

Anna Astorga

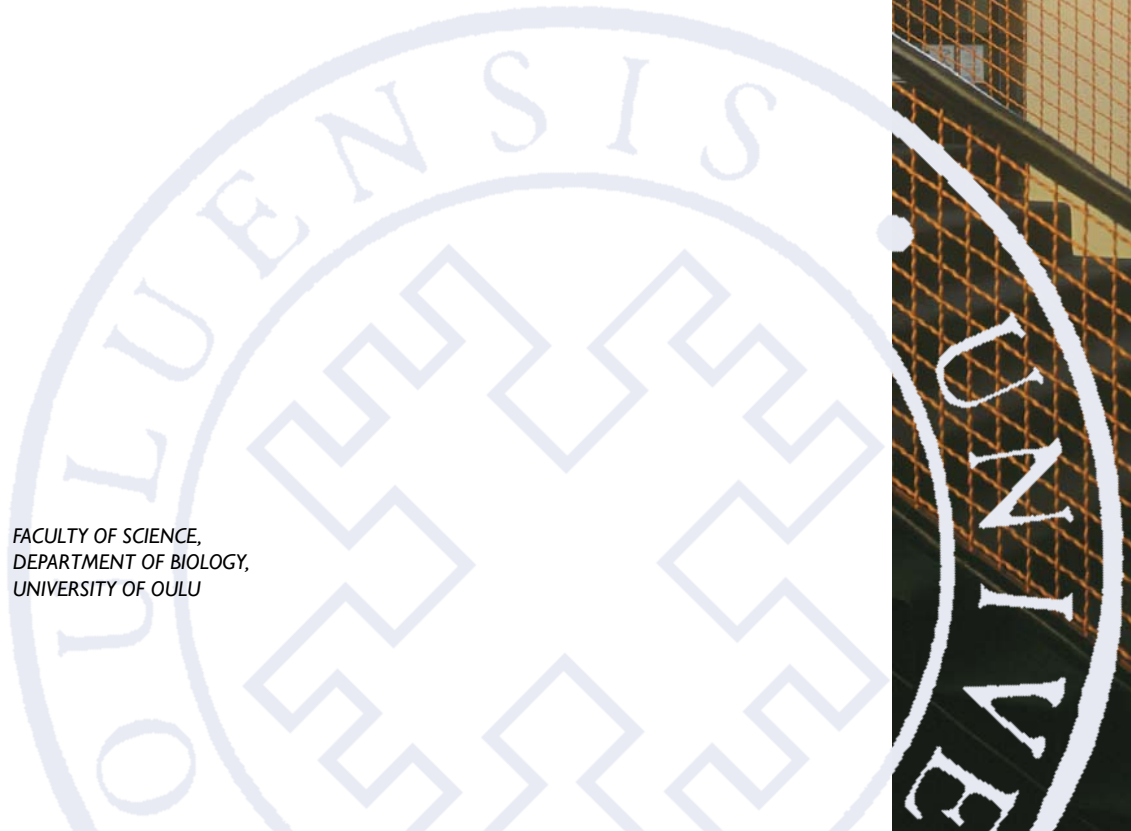
DIVERSITY PATTERNS IN MARINE AND FRESHWATER ENVIRONMENTS

*THE ROLE OF ENVIRONMENTAL AND SPATIAL
FACTORS ACROSS MULTIPLE SCALES*

FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY,
UNIVERSITY OF OULU

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**DIVERSITY PATTERNS IN MARINE
AND FRESHWATER ENVIRONMENTS**

The role of environmental and spatial factors across
multiple scales

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Abstract

Recognition of the importance of a regional perspective for understanding the structure and dynamics of local assemblages has stimulated the emergence of the field of macroecology. Most attention has been directed to terrestrial ecosystems, while large-scale patterns in biodiversity of aquatic organisms have received less attention. In this thesis I examined patterns of aquatic diversity across several geographic areas and scales, in an effort to understand some of the environmental and spatial factors determining species diversity in aquatic environments. The main objectives of this thesis were: (i) to examine the latitudinal diversity patterns of marine crustaceans and molluscs and their relationship to large scale environmental gradients, (ii) to study macroinvertebrate species richness in headwater streams at two spatial extents, within and across drainage systems, and assess the relative importance of local, landscape and regional variables, and (iii) to study diversity patterns of macroorganisms vs microorganism, comparing distance decay patterns of stream diatoms, macroinvertebrates and bryophytes.

Latitudinal diversity patterns of crustaceans and molluscs were clearly related to larval developmental mode. An increase in species richness towards high latitudes was found for species with direct development, whereas richness of species with planktotrophic development decreased poleward. Sea surface temperature was the most important environmental gradient related to species richness of both phyla and each developmental mode, but with different effects on each mode.

Stream macroinvertebrate species richness at the bioregion extent was negatively related to water humic content. Another factor related to species richness at the bioregion extent was elevation range, a variable linked to stream topographic heterogeneity. Local environmental variables explained most of the variation in species richness at the drainage system extent, however high among-region variability was evident.

Patterns between macro- and microorganism may not be fundamentally different, but the level of environmental control varied, being strongest for diatoms, while some groups of benthic macroinvertebrates exhibited relatively strong dispersal limitation. The relative importance of niche vs. dispersal processes is not simply a function of organism size but other traits (*e.g.* life-history type, dispersal capacity) may obscure this relationship.

Keywords: biodiversity, community similarity, environmental gradients, latitudinal patterns, marine, spatial scale, spatial structure, species richness, streams

To Ranchillo's stream

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Curiosity on stream ecology and my Finnish roots lead me to Finland in 2004. Then I started officially doing my Ph.D. thesis in Timo Muotka’s research group. I am grateful to Timo for invaluable guidance during these years, for his trust in me and for his enthusiasm in stream community ecology that have inspired me to keep on doing research as a freshwater ecologist. Jani Heino and Riku Paavola have also been actively part of the supervision, thank you for your helpful advice, discussions and guidance in the field of stream ecology.

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List of original papers

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

- I Astorga A, Fernández M, Boschii E & Lagos N (2003) Two oceans, two taxa and one mode of development: latitudinal patterns of South American crabs and test for causal processes. *Ecology Letters* 6: 420–427.
- II Fernández M, Astorga A, Navarrete S, Valdovinos C & Marquet P (2009) Deconstructing Latitudinal Diversity Patterns in the Ocean: Does Larval Development Hold the Clue? *Ecology Letters* 12: E12–733.
- III Astorga A, Heino J, Luoto M & Muotka T (2009) Freshwater biodiversity at a regional scale: determinants of macroinvertebrate species richness in headwater streams. Manuscript.
- IV Astorga A, Oksanen J, Luoto M, Soininen J, Virtanen R & Muotka T (2009) Distance decay of similarity in stream communities: do macro- and microorganisms follow the same rules? Manuscript.

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1 Introduction

Biodiversity, the variety of life, is distributed heterogeneously across the earth. Some areas teem with biological variation, while others are less diverse. Why do the number and kinds of species vary from one place to another and what determines the number and kinds of species that co-occur in one place? These deceptively simple questions have captured the attention of scientist for centuries, becoming one of the main objectives in ecology and biogeography (Brown & Lomolino 1998). Traditionally, the approach for answering such questions has been to document events and interactions occurring within a local community, focusing on how ecological systems are structured by local scale environmental variables and biological processes (Paine 1966, Huston 1994). However, during the past 15 years an important development has been made in studies documenting large-scale spatial patterns in biodiversity, attempting to explain them and to explore their implications (Blackburn & Gaston 2003). Two main reasons lie behind this development: First, it reflects the increased general concern over the future of biodiversity, and the resultant need to determine its current status and identify the most effective schemes for conservation. Second, it reflects the improvements in data availability and analytical tools (Gaston 2000, Magurran 2004).

