximum depth was the most important variable, whereas total phosphorus, water colour, mean annual temperature and area accounted for progressively less of the variation. 10.6% of the variation was shared between the environment and connectivity, the bulk due to the co-variation between stream order and area (Fig. 10).

We also looked more closely at what species were associated to which variable. We found a group of fish that were found more often in deep lakes (smelt, vendace, burbot, bleak and whitefish). In contrast, roach and rudd were positively associated with shallow lakes. Bleak, bream, white bream, ruffe and zander were positively associated with total phosphorus, whereas
pike, perch and roach were significantly negatively associated with the variable. Bream, zander, bleak, ruffe, and white bream were favoured in lakes with a large river at the outlet, whereas pike, perch and roach were disfavoured there. Pike, perch and roach were found more often above the highest coastline and bream, white bream, zander and bleak below it. White bream was negatively affected by barriers in the river between the lake and the next lake downstream and altitude, but perch was positively affected by the two variables.

Figure 10. Canonical correspondence ordination of the number of fish of different species in relation to significant environmental and connectivity related variables. The species abbreviations (see figure 9 for full name) indicate the location of species centroids. Arrows represent the vectors of the variables. For clarity only the statistically significant variables are shown.

Genetic and morphological differentiation in perch (V)

We investigated perch spawning in two littoral and one pelagic habitat (figure 11).
Figure 11. Map over the three sampled sites in Hjulstafjärden, Lake Mälaren. The habitat at Site 1 was of a pelagic variety, whereas sites 2, 3 were littoral.

In May we found a significant genetic differentiation between all sites. There was also significant spatial genetic differentiation in the August sample. In addition, there was a pattern of temporal differentiation within each site. It seems that the sampled fish represented six genetically differentiated groups of fish corresponding to the three sites and two sample dates. When estimating the number of correctly classified individuals to the six genetic clusters only 1 out of the 177 individuals was misclassified. Furthermore, a pattern of isolation by distance was found at each sampling date, i.e. more genetic material was shared between closely situated sites than between sites separated by larger distances.

There was an effect of sampling date on morphology where fish caught in August had a more up-ward bent morphology compared to the fish caught in May. There was also a significant effect of capture site on morphology.

When comparing the morphological differences between sites and dates with the spatial and temporal genetic differentiation, the two measures of differentiation between sites in August coincided. There was also a substantial overall temporal differentiation at both the molecular and morphological level, but the patterns found in May did not concur with each other.
General Discussion

Fish richness/diversity in Swedish lakes

Species richness was found to be controlled by both regional and local processes. The effect of the last ice age was one evident regional factor. During the ice age Sweden was covered in ice. During the period after the ice retreated, some 15000 years ago, the Baltic Sea underwent a series of stages (figure 12) with varying water levels and salinity (Bjorck 1995).

![Figure 12. The time-scale where all colonizations of Swedish lakes have taken place.](image)

The pressure exerted from the ice compressed the ground under it. The combination of a higher water level in the Baltic Sea and a lower land allowed fish to move freely far above the current coast line. When the land ascended, due to isostatic rebound, lakes were formed, potentially trapping several fish species in them. The water from the melting glaciers also formed large temporary lakes (i.e. ice dammed lakes). Any present-day lake previously covered by the ice dammed lakes could have been colonized through the melt-water drainage, as some fish species are believed to have colonized the water soon after the ice retreated (Ekman 1922). The border between areas that have been under water at some stage and the areas that have never been under water is called the highest coastline (Fig. 6).

It is likely that fish colonized Sweden in three steps, at first through the melt-water drainage at the end of the last ice-age, subsequently when the water-level of the Baltic Sea peaked (and gave rise to the highest coast-line) and finally through the rivers. The first two are evident through the high
diversity below the highest coast line (paper I & II). The third way is obvious through the high diversity in lakes that are connected by a stream of high stream order (paper II), and the low diversity in the seepage lakes (paper I). Many studies incorporating lake connectivity disregard the size of the river (e.g. Olden et al. 2001), which we have found to be the most important connectivity variable. Altitude of the lake is also of importance. Besides affecting diversity through restricting migration through an increased slope for the fish to navigate, high altitude sites have harsher climate and generally are of lower productivity, which is supposed to decrease diversity. But considering that neither productivity (total phosphorus, paper II, and secchi depth, paper I) nor climate (MAT) affect diversity here we assume that altitude primarily influences diversity and richness through restricting migration.