For describing, and ultimately understanding the abundance and distribution of species at large spatial scales, attention has been focused on the identification of general spatial patterns of biodiversity. Amongst these patterns are, for example, the variation of diversity across latitude, altitude, depth and isolation (Brown & Lomolino 1998). Other studies have been concerned with comparing diversity across different biogeographic regions (Reid 1998), as well as on variation of diversity across spatial scales, for example, the species-area relationship (Rozenweig 1995), and the relationship between local and regional species richness (Cornell & Lawton 1992). Both contemporary and historical, local ecological and regional factors can regulate biodiversity patterns (Brown and Lomolino 1998, Quian *et al.* 2007). The main environmental gradients that have been associated with variation in species diversity are energy-related variables (*i.e.*, temperature), precipitation, productivity and habitat heterogeneity (Currie 1991, Rahbek & Graves 2001, Hawkins *et al.* 2003a, Francis & Currie 2003). The main historical and regional factors associated with species diversity patterns include glaciations and historical idiosyncrasies among regions, independent of contemporary environmental conditions (Hawkins *et al.* 2003b,

Graham *et al.* 2006, Vyverman *et al.* 2007). Although many ecologists now accept that there probably is no single explanation for these biodiversity patterns, the central question becomes not which of the competing explanations is the correct one, but what is their relative importance, and when and where and why does this change (Blackburn & Gaston 2003).

Efforts to understand spatial patterns of diversity have concerned a relatively small number of well-known taxa, especially plants, birds and mammals in the terrestrial realm and, to a lesser degree, molluscs and fish in the marine realm (Gaston & Spicer 1998). In marine systems, the generality of some diversity patterns, such as the latitudinal gradient in species richness, is unclear. While some groups exhibit clear clines of decreasing diversity towards lower latitudes, many other groups exhibit the opposite pattern (Kendall & Aschan 1993, Clarke & Crame 1997, Valdovinos *et al.* 2003). These different patterns may be related to different evolutionary and historical processes between regions (Rosa *et al.* 2008), but they might also be related to the coarse way in which species richness is usually quantified. Different patterns can be expected between different taxa or regions, as a result of the interaction between species attributes and the environmental context in which they are embedded (Marquet *et al.* 2004). In freshwater systems, knowledge of large-scale diversity is less well developed, except perhaps for fishes (Guegan *et al.* 1998, Zhao *et al.* 2006). Moreover, a recent review suggests that geographical patterns in freshwater invertebrate diversity may be relatively weak, and local environmental variation overrides the influences of historical and climatic factors (Heino 2009). However, the spatial extent of freshwater diversity studies is often quite small compared with terrestrial or marine systems, and evidence from the few larger scale studies stress the importance of considering the climatic environmental factors and the history of regions and lineages for understanding freshwater biodiversity patterns (Harding *et al.* 1998, Bradley & Ormerod 2001, Vinson & Hawkins 2003, Beauchard *et al.* 2003, Hof *et al.* 2008, Bonada *et al.* 2008).

The primary goal of this thesis was to examine patterns of aquatic species diversity across several geographic regions and scales. Papers I and II examine the latitudinal diversity gradient of marine invertebrates in an attempt to reconcile the contrasting latitudinal patterns reported for marine taxa at a hemispheric extent in South America. In paper III we studied species richness of stream macroinvertebrates at two spatial extents, analyzing how much of the variation in species richness is explained by local environmental factors, landscape variables and regional climatic variables, and how species richness is structured in space

across Finland. In paper IV we examined the community similarity of stream macroinvertebrates, bryophytes and diatoms, examining how species turnover is related to environmental factors and geographic distance between sites. One key aspect that integrates the four articles included in this thesis is the recognition of the importance of a wider perspective, by studying species richness variation across different spatial scales, from individual drainage systems to continents. Studies of biodiversity in aquatic environments are urgently needed, because aquatic ecosystems are globally among the most threatened ones, even more so than most terrestrial systems (Jenkins 2003). The following sections introduce each paper and their specific objectives.

1.1 Marine latitudinal diversity gradients

Perhaps the boldest signature of spatial variation in biodiversity is that associated with latitude. Studies along latitudinal gradients have contributed greatly to our understanding of the geographic distribution of species richness (Currie 1991, Hillebrand 2004). These studies have primarily addressed patterns of richness at very broad geographical extents, based on data compiled from distribution maps and atlases. This pattern is widely reported for terrestrial organisms but is less clear in marine systems, showing notable differences to the north and south of the equator (Clarke & Crame 1997, Roy *et al.* 1998, 2000, Clarke & Lidgard 2000, Gray 2001). In the northern hemisphere, a consistent trend of decreasing diversity towards the pole has been reported (Rohde *et al.* 1993 and references therein, Roy *et al.* 1998, 2000, Rutherford *et al.* 1999). There appears to be a contrasting or asymmetric tendency in the southern hemisphere, many taxa showing an increase in species diversity towards high latitudes (Clarke & Crame 1997, Lancellotti & Vásquez 2000, Macpherson 2002, Valdovinos *et al.* 2003).

The consistency amongst the environmental descriptors of species richness also differs among regions, further complicating the problem of identifying the main causes behind the different patterns of diversity between hemispheres. Marquet *et al.* (2004) hypothesized that the opposing patterns of species richness, and the causal factors identified to explain them, might be related to the coarse way species richness is usually quantified. The approach proposed by Marquet *et al.* (2004) is based on the observation that, in general, species assemblages are not symmetric or homogeneous in the biological attributes of their constituent species, and that the prevalent approach of simply counting numbers neglects among-species biological differences that may be fundamental to understanding

ecological patterns in general and latitudinal patterns in particular. Deconstructing species richness according to biological attributes may thus help to understand differences in patterns of species richness and also to reveal underlying processes.

Larval developmental mode has been shown to be a critical life history attribute of marine species with ecological, biogeographical and evolutionary consequences affecting population dynamics, potential for dispersal, speciation and extinction rates, as well as range size distributions (Jackson 1974, Hansen 1980, Jablonski & Lutz 1983). Moreover, some of the taxa failing to conform to the classic latitudinal diversity pattern exhibit non-feeding larvae or lack of larval phase (Roy *et al.* 2000, Valentine & Jablonski 1983). In the first two papers of this thesis we examined latitudinal diversity patterns of marine invertebrates in the southern coasts of South America. In paper I, we studied two groups of crabs sharing the same mode of larval development, along both the Pacific and Atlantic coasts of South America. Specifically we examined (i) the consistency of latitudinal diversity patterns of two groups with one developmental mode across both coasts; (ii) the relationship between diversity and sea surface temperature (SST) and continental shelf area; and (iii) the relationship between the species' geographic range size and latitude for each taxonomic group (Rapoport's rule). In paper II, latitudinal diversity patterns of molluscs and crustaceans were deconstructed according to their mode of larval development. Specifically, we examined (i) diversity patterns of planktotrophic versus directly developing species of molluscs and crustaceans; and (ii) the relationship of each group within each larval developmental mode to SST, continental shelf area, and chlorophyll-a concentration.

1.2 Stream macroinvertebrate species richness and its local, landscape and regional determinants

The number of species coexisting in local communities is the consequence of factors operating on both local and regional scales (Ricklefs & Schluter 1993). Stream ecologists have traditionally dealt with local (*i.e.*, patch to reach) scales, and only during the last decade have they expanded the spatial coverage of their research to include patterns across catchments, ecoregions and other regional entities (Heino *et al.* 2003, Sandin 2003, Vinson & Hawkins 2003, Marchant *et al.* 2006). However, notwithstanding the long traditions of ecological research on stream organisms, we still know little about their broad-scale richness patterns and their regional determinants. Streams are optimal systems to address these

questions, given that they are organized as natural spatio-temporal hierarchies, where species richness is influenced by local in-stream and riparian variables, catchment characteristics, and regional environmental factors, thus calling for a multi-scale approach to stream research (Poff 1997, Bonada *et al.* 2008, Heino 2009). At small spatial extents, local factors, such as water chemistry and habitat heterogeneity, may exert strong control over species richness. However, it is also possible that regional climatic variability may completely override any effects of local habitat conditions (*e.g.*, Bradley & Ormerod 2001).

In paper III we assessed the relative importance of local environmental factors, catchment characteristics and regional variables to species richness variation of stream macroinvertebrates at two spatial extents: bioregion and seven drainage systems. We thus aimed at establishing links between two spatial extents: broad-scale species richness patterns and their partly local-scale determinants. We specifically asked whether (i) the same variables proposed to control broad-scale richness patterns of terrestrial organism (temperature, topographic variability) are important determinants of species richness also in streams, or whether (ii) environmental factors effective mainly at local scales (in-stream heterogeneity, potential productivity) set a strong environmental filter, constraining the membership in local communities of species present in the regional pool.

1.3 Community similarity and its relationship to environmental and geographic distance

The proportion of species shared between two communities often decreases as the distance between them increases (Nekola & White 1999). Two explanations have been proposed for this trend. Niche theory predicts that community composition will change as a result of species-specific differences in adaptive responses along environmental gradients, thus a decrease in community similarity with distance would be caused by increasing environmental distance among sites (Tilman 1982). In contrast, because of the spatial effects of dispersal limitation, neutral theory predicts that the compositional similarity between communities will decrease as the geographic distance between two sites increases (Hubbel 2001).

The relative importance of geographic distance and environmental distance to community similarity should exhibit predictable variation across organisms with different dispersal ability. Very effective dispersers (such as many unicellular organisms) should be less affected by barriers and thus able to reach most appropriate habitats within a region, while organisms with poorer dispersal ability

should have a greater decay in community similarity with increasing distance between sites. In paper IV, we studied community similarity and its relationship to geographic and environmental distance in three stream organism groups: benthic diatoms, macroinvertebrates, and bryophytes. Our objectives were: (i) to test the relative importance of geographic distance (dispersal limitation) and environmental distance (niche partitioning) to community similarity; (ii) to evaluate the relationship between community similarity and geographic distance for each taxa at closely similar vs. highly dissimilar environments, in an attempt to decrease distance-to-environment covariance (see Gilbert & Lechowicz 2004); and (iii) to examine the relative importance of geographic distance for three groups of macroinvertebrate species with different dispersal abilities.

1.4 Predictions

In paper I we studied latitudinal diversity patterns of Anomuran and Brachyuran crabs and predicted that both taxa should exhibit similar latitudinal patterns and responses to environmental gradients given their unique mode of larval development. Being a descriptive analysis, no clear patterns were expected for the relationship with environmental variables. However, as predicted by the energetic hypothesis and the species-area hypothesis, species richness should exhibit a positive relationship with sea surface temperature (as a surrogate for energy availability) and a positive relationship with continental shelf area (as a surrogate for habitable area). Rapoport's rule predicts an inverse relationship between range size and latitude.

In paper II we hypothesized that the disparate latitudinal patterns of species richness of marine invertebrates reported for the southern hemisphere reflects differences in species' attributes, namely mode of larval development, which in turn determine their contrasting responses to environmental variables. Cold water temperatures decrease developmental rate (Gillooly *et al.* 2002) which in turn increases the residence time of larvae in the plankton (O'Connor *et al.* 2007). Long larval residence time may reduce the opportunities for isolation and speciation. Whereas direct developers might face lower reproductive costs, and therefore potentially greater ecological success towards higher latitudes as lower water temperatures support higher oxygen concentration, and dissolved oxygen is a limiting factor affecting the capacity to aggregate embryos and larvae as well as the costs of brooding (Brante *et al.* 2003). We predicted (1) a strong positive association between richness of planktotrophic species and SST, and a weak or

negative association between SST and richness of direct developing species; (2) a positive relationship between Chl-a concentration for planktotrophic and direct developers; and (3) a strong positive association between species richness of direct developing species and shelf area as a consequence of restricted dispersal and the heterogeneity and opportunities for isolation that characterizes the Fjord region in southern Chile (Valdovinos *et al.* 2003). No clear pattern was expected for planktotrophic species and shelf area.

In paper III we evaluated the importance of local, landscape and regional variables to stream macroinvertebrate species richness variation at bioregion and drainage system extent. We predicted that (1) regional-scale variables and catchment characteristics should override the influence of local environmental variation at the largest extent (*i.e.*, bioregion), while local environmental variables should be important in explaining species richness variation within each drainage system; and that (2) the relative importance of pure spatial component should increase from smaller to larger extent.

In paper IV we studied the relationship between community similarity and environmental and geographic distance in stream benthic communities. We predicted that (1) diatoms, being unicellular organisms, should exhibit the strongest relationship to environmental distance between sites, followed by bryophytes and macroinvertebrates; (2) among macroinvertebrates, species exhibiting poor dispersal ability should exhibit the strongest relationship to geographic distance between sites, while species with good dispersal ability should exhibit stronger relationship to environmental distance between sites.

2 Materials & Methods

2.1 Geographic areas and study extent

The papers in this thesis were based in marine and stream environments, in northern Europe and southern South America. Paper I extended from 10°S to 56°S in the Southeastern Pacific (SEP) and Southwestern Atlantic (SWA) coasts of South America, and paper II extended along the Chilean coast, from 18°S to 56°S. Paper III was conducted in Finland (60°N to 70°N and 20°E to 32°E), evaluating variation in species richness at two spatial extents, bioregion and individual drainage systems. The largest study extent, bioregion (B), spanned a north-south gradient of ca. 800 km (including 172 streams). The drainage systems extent consisted of seven drainage systems (24 or 25 streams each): Muoniojoki (DS1: 68°N, 24°E), Kemijoki (DS2: 67°N, 28°E), Koutajoki (DS3: 66°N, 29°E), Kiiminkijoki (DS4: 65°N, 26°E), upper Oulujoki (DS5: 65°N, 29°E), Kyrönjoki (DS6: 63°N, 23°E), and upper Kymijoki (DS7: 62°N, 25°E). Paper IV was conducted in Finland, and it spanned a north-south gradient of 1100 km (including 119 streams; 14–15 stream riffles in each of eight drainage systems).

2.2 Species data

Diversity covers both α diversity (species richness of spatially defined units) and β -diversity (differences in the species composition between different units) (Magurran 2004). In this thesis, I analyzed variation in species richness (papers I–III) and variation in species composition between communities (paper IV).

In papers I and II, species' latitudinal distribution were compiled through an exhaustive literature search, as well as museum collections and records of scientific expeditions. Based on these latitudinal distributions, species richness was determined as the sum of all species whose ranges crossed a given 1-degree latitudinal band. In paper II, data on larval developmental mode were available for all crustaceans since each clade is locked to a single mode of larval development; Anomura and Brachyura exhibit planktotrophic development, whereas all species of Isopoda and Amphipoda exhibit direct development. In the case of molluscs, information on modes of larval development was obtained from an intensive literature search and interviews with expert scientists on invertebrate zoology, taxonomy, ecology or aquaculture at 11 major universities in Chile. The

data obtained from the interviews were based on observation or unpublished data and in no case did we assign a species to a larval development category based on information from related species.