There were more species in lakes close to the largest lakes and the Baltic Sea coast (paper I). The increase in species numbers close to these species rich areas is likely due to a combination of two mechanisms. On the one hand, some species may have had the opportunity to colonize the smaller lakes through rivers connecting to these water-bodies (paper II). On the other hand, the well connected lakes could function as sinks in a metapopulation with the rescue effect and re-colonization after local extinctions maintaining the higher species richness (Hanski 1999), however as richness was unaffected by the presence of barriers (paper II) this is unlikely. There were fewer species along the west coast (Fig. 6). Lake acidification is a big problem in south western Sweden (Bernes 1991) and could explain part of the lower species richness (paper II). Although the lakes have started to recover from acidification (Skjelkvåle et al. 2001) the salt barrier may prevent natural recolonization of fish into the lakes. In addition, the Baltic Sea (eastern coast) has likely been colonized from several different glacial refuges, whereas the west coast probably has only been colonized from one refuge (Nesbo et al. 1999). Thus, we were surprised to find that the richness of the species pool was of no consequence for local richness (paper II).

The non-existent link between regional and local richness might in this case be explained by the restricted migration. The high diversity only affected the most well connected lakes. Many lakes are still likely to be dependent on the inoculation of species after the ice-age but neither the size of the species pool nor the number of species in the catchment affected richness. The distance to the lake was of no consequence, nor were the presence of anthropogenic dispersal barriers. We had expected to find an effect of barriers, as comparatively short lived barriers, in the form of beaver dams, have been shown to decrease lake fish diversity (Bertolo and Magnan 2006). Still, considering the time since colonization of the lakes started the barriers have been in place a very short time (Fig. 12), perhaps too briefly for local extinctions to take place. So, evidently, the size of the river, and to some extent slope (through altitude), is of great importance for fish migration. The most isolated of lakes, i.e. the seepage lakes, were species poor, as expected.
Several factors affect survival once the fish reach the lake. Lake size was important, as was maximum depth. An increase in maximum depth may, besides increasing the amount of available habitat, also decrease the likelihood of winter fish kills due to anoxia. Low pH lakes had lower richness and diversity, indicating that some species have gone locally extinct. Latitude is one of the most widely recognized large-scale diversity gradients, diversity generally decreases at higher latitudes (Hillebrand 2004). Still, gradients in climate and productivity have often been proposed as explanations (see Ricklefs and Schluter 1993). Yet, in these studies the proxies of productivity (i.e. secchi disc depth and total phosphorus) and climate (mean annual air temperature) explained little of the variation.

The results indicated that fish species richness in Swedish lakes is the result of both regional and local factors. The local variables explained most of the variation, suggesting that many species have had access to lakes without successfully colonizing them.

Differences between fish diversity and fish community composition

Both community richness and composition was determined by a combination of local and regional factors, though there were some differences between what factors were of importance for community richness and composition.

The highest-coastline, stream order, area, water-colour, altitude and mean annual temperature affected both richness and composition (paper I, II, & IV).

Anthropogenic dispersal barriers affected species composition (paper IV), but not diversity and richness (paper II). A barrier stopping migration between the lake and the next lake downstream affected white bream (Blicca bjoerkna) negatively and perch (Perca fluviatilis) positively. Especially perch seem to be favoured by all form of barriers – past and present – whereas white bream appear to be negatively affected by barriers. White bream might be a later colonizer than the other species, still advancing along the rivers or it could be more dependent on re-colonization or a rescue effect for local persistence.