In papers III and IV, species datasets were obtained through field surveys at each stream in late autumn between years 1992–2004. To delineate our analyses to a single habitat type, we focused on near-pristine (no point sources of pollution, no obvious signs of human impact in the riparian zone or the stream channel, < 15% of catchment under anthropogenic impact) forest streams (orders 1 to 3, base flow < 0.6 m³ s⁻¹). Streams were also selected based on their accessibility, and only streams within 2 km of the nearest road were included. Benthic macroinvertebrates were sampled by taking a two-minute kick-net sample (net mesh size 0.3 mm) at each site, aiming to cover most benthic microhabitats present in a stream section of approximately 100 m². Such a sample typically captures more than 70% of all species present in a riffle, missing mainly species that occur only sporadically in streams (Mykrä *et al.* 2006). Macroinvertebrates and associated material were preserved in 70% alcohol in the field, and were later sorted and identified to the lowest feasible taxonomic level, usually species, in the laboratory. Our analysis included all other major groups of macroinvertebrates except chironomids, which were not identified to species level and were therefore excluded from all analyses. Species richness of macroinvertebrates was calculated for each site based on presence-absence data (paper III). In paper IV, samples of benthic macroinvertebrates, bryophytes and diatoms were collected in each stream site. Macroinvertebrates were sampled in the same way as in paper III (see methods above). Bryophytes were sampled in ten randomly placed 50 cm × 50 cm quadrants in those areas of the stream bed that remain submerged at base flow. This sampling method allows the detection of about 75% of the bryophyte species present in a stream reach (Mykrä *et al.* 2008). All bryophyte species and their percentage cover were recorded in the field. For diatom sampling, each study site was divided into five or ten cross-stream transects, depending on stream width. Ten stones were randomly selected in each transect, and diatoms were scraped off the stones from a predefined area (3.1 cm²) using a plastic template. Subsamples were then pooled into a composite sample for each site. In the laboratory, fresh samples were carefully checked to guarantee that most diatom frustules were alive before acid combustion. Cleaned diatoms were mounted in Dirax or Naphrax. A total of 500 frustules per sample were identified and counted using phase contrast light microscopy (magnification 1000×). Diatoms were identified to species according to Krammer & Lange-Bertalot (1986–1991) and

Lange-Bertalot & Metzeltin (1996). Community similarity matrices were calculated separately for macroinvertebrates, bryophytes and diatoms using the Sørensen similarity index on presence-absence data (paper IV).

2.3 Environmental data

The environmental data were obtained from several sources. As papers I and II comprised such a large extent, we obtained sea surface temperature (SST) and chlorophyll-a concentration (Chl-a) from satellite data available on the web. Temperature was obtained from the FERRET server of the National Centers for Environmental Prediction (<http://ferret.wrc.noaa.gov/Ferret/las>). Chl-a data were obtained as 8-day averages from SeaWiF's satellite images for four years (1997–2000), averaged alongshore for the first 12 km cross-shore per degree of latitude (Thomas 1999). Continental shelf area (including the Chilean fjord area) was calculated by digitizing a 1:106 scale Lambert Zenithal Azimuthal equal area projection map for the southeastern and southwestern coasts of South America down to the 200 m isobath.

In paper III we evaluated the relative importance of local, landscape and regional scale environmental variables to variation in species richness of benthic macroinvertebrates. Local environmental variables were sampled during field surveys. Macrophyte cover and shading by overhanging riparian vegetation were measured at each site. Water samples were collected simultaneously with benthic sampling, and they were analyzed for pH, conductivity, total nitrogen, total phosphorus, and color following Finnish national standards. Environmental variables describing landscape-level catchment characteristics of each site were modeled using geographical information system. Streams were first digitized using 1:20000 vector data of water bodies in Finland (National Land Survey of Finland, NLS). Catchment boundaries were delineated and digitized using 1:50000 digital topographic base maps (based on digital elevation model and vector data of drainage basins; Finnish Environment Institute) and catchment sizes were determined. Land cover features were calculated using land use and forest classification 25-m raster databases (NLS). As the most likely candidates for landscape-scale regulators of stream biodiversity, we selected (i) percent cultivated and urban area (combined as % anthropogenic influence), (ii) percent forest cover, and (iii) percent lakes in the catchment. Climatic variables for each site were obtained using multivariate linear regressions to relate mean summer temperature to latitude, longitude and altitude of each study site, downscaling

climate data from a 10 × 10 km resolution grid (Finnish Meteorological Institute, Venäläinen & Heikinheimo 2002) to a 1-km² grid. Climatic variables thus obtained are fine-tuned to better describe local-scale variation in climatic conditions, although they still reflect regional variation in climate. The following climatic variables were included: mean summer (June 1 – September 30) air temperature and coefficient of variation (CV) of monthly precipitation (June 1 – September 30), and elevation range.

In paper IV, environmental variables included were: shading, depth, current velocity, moss cover, substratum particle size, pH, conductivity, TP, water color, mean summer air temperature, coefficient of variation (CV) of monthly precipitation, and elevation range. These variables were obtained in exactly the same way as in paper III (see above). Table 1 summarizes the species and environmental data for each subproject.

Table 1. Species and environmental data used in paper I to IV. The complete list of environmental variables included in paper III and IV is given in Materials & Methods (section 2.3). GIS data were modeled with Geographic Information System; Literature data were compiled through literature search; Survey data were obtained through field surveys.

Paper	Type of data	Variables	Data source
I	Species' latitudinal distribution	Species richness	Literature
	Environmental	Sea surface temperature	Satellite
		Continental shelf area	GIS
II	Species' latitudinal distribution	Species richness	Literature
	Environmental	Sea surface temperature	Satellite
		Continental shelf area	GIS
		Chlorophyll-a concentration	Satellite
III	Species' presence-absence data	Species richness	Survey
	Environmental	Local	Survey
		Landscape	GIS
		Climatic	Downscaled climatic
IV	Species' presence-absence data	Compositional similarity (Sørensen index)	Survey
	Environmental	Local and climatic	Survey and downscaled climatic data

2.4 Spatial analysis

Ecological variables often vary synchronously over wide geographical areas, a phenomenon known as spatial autocorrelation; its most common forms are patches and gradients (Koenig 1999). Spatial variation in diversity may result from the direct effects of local environmental variables, from shared variation between space and the environment, or from spatial autocorrelation of diversity itself (*i.e.*, other biotic or abiotic processes that produce a given spatial structure in diversity). Therefore it is important to describe these spatial structures and measure the autocorrelation present in diversity data.

Two types of analytical approaches were used in this thesis. First, the “raw-data approach” (papers I–III), where the input data are in the form of raw-data tables, such as estimates of species richness at study sites and measurements of environmental variables at the same study sites (Tuomisto & Ruokolainen 2006). In this approach, the spatial structure was modeled using a third-order polynomial equation ($f(x,y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$), where x and y represent the geographic coordinates of the locations (used in papers I and II). In paper III, instead of using a third-order polynomial, the spatial variables were obtained by principal coordinates of neighbor matrices (PCNM), a technique proposed for detecting and quantifying spatial patterns in species data across a wide range of scales (Borcard & Legendre 2002). This consists of extracting eigenvectors from a distance matrix between sites. In the raw-data approach we test through multiple regression whether the variation in the response variables (*i.e.*, species richness) can be explained by variation in the independent variables (environmental and spatial variables). Additionally, in order to graphically understand the spatial structure of diversity in paper I, we created autocorrelograms using Moran’s I coefficients at 10 distance classes, covering the full spatial extent of the data (Legendre & Legendre 1998).

The second spatial approach can be called the “distance-approach” because the input data are in the form of distance matrices based on the raw data (paper IV, Tuomisto & Ruokolainen 2006). Here, community distance matrices are related to environmental distance matrices and to geographic distances between sites. Thus, the spatial structure in the distance approach is represented by the geographic distance between locations.

2.5 Statistical analysis

Table 2 summarizes the statistical analysis used in each paper and the main objective of each analysis. In papers I to III we examined the relationship between species richness and a set of environmental and spatial variables through linear regression (semi-partial linear regression and General Linear Models, see Table 2). In paper III, to examine the effects of each group of environmental variables on species richness, three different models, each with a different set of variables (*i.e.*, local, landscape and climatic variables), were first built for each spatial extent, *i.e.*, bioregion and each drainage system. Stepwise backward regression with Akaike's Information Criteria (AIC) was used to select the best-fit model: the model with the lowest AIC value was considered to be the best. In the next step, all significant explanatory variables from each of the three groups were simultaneously included in a "hybrid environmental model" (see Kivinen *et al.* 2006) to assess the total contribution of local, landscape and regional variables to species richness variation.