Lake depth had but a minor affect on the number of species (paper I & II), but changed the composition radically (paper IV). Larger depths can lead to an increased size of the pelagic habitat, thereby facilitating the occurrence of pelagic species and provide a cold-water refuge for cold-water species in the summer. This is supported by the fact that several well known pelagic and/or cold-water species were favoured by an increasing depth. On the contrary, shallow lakes warm up quickly in the spring, and should therefore favour warm water species. Accordingly, two warm water species were
associated with a low maximum depth. Shallow lakes are also, commonly, associated with oxygen deficiency in the winter (Magnuson et al. 1998), during the ice covered period, and we found that crucian carp was associated negatively, albeit insignificantly, with depth. Crucian carp is well known to be extremely tolerant of low oxygen conditions (reviewed in Holopainen et al. 1997), and has been shown to occur more often in lakes with low oxygen conditions during the winter (Öhman et al. 2006).

pH has been shown to be important for species configuration within lakes (e.g. Persson 1997, Öhman et al. 2006). However, here pH affected only the number of species, not the composition. In paper II it is evident that richness and diversity increases linearly with an increase in pH. We would have expected to find that richness decreased rapidly at a threshold corresponding to local extinctions of sensitive species, as the pH in some lakes is low enough to severely affect several of the species included in the study (Appelberg et al. 1993, Öhman et al. 2006). But the results (or rather lack thereof) in paper IV would suggest that the effect of pH affects all species in a similar manner.

There was a large effect of productivity, in the form of TP, on composition, but not on richness and diversity. Total phosphorus (TP) was the second most important structuring factor for FCC. TP is a good proxy for primary productivity in aquatic systems (Peters and Bergmann 1982), and it has been shown a number of times that productivity is of importance for both the richness and composition of species in a range of different systems (reviewed in Waide et al. 1999). Yet, no fish species were reported to have become locally extinct due to the adverse impacts, such as anoxic conditions and degradation of the habitat, caused by eutrophication in an extensive study of fish stocks in Sweden, Norway and Finland (Tammi et al. 2003). Still, the composition of the fish communities has been found to change towards a dominance of the cyprinid species (Persson et al. 1991). Our analysis showed that this was the case, the cyprinids bream, white bream and bleak occurred more often in high TP lakes. A high productivity is generally associated with a high turbidity, which should favour species that are adapted to foraging in low light conditions. Zander and ruffé can even feed at night (Froese and Pauly 2007) and were favoured in the high TP lakes, whereas species that rely more on sight (pike, perch and roach) were disfavoured.

Comparison between community composition in fish and bacteria

There were striking, and surprising, similarities in the control of fish community composition and bacterial community composition (figure 13). We
predicted fish to be very limited by dispersal, as they have to disperse through water-ways and are generally poor dispersers (see Lucas and Baras 2001). Bacteria, on the other hand, are predicted to be unrestrained by dispersal (e.g. Finlay 2002, Van der Gucht et al. 2007), see introduction.

![Figure 13](image.png)

Figure 13. The fractions of community composition explained by the local environment and the spatial/connectivity related factors for fish (left) and bacteria (right).

Still, both would be described as being assembled by a combination of mass-effect and species-sorting (see Cottenie 2005) metacommunity dynamics (paper III & IV). Maybe the difference in scale of the studies renders similar patterns (~500 meters for bacteria, ~500 000m for fish).

SS is the traditional explanation for BCC: as everything is everywhere, patches with favourable environment will be occupied. However, we also found evidence of mass effects (see Leibold et al. 2004), which distribute taxa steadily within a region of highly connected habitats. More specifically, pools close to each other are more likely to share a common colonization event, such as simultaneous spray water inputs and/or higher connectivity resulting in occasional exchange of bacteria via rivulets connecting them (e.g., during rainfall periods), potentially yielding more similarly composed bacterial communities due to spatial factors alone. Lindström et al. (2004, 2006) found that in lakes with short retention time the bacterial composition of the inlet water structured the composition within the lake. The rock pools may be similarly controlled, either through water from the Baltic, or groundwater from the surrounding forest, or most likely from surrounding pools. However, the distance from the pools to the shore, which presumably reflects the likelihood to receive spray water inputs, was not a significant factor in explaining the variation in BCC between pools, indicating that distance from the sea per se was not important.
This result is remarkable because previous studies investigating the effect of local environmental conditions and dispersal on community structure in landscapes of lakes found that BCC was only significantly influenced by the environmental condition but not by spatial factors (Beisner et al. 2006, Van der Gucht et al. 2007). Bacteria might be able to disperse freely, but it is likely quicker and more efficient to disperse short distances, through water.

Van der Gucht et al. (2007) argued that spatial factors are not important, despite the large scale of their studied system. However, I would rather suggest that most studied systems are too large for spatial effects to be evident. Mass-effects for bacteria should perhaps not be evident on much larger scales than what we have studied (see also Lindström et al. 2006), as a surplus of a “species” of bacteria is unlikely to be dispersed very far.

An indication of ME on fish community composition may be found in figure 14. The locally abundant species are the same species that are present in many lakes, which might indicate that abundant species are more likely to disperse to surrounding lakes. For ME to be a realistic explanation dispersal has to be fairly high (see Holyoak et al. 2005), and the effect from the dispersal barriers (paper IV) should indicate that disconnecting a lake from the metacommunity had an effect on at least some species in the community. Several environmental gradients were also shown to be of importance for composition, which means that some species have been excluded from communities by unfavourable local conditions, suggesting SS dynamics. Several connectivity related factors were important for FCC, potentially affecting the chance of colonization, re-colonization, and facilitate a rescue effect. The spatial effect on BCC might have been even larger, had the inter-pool connectivity been described and analyzed.

These studies show that both the composition of aquatic bacterial communities and lake fish communities are affected by similar factors, both environmental and spatial.

The commonness and rarity of species

It is a well-known phenomenon that locally abundant species are also, generally, widely distributed. The most common explanations for this relationship, the distribution-abundance curve, are Brown’s niche breadth hypothesis and metapopulation dynamics. Brown (1984) propose that generalist species, on the one hand, are generally both locally common and have wide distributions. Specialists, on the other hand, tend to be locally sparse and have narrow distributions. In addition, metapopulation models predict that locally abundant species become widely distributed as they are unlikely to go extinct locally, due to their high numbers, and have a high rate of colonization, through mass-effects, of surrounding localities (Hanski 1999). The most common fish species in the surveyed lakes are pike, perch and roach.
(Fig. 14). None of the three are well known for having extraordinary dispersal abilities (Lucas and Baras 2001), hence it is likely that they are common due to them being good at colonizing lakes once they reach them and/or very rarely go locally extinct.

\[ \text{Log CPUE} \]

\[ \text{Log presence [\% of lakes]} \]

Figure 14. Plot of the mean catch per unit effort (CPUE) of species in lakes where they are present vs. the percent of the total number of lakes they are present. $R^2 = 0.3615$, $P=0.024$

In addition, the most common species were not negatively affected by anthropogenic dispersal barriers (paper IV). If local extinctions are very rare then the relatively short time that the barriers have been in place (see figure 12) are likely too short for an effect to be evident. In addition, perch populations appear to be divided into distinct subpopulations (paper V). As there seems to be an exchange of genes, and thus individuals, between the populations, there could be within-lake metapopulation dynamics. We sampled a small area of Lake Mälaren, roughly equivalent of a small lake, and found one distinct population per site. Lake Mälaren is about 1 000 times larger (1 120 km$^2$) than the sampled area, a conservative estimate of the number of subpopulations would then be 3 000. The risk of them going extinct simultaneously should be rather slim.
Small-scale genetic and morphological differentiation

Lake fish in previously glaciated areas of the Northern hemisphere often display an individual variation in morphology within populations coupled to different habitats of the lakes (Robinson and Wilson 1994, Schluter 1996). Perch, for example, commonly exhibit dietary and morphological variation between the littoral and pelagic habitats of lakes (Svanbäck and Eklöv 2002, 2003). These habitat specific morphologies are suggested to be adaptive (Svanbäck and Eklöv 2003, 2004), but phenotypic plasticity seems to play a leading role during the morphological development (Hjelm et al. 2001, Olsson and Eklöv 2005).