Variation partitioning provided the statistical means to quantify the relative effects of environmental and spatial variables on species richness (papers I to III). Variation in species richness was partitioned into four components: (a) pure environmental variation (variation in species richness explained solely by environmental variables); (b) spatially-structured environmental variation (variation shared by spatial and environmental variables); (c) pure spatial variation (variation explained solely by spatial variables); and (d) unexplained (residual) variation (Legendre & Legendre 1998). In paper I, we also determined the relationship between latitude and geographical range size (Rapoport's rule), using Stevens' 1989 method as well as the midpoint method (Rohde *et al.* 1993) to avoid the problem of non-independence of the data. We estimated the mean range size using the latitudinal range of species whose midpoints fall in a given 5° latitudinal band. In paper IV, we first selected the best set of environmental variables related to community similarity using BIO-ENV analysis (Clarke & Ainsworth 1993). We then examined the relative importance of environmental distance and geographic distance to community similarity through partial Mantel tests (Table 2).

Table 2. Statistical analysis performed in paper I to IV and objectives of each analysis.

Paper	Analysis	Objective of analysis
I	r-Pearson correlation	Correlation between environmental variables and diversity
	Semi-partial correlation (sr^2)	To estimate the single contribution of each environmental variable to the total variance of diversity
	Variation partitioning	To partition the diversity variation explained by the environmental variables and that explained by the spatial structure alone.
	Autocorrelation (Moran's I)	To graphically understand the spatial structure of diversity and to evaluate the scale specific effect of each environmental variable
	ANOVA	To compare mean species range size between groups and between oceans (Rapoport's rule)
II	Semi-partial correlation (sr^2)	As in paper I
	GLM	To construct environmental, spatial and combined models
	Variation partitioning	As in paper I
III	GLM	To construct local, landscape, regional and combined models
	Variation partitioning	As in paper I and II
IV	BIO-ENV	To select the best set of environmental variables correlated to community similarity
	Partial Mantel test	To test the relationship between community similarity and environmental distance controlling for the geographic distance and vice versa

3 Results & Discussion

3.1 Marine latitudinal diversity gradients

Diversity of Brachyuran and Anomuran crabs showed the typical decreasing trend with increasing latitude in both oceans (Fig. 1). The SWA exhibited higher diversity of both groups north of 28°–35°S, while towards the south, the SEP showed a slightly higher diversity (Fig. 1).

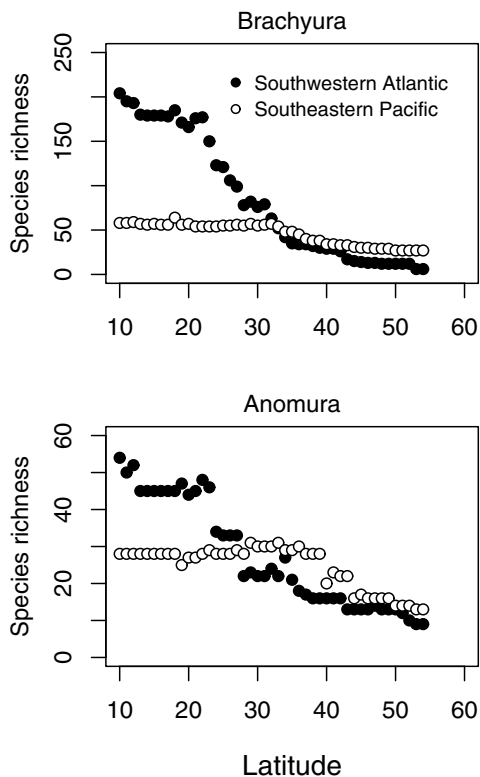


Fig. 1. Latitudinal patterns of Brachyuran and Anomuran crabs along both coasts of South America, the Southwestern Atlantic and the Southeastern Pacific (Paper I Figure 2, modified by author).

A large proportion of the variation in diversity of both groups in both oceans was explained by the two spatially structured environmental variables (shelf area and

SST), although each variable had a different contribution. Semi-partial correlation showed that the single contribution of SST to the total variance of crab diversity was always positive and significant, while the single contribution of shelf area was negative and its significance varied between oceans. The strong relationship with spatially structured SST obscured the positive effect that the species-area hypothesis predicts.

The important effect of SST gradient on diversity was also evident in the correlograms. *Anomura* and *Brachyura* diversity showed positive and significant spatial autocorrelations up to 1500–2000 km in the SEP and 2000–2500 km in the SWA, and a strong negative spatial autocorrelation at the largest distance classes. After removing the scale-specific effect of SST, the shape and the scale of the spatial pattern of residuals were strongly modified with respect to the spatial correlogram of the raw diversity data. In contrast, when shelf area was included in the model, the residual spatial pattern showed little or no change with respect to the previous patterns. However, a positive autocorrelation in the residuals remained at $< 5^\circ$ latitude, even after including the spatial trend (polynomial of x and y) in the model. The inclusion of the relevant environmental factors acting at each scale in the regression model should be sufficient to completely remove autocorrelation from the residuals at all scales (Diniz-Filho *et al.* 2003). We believe that variations at smaller spatial scales of circulation patterns, geography, upwelling regimes, and nutrient inputs, among others, might influence the relationship between SST and diversity at scales $< 5^\circ$ latitude. No relationship between latitude and mean range size (Rapoport's rule) was found for Anomuran or Brachyuran crabs.

Yet, it is unclear how factors such as shelf area explain diversity of molluscs in the SEP (Valdovinos *et al.* 2003), but not in the northeastern Pacific (Roy *et al.* 1998), where SST seems to be the primary causal factor affecting diversity. SST, in turn, does not explain diversity of molluscs in the SEP (Valdovinos *et al.* 2003), where it explains the diversity of *Brachyura* and *Anomura*. Based on sparse evidence from other studies and on the results from paper I (Table 3), we hypothesized that the mode of larval development may be an important factor influencing patterns of diversity, and species exhibiting different developmental modes may be differentially affected by environmental factors.

Table 3. Summary of existing evidence on latitudinal patterns of species richness following the normal (decrease towards the poles) and reverse trends for benthic biota (Paper II Table 3, modified by author.)

Taxonomic group	Developmental mode	Latitudinal gradient	Source
Brachyura and Anomura	Planktotrophic	Normal	Macpherson 2002 Astorga <i>et al.</i> 2003
Brachiopoda Inarticulata	Planktotrophic	Normal	Valentine & Jablonski 1983
Gastropods	Direct	Inverse	Gallardo & Penchazadeh 2002
Isopoda	Direct	Inverse	Lancellotti & Vásquez 2000 Lopez Gappa <i>et al.</i> 2006
Amphipoda	Direct	Inverse	Myers <i>et al.</i> 1996 Lancellotti & Vásquez 2000
Protobranch Bivalves	Non-feeding larvae, low fecundity	Inverse	Roy <i>et al.</i> 2000
Polyplacophora	Primarily Non- planktotrophic	Inverse	Valentine & Jablonski 1983
Modern Articulata	Non-planktotrophic	Inverse	Valentine & Jablonski 1983

This hypothesis was addressed in paper II by comparing molluscs and crustaceans exhibiting planktotrophic and direct developmental modes. The overall latitudinal trend of mollusk species richness was nearly constant from 20 to 40°S increasing steeply towards higher latitudes (Fig. 2, All Molluscs). In contrast, crustaceans showed a smooth increase in species richness from 18 to 30°S, then remaining relatively constant toward the south (Fig. 2, All Crustaceans). However, when overall species richness was deconstructed by larval developmental mode, similar and clear patterns were found within each mode of larval development for both phyla. Monotonic increases in species richness toward high latitudes were found for species with direct development (Fig. 2, Molluscs and Crustaceans direct), whereas richness of species with planktotrophic development remained relatively constant between 18 and 35°S, and then decreased poleward (Fig. 2, Molluscs and Crustaceans planktotrophic). By deconstructing the latitudinal pattern of species richness by the mode of larval development, the formerly opposing trends of species richness reported along the coast of Chile became remarkably similar.