There is evidence of genetic differentiation between morphological forms, for some species (reviewed in Schluter 1996), despite the fact that this differentiation to a large extent is attributable to phenotypic plasticity (e.g. Robinson and Parsons 2002). And such polymorphisms could be of great evolutionary significance if there is a tight connection between morphological and genetic divergence (West-Eberhard 1989, Smith and Skulason 1996), since the build-up of reproductive isolation between genetically differentiated morphotypes could lead to future speciation (Fig. 3). Thus, in order to shed some light on the very early stages of speciation we investigated the potential for genetic and morphologic differentiation of perch at small scales.

Perch has been proposed to be a likely candidate for speciation in the future (Behrmann-Godel et al. 2004). We found genetic and morphologic differentiation in perch between three sites and two dates (paper V). But we believe that speciation between littoral and pelagic perch from the studied lake is unlikely at a short time scale since the result presented in paper V indicate that the heritable component of morphology is rather weak (see also Svanbäck and Eklöv 2006). Indicating that the differentiation in morphology might rather have been driven by a plastic response to variation in the environment between sites, and the time effect may have been due to variable resources between sample occasions. Furthermore, the small scaled genetic differentiation could have evolved due to kin-association and/or site-fidelity. Perch is known to exhibit strong site and shoal fidelity (e.g. Kipling and Le Cren 1984), and we found indications of that the majority of the sampled groups consisted of individuals that were more related to each other than expected by chance alone. Thus, the sampling of to some extent genetically isolated groups consisting of close relatives could serve as a possible explanation for the small scaled genetic differentiation found in this study.

Still, genetic differentiation at small spatial scales has been considered to be negligible due to extensive exchange of individuals, and thus genes, yet we found genetic differentiation in Eurasian perch between three sites separated by less than 400 hundred meters. The maintenance of genetic variation within and among populations locally is potentially important for maintaining diversity in a longer-term perspective.
Conclusions and perspectives

The major results of the papers presented in this thesis can be summarized as follows:

- Both local and regional processes affect local fish species richness, diversity and composition (paper I, II, & IV)
- Fish and bacterial community composition is the result of both local and regional factors. The metacommunity dynamics of both groups are best described by a combination of species sorting and mass-effect dynamics, despite widely differing dispersal abilities (papers III-IV)
- Speciation between littoral and pelagic perch is unlikely, as the heritable component of morphology was marginal (paper V)

During my work on this project I have raised a number of questions, questions that I have not had time to answer myself, but hope will be answered sometime in the future. The few that I deem interesting enough to merit addressing in future studies are:

- Is it possible to predict species richness and composition in lakes? A predictive model would be constructed and evaluated
- Why are certain species common and other rare? Investigate the commonness and rarity of fish species throughout Sweden. Classify the species according to if they are at an end of their respective ranges, whether they are specialists or generalist and if they are good or poor dispersers.
- How large part of the area effect on fish species richness can be attributed to habitat heterogeneity? The habitat would be mapped using a GIS-GPS unit in lakes of similar size and similar connectivity.
- Metapopulation dynamics of aquatic bacteria. An experimental study would be performed, with identical pools with known connectivity. Different dispersal rates could be tested.
- Do subpopulations of perch function as a metapopulation? Sample more locations in Lake Mälaren.

*The best laid schemes o' Mice an' Men, Gang aft agley*

Robert Burns
Relevance of the thesis

This is my time for reflection. What have I produced, and why? “Understanding biodiversity and its origin, maintenance, and loss on Earth is an issue of profound significance to the future of humanity and life as we know it” (Hubbell 2001). An indication as to how important the issue is considered to be is given by the fact that no less than 187 countries have agreed on a Convention of Biological Diversity. Even though biodiversity evidently is of so profound importance, research is still in its cradle. We still do not even know the number of species inhabiting this world – not even the order of magnitude thereof. Fluctuations in diversity are normal; species should go extinct now and then – both locally and globally. But one invasive species have changed these fluctuations fundamentally. The culprit, Homo Sapiens, has a greater impact on the stability, dynamics, composition, structure, and functioning of ecosystems and communities than any other species (Tilman 1999).