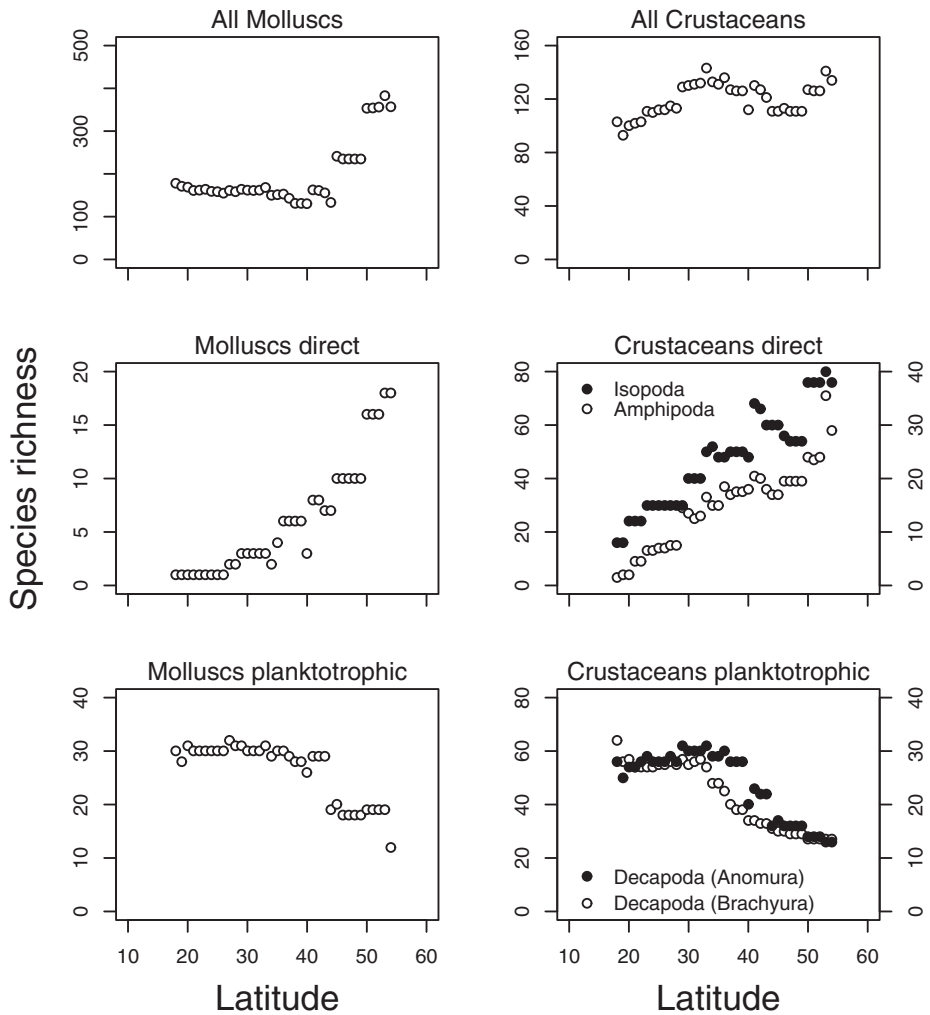


Fig. 2. The overall latitudinal patterns of species richness for all molluscs and crustaceans along the coast of Chile was deconstructed by larval developmental mode between species exhibiting direct development and planktotrophic larvae. For crustaceans we plotted separately amphipods and isopods (Crustaceans direct) and decapods (Anomura and Brachyura, Crustaceans planktotrophic). In Crustaceans planktotrophic, the y-axis on the right corresponds to Anomura and on the left to Brachyura. Similarly in Crustaceans direct, the y-axis on the right corresponds to Isopods and on the left to Amphipods (Paper II Figure 1, modified by author).

Considering the purported interaction between temperature and development mode, we predicted a positive relationship between temperature and species richness for planktotrophic species, and a weak or negative relationship for direct developers. Our results support these predictions. SST was the most consistent and important environmental variable for both taxa and also for both larval developmental modes, although species with direct development showed a strongly negative relationship with SST. Large-scale patterns of SST are not only an indicator of solar radiation and potential energy, but also a critical factor affecting rates of development (Wear 1974, Gillooly *et al.* 2002) and physiological processes (Pörtner 2002). The slower metabolic and developmental rates in the colder water temperature characteristic of high latitudes (Wear 1974, Vermeij 1978, Morgan 1995) might indirectly contribute to increased larval mortality by prolonging the duration of exposure to predation in the plankton (O'Connor *et al.* 2007, Pechenik & Levine 2007). The prediction from these, admittedly simple relationships, is that species with planktonic larvae would not perform well at high latitudes (Thorson 1950), which could explain the decline in species richness of these species toward the poles and the prevalence of species without planktonic larvae. Temperature may also reduce the opportunities for isolation and speciation of planktotrophic species. On the other hand, low temperature at high latitudes might generally favor direct developers since the cost of brooding increases with temperature (*e.g.*, oxygen provision; Brante *et al.* 2003). Our results and the high prevalence of brooding species in Antarctica support this contention (Thorson 1950, Clarke & Crame 1997, Gallardo & Penchaszadeh 2001). As the cost of brooding decreases poleward, more energy invested in reproduction can be devoted to egg production (Brante *et al.* 2003, Fernández *et al.* 2007) fostering higher local abundance, increasing population persistence and probably species diversity by reducing extinction.

Our second prediction entailed a positive relationship between productivity, measured as Chl-a concentration, and species richness of planktotrophic and direct development species. Results suggest that Chl-a plays a role in the distribution of both phyla, but the amount of variance in species richness explained by Chl-a was much lower than that explained by SST. As expected if Chl-a concentration represents food availability for larvae, Chl-a was positively related only to richness of species exhibiting feeding larvae and it explained a higher proportion of the variance in diversity of planktotrophic than of direct developing species. Both planktotrophic molluscs and anomura species showed a significant and positive association between species richness and Chl-a. This

result is consistent with the prediction that reduced availability of Chl-a levels may limit the development of planktotrophic larvae over extended periods, and thus the distribution of planktotrophic taxa at higher latitudes (Thorson 1950). The lack of association in the case of brachyuran crabs might be related to the high species richness of Brachyura in a region of comparatively low Chl-a minimum (0.1 and 0.2 mg/m³) in northern Chile (18–32°S), which suggest that the influence of Chl-a on species diversity might be weak and more complex than the effect of SST. The predicted pattern was observed only in planktotrophic groups and most taxa with direct development exhibited a negative association with Chl-a.

Shelf area was not significant in most cases and did not show a consistent pattern within region or larval developmental mode (see also Roy *et al.* 1998), which provides only partial support to our predictions. Valdovinos *et al.* (2003) showed a distinctly different result, where shelf area was the main causal factor behind species richness of benthic molluscs along the Chilean coast. However, they pooled all species together, regardless of the larval developmental mode. These authors hypothesized that the high heterogeneity of the southernmost fjord area created a highly vicariant landscape that fostered isolation and speciation, which is reflected in a high ratio of species per genera as compared to northern areas. If this were so, direct development species would be expected to be especially sensitive to area effects given their restricted dispersal. Since direct developing crustaceans fit this prediction, the lack of consistent support in the case of molluscs may be related to the reduced sample size.

3.2 Stream macroinvertebrate species richness and its local, landscape and regional determinants

Our key finding was that, at the broadest study extent, the humic content of stream water (as indicated by water color) was the strongest correlate of stream invertebrate species richness (Fig. 3a). This is not the first time that water color has been shown to be negatively related to stream invertebrate diversity, but all previous studies have been conducted on much more restricted spatial extents (*e.g.*, Otto & Svensson 1983, Malmqvist & Mäki 1994). More importantly, our finding that water color showed strong spatial structuring, paralleled by corresponding geographical variation of macroinvertebrate species richness, is a novel one. In fact, many of the key determinants of macroinvertebrate species richness of boreal streams exhibit relatively strong spatial patterning, as indicated

by the high proportion of the spatially structured environmental component in variation partitioning. It should be noticed, however, that many environmental variables are strongly inter-correlated; for example, water color is intimately linked with other water chemistry variables, particularly nutrients, iron and pH (see Vuori & Muotka 1999). This intertwining of variables goes even further: the strongest landscape-level determinant was the proportion of forests in the catchment, which in turn mirrors the amount of humic contents of stream water. Thus, assigning a variable to only one of a set of hierarchical scales is not often clear-cut, complicating the application of the theory of environmental filters (see Poff 1997) to stream invertebrate communities.

Another factor of importance to species richness at the bioregion extent was elevation range, a variable strongly linked to stream topographic heterogeneity (Fig. 3b). It is often assumed that range in elevation represents a surrogate for habitat heterogeneity, and that an increase in topographical heterogeneity results in an increase in the number of ecological niches (Rahbek & Graves 2001, Hawkins & Porter 2003). In topographically heterogeneous drainage systems, the high rate at which habitats change along an elevational gradient produces high between- and within-habitat diversity, sometimes even along short spatial gradients. Topographic variability has been frequently indicated as a close correlate of species richness in many terrestrial studies (Rahbek & Graves 2001, Kerr *et al.* 2001), as well as in studies on freshwater fishes (Guegan *et al.* 1998).

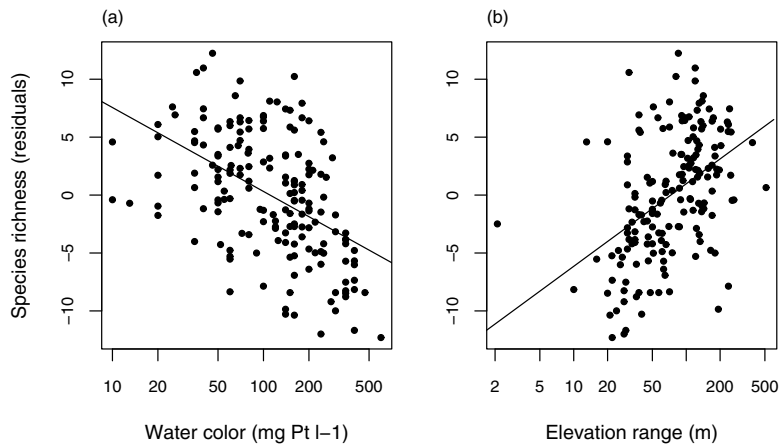


Fig. 3. Univariate relationships between macroinvertebrate species richness residuals (richness = $\log(\text{catchment area})$) and the two of the key environmental gradients for the bioregion. (a) water color (x axis in log scale; $r^2 = 0.24$, $P < 0.001$) and (b) elevation range (x axis in log scale ; $r^2 = 0.21$, $P < 0.001$) (Paper III Figure 3, modified by author).

The purely spatial component of variation in macroinvertebrate species richness at the bioregion extent was relatively large (20%). We suspect this is related to the widely differing history of land-use in different parts of the country, more southerly regions having been under intensive agriculture and forestry for hundreds of years, whereas northern parts of the country still remain relatively pristine. Past land use activity has been reported to cause a long-term reduction in the diversity of stream macroinvertebrates (Harding *et al.* 1998), amphibians (Piha *et al.* 2008) and terrestrial plants (Lindborg & Eriksson 2004), but its impacts are difficult to detect using only contemporary environmental variables. Alternatively, post-glacial re-colonization may have varied among our drainage systems. The last glaciation has profoundly modified biotic communities in Northern Europe, including freshwater ecosystems (Sandin & Johnson 2000, Ilmonen *et al.* 2009), and postglacial colonization routes may still bear a historical imprint on freshwater invertebrate communities of boreal streams.

As expected, local environmental variables explained most of the variation in species richness at the drainage-system extent. Factors related to species richness at this extent reflected gradients in water humic content, with a negative effect on species richness, and in-stream habitat heterogeneity (macrophyte cover), with a

positive effect on richness. These environmental gradients have been repeatedly shown to be related to local richness of stream invertebrates (Vinson & Hawkins 1998). The importance of the pure spatial component was strongly region-dependent, having high values in two drainage systems (*i.e.*, DS6 and DS7). In these systems, species richness displayed not only broad-scale variation, but also fine-scale patchiness, as indicated by the presence of several significant fine-scale spatial vectors. Overall, these results underline the high among-region variability of headwater streams (see also Clarke *et al.* 2008), and to gain better insight into factors underlying species richness variation at the scale of drainage systems, several drainages across a broad spatial extent should be included.

To this end, our results emphasize the need for spatially-explicit, regional (or broader) study designs aiming at understanding the geographical variation of freshwater biodiversity. We concur with Vinson & Hawkins (2003) in emphasizing the need for more regional-scale studies of freshwater biodiversity, relating species richness to both local factors and broad-scale climatic variables, and recognizing the presence of spatially-structured environmental variation, not only as a nuisance but as an ecologically relevant factor to be carefully considered in study design and interpretation of results.

3.3 Community similarity and its relationship to environmental and geographic distance

The best set of environmental variables (as selected by the BIO-ENV analysis) related to community similarity of all three taxonomic groups included water chemistry variables (*e.g.*, pH, conductivity, total phosphorus, water color) and regional scale environmental variables (*e.g.*, CV of precipitation, temperature, and elevation range). Water chemistry variables, especially pH, have been previously related to regional-scale diversity of streams for macroinvertebrates (Heino *et al.* 2003, Mykrä *et al.* 2007, Petrin *et al.* 2007), and at regional to global scales for diatoms and other unicellular organisms (Telford *et al.* 2006, Fierer *et al.* 2007). Community similarity was negatively related to both environmental and geographic distance between sites in all three groups. These relationships were best approximated by a logarithmic model (Fig. 4). Partial Mantel test further indicated strong environmental control in all three groups, the effect of geographic distance being non-significant for diatoms and macroinvertebrates, and only weakly significant for bryophytes. However, more detailed analysis of these relationships among closely similar vs. dissimilar environments and for

different dispersal categories of macroinvertebrates revealed some important differences between these three groups.

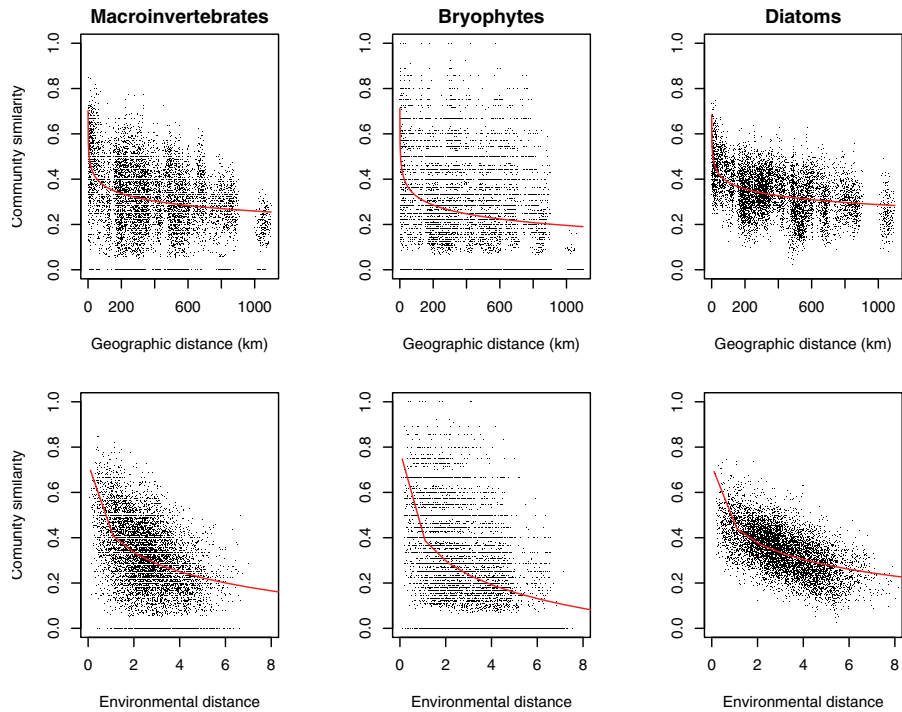


Fig. 4. Relationship between community similarity and geographic and environmental distance for stream macroinvertebrates, bryophytes and diatoms. The relationship was best approximated by a logarithmic model in each case (for regression equations see paper IV).