Habitat degeneration and fragmentation has been proposed to be the biggest threat to diversity. At the same time as it leads to an increased rate of extinction, the rate of speciation is decreased (Rosenzweig 2001). In this thesis I present results that indicate that the area and connectivity of lakes is of the utmost importance for fish species richness, diversity and composition. Still, I could not find a large effect of contemporary dispersal barriers, but if global warming takes place as feared (or worse) warm water species will try to advance their fronts (Parmesan 1996, Wilson et al. 2005) - at the cost of other species. In addition, the predicted increased precipitation and increased likelihood of extreme flows (e.g. Palmer and Räisänen 2002), which might facilitate dispersal in fish through increasing the size of the rivers that connects the lakes and flush out natural dispersal barriers. Thus, in the future the effect of dams might be more prominent.

I end this thesis with a quote, a quote that captures the very essence of biodiversity: “What a struggle must have gone on during long centuries between the several kinds of trees, each annually scattering its seeds by the thousand; what war between insect and insect - between insects, snails, and other animals with birds and beasts of prey - all striving to increase, all feeding on each other, or on the trees, their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees” (Darwin 1859).

Eftersom huvuddelen av avhandlingen har fisk som fokus börjar jag med ett exempel på hur artrikedomen kan tänkas styras i sjöar. Sedan går jag igenom vad jag kommit fram till i de olika undersökningarna.


För ungefär 15 000 år sedan var hela Sverige täckt av is. Då fanns inga sjöar – och därmed inga fiskar! När isarna började smälta steg vattennivån i Östersjön. Den högsta nivån vattnet nådde kallas för högsta kustlinjen.

Det dröjde inte länge innan fiskar började vandra in från öster. De kunde simma fritt ända upp till högsta kustlinjen. När isen smalt bort började mar-

Många arter kom till Sverige efter att vattennivån sjunkit. Eftersom många arter är dåliga på att hoppa stoppades de av naturliga vandringshinder – vilket återspeglar sig i den höga rikedomen nära kusten.


De viktigaste resultaten från den tredje (III) undersökningen är att även bakterier är beroende av spridningsvägar. Traditionellt set fanns bakterier som bindes ihop med resten av vattendraget. Nu är de mer öppna för att komma in i insjöar.
trivts på en viss plats. Vi visade dock att bakteriesamhällen i hällkar var mer lika varandra om hällkaren var nära varandra än annars.

I den fjärde (IV) undersökningen studerade vi artsammansättningen i svenska sjöar. Där kom vi fram till att spridningsbegränsning var av nästan lika stor vikt som lokala förutsättningar för sammansättningen av fisksamhällen.

I arbetet som får avsluta den här avhandlingen (V) undersökte vi om vi kunde hitta ett förstadium till artbildning hos abborrar i Mälaren. Abborrar är Sveriges vanligast förekommande insjöfisk, och det skulle därför vara väldigt intressant om de skulle bilda nya arter. Eftersom abborrar som lever i den fria vattenmassan har annorlunda kroppsform jämfört med de som lever i vegetationen så skulle det kunna tyda på att de är även genetisk skilda. Om det dessutom skulle visa sig att abborrar från pelagialen leker med andra abborrar från pelagialen, och vice versa, skulle detta kunna leda till artbildning. Resultaten visade att abborrar fångade på olika platser också var genetisk skilda, men det gick inte att koppla till kroppsform eller habitatval - utan snarare handlade om besläktade individer som bildar stim och anpassar kroppsform efter vilket habitat de lever i. Vi kunde alltså inte finna något förstadium till artbildning.
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*Casus ubique valet; semper tibi pendeat hamus*

*Quo minime credas gurgite, piscis erit*

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