A hotly debated issue in macroecology is whether microorganisms exhibit predictable biogeographical patterns similar to those of macroorganisms (Hillebrand 2001, Finlay 2002, Fenchel 2003, Green *et al.* 2004, Van der Gucht *et al.* 2007). Recently, the global-scale diversity of diatoms was shown to be explained by historical factors rather than by contemporary environmental factors (Vyverman *et al.* 2007). Other authors have shown that stream bacterial communities at the landscape scale (*i.e.*, within a drainage system) are strongly controlled by pH, arguing that environmental attributes of microbial habitats have to be thoroughly characterized and accounted for before examining any

correlation between geographic distance and community distance (Fierer *et al.* 2007). Our results show that while diatoms are strongly controlled by the set of environmental variables included, they do exhibit a slightly different decay pattern than macroinvertebrates and bryophytes (Fig. 4). Firstly, diatoms always have some degree of similarity between pairs of sites, independent of the distance between them. Secondly, geographic distance seems to be important but only when the relationship between community similarity and geographic distance is examined among closely similar environments.

Bryophyte community similarity was significantly related to both environmental and geographic distance. The Mantel correlation coefficient was, however, much lower for geographic than environmental distance. The high beta-diversity and strongly scattered pattern of bryophyte community similarity indicates that even geographically closely situated sites with similar environments can have completely different bryophyte communities (Fig. 4). This result may be related to the randomness of dispersal in bryophytes. It has been proposed that bryophyte spore dispersal is limited in space, spores being mainly deposited in the immediate surroundings of the “mother plant” (Zartman & Nascimento 2006, Pharo & Zartman 2007). However, recent studies have proposed thermal updrafts as an important mechanism of long-distance dispersal, where propagules from a much larger geographic area might be available for colonization (Sundberg *et al.* 2006, Hylander 2009).

After controlling for environmental distance, macroinvertebrate community similarity was not significantly related to geographic distance. A more detailed analysis, however, revealed that geographic distance between sites was strongly related to community similarity in closely similar environments, suggesting dispersal limitation in this group. Different dispersal categories of macroinvertebrates responded differently to environmental and geographic distance. As expected, species with low dispersal ability showed a significant relationship to geographic distance, while more effective dispersers showed non-significant relationship to geographic distance but were strongly related to environmental distance. Thompson & Townsend (2006) documented a similar pattern at a much smaller spatial scale, emphasizing the role of dispersal and local environmental conditions in explaining local patterns of benthic macroinvertebrate diversity.

There is an ongoing debate on whether microorganisms exhibit predictable biogeographical patterns similar to those of macroorganisms. Our study contributes to this debate by comparing community similarity of three taxonomic

groups, including micro- and macroorganisms, across the same set of sites and a large environmental and geographical gradient. Our results provide support for the primacy of niche processes, although geographic distance also was important at different scales and different levels of environmental heterogeneity, and for species with poor dispersal ability.

3.4 Conclusions

This thesis was inspired by the maxim that ‘wherever there is a widespread pattern, there is likely to be a general explanation which applies to the whole pattern’. This idea seemed appealing, and finding such general explanations would be the key to understanding species diversity distribution. What seemed then a possible task, has demonstrated to be an enthralling but enormously challenging endeavor. Data collection, field work and data analysis have exposed the complexity of biological systems, determined by a multitude of processes that vary across organisms and habitats, and the difficulty of analyzing such variability in a proper way. However, there are some patterns and processes that do repeat themselves when spatial variation in species biodiversity is studied, being perhaps even “universal”. This thesis examined some of these patterns in marine and freshwater environments, namely, latitudinal diversity gradients in marine environments, the relationship between local species richness and its local, landscape and regional determinants, and the distance decay of community similarity in stream communities.

The first step along the way to understanding the determinants of species diversity is to accurately characterize the geographical patterns themselves. The diversity patterns that are apparent along spatial and environmental gradients are abstractions from a broader spatial variation (Gaston & Spicer 1998), and are thus dependent on the spatial scale, *i.e.*, extent and grain. The definition and choice of scale can directly affect the results of any given analysis and the comparability of results between similar studies (Rahbeck 2005). Thus, it is important to explicitly consider the scale of both biodiversity and the associated environmental data. Range map data describe coarse-grained patterns of diversity, where climatic and historical factors will be the main determinants, whereas survey type of data often leads to weaker patterns, with more variability and a stronger local control of species diversity (Hurlbert & White 2005). Therefore, a great contribution would be to carry out geographically more extensive surveys (*i.e.*, continental scale) to see whether at these extents climatic and historical factors override the influence

of local or regional scale habitat conditions. Ultimately, both types of data (*i.e.*, range maps and surveys) are important, and the understanding of species diversity distribution will be addressed satisfactorily only when data are integrated across multiple spatial scales.

Life history traits are as well important when characterizing the geographical patterns of taxonomic groups. These traits may be closely related to species responses to environmental variables, thus potentially producing different geographic patterns depending on the trait under consideration. For marine crustaceans and molluscs, mode of larval developmental was a fundamental trait related to the direction of the latitudinal diversity gradient (*i.e.*, normal vs. inverse direction). For stream communities, different dispersal ability categories were associated with different distance decay patterns, as well as the relative importance of environmental and spatial distances in explaining benthic macroinvertebrate community similarity.

The second step is to relate these geographical patterns of diversity and its determinants. In this thesis I have evaluated contemporary environmental variables at different scales, and analyzed the relative contributions of environmental vs. spatial variables. Amongst the large-scale contemporary environmental gradients, available energy (*i.e.*, temperature) has been frequently shown to be related to species richness. The form and cause of this relationship are some of the most hotly debated topics in the study of global biodiversity (Gaston 2000). Diversity patterns of crustaceans and molluscs at a continental-scale were strongly related to spatially-structured sea surface temperature. Even so, an important contribution for further understanding of these large-scale diversity patterns would be not only to relate them to contemporary environmental gradients but also to evolutionary processes that have occurred through time on the pacific coast of South America. Thus, a central question becomes: What are the relative roles of contemporary environmental and historical processes for latitudinal patterns of mollusks and crustaceans with planktotrophic and direct development?

Freshwater diversity and its determinants were studied at a much smaller scale than the marine patterns. Both freshwater studies, however, were based on a large number of sites across a regional extent, including detailed environmental characterization of each stream. At this scale, local and regional environmental conditions were identified as the main determinants of species richness. An interesting questions then becomes, are the same environmental variables

identified in our study important for regional species richness of streams from other geographic areas?

Studying community similarity simultaneously for three stream taxonomic groups across the same set of sites was important for understanding some of the environmental and spatial factors related to the generation of diversity of micro- and macroorganism in freshwater communities. These results stimulate the further exploration of diversity of freshwater communities across widely separated geographic areas but with a similar environmental setting or shared geological history.

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