# Summary

## Environmental filtering vs. Natural variation and plant strategies: key components of plant trait modulation by nutrient supply.

Climate change and the intensive use of natural ecosystems cause profound alterations in the functioning of these ecosystems and their vegetation composition. Although for many of these effects on vegetation observations exist, quantitative predictions of vegetation responses to climate change (e.g. as in habitat distribution models) are more difficult. Predictions using current habitat distribution models are problematic because of the lack of causal relationships with a general application. The aim of this thesis is to develop causal relationships that quantify plant responses to nutrient availability in natural plant communities that can be used to improve habitat distribution models. For the quantification of these relationships plant traits, instead of existing approaches that use Plant Functional Types or plant taxa, are used. Given the functional significance of plant traits, they can potentially be used to develop relationships with a causal basis that are generally applicable and are more likely to hold under climate change.

A first analysis to quantify the relationships of leaf traits vs. soil nutrients and climatic factors was carried out using a global dataset that covered almost all biomes and growth forms present on earth (Chapter 2). Despite the large observed variability in this relationship, it was possible quantify the trade-off between traits associated with growth and resource-conservation ‘strategies’ in relation to soil fertility. Soil nutrient measures explained more variance in leaf traits among sites than climate in bi-variate analysis. In multivariate analysis, precipitation interacted with soil nutrients for specific leaf area (SLA) and area-based leaf nitrogen concentration (LNCarea). Mass-based LNC and leaf phosphorus concentration (LPC) were determined mostly by soil fertility, but soil P was highly correlated to precipitation.

Large unexplained variability characterizes the relationships of leaf traits and measures of nutrient supply and climate. The factors underlying the large variability observed in relationships between plant traits and nutrient supply were studied at two levels: among sites and within sites. In Chapter 3, the contribution of factors in determining the variation in plant traits among sites, were assessed by combining various soil fertility indicators and water supply, as well as intrinsic plant trade-offs using structural equation modeling (SEM). In SEM the coordination of plant traits and measures of abiotic factors, as observed in natural communities, was compared to a hypothesized multivariate model based on current theory of plant strategies. Hypothesized models were not consistent with the observed data and the combined effects of various abiotic factors were significant, but moderate. The reasons for these outcomes included: i. strong correlations among traits that supposedly belong to different strategy components, ii. poor understanding of mechanisms determining the co-variation of plant maximum height, leaf size and stem density, and iii. lack of integrative and long-term measures of nutrient supply needed to predict coordinated plant trait responses.

Factors affecting within sites variability were studied in Chapter 4 and Chapter 5. In Chapter 4, data collected in 50 sites in The Netherlands was used to evaluate the role of alternative solutions to cope with the same environmental conditions. Here, categorical classifications such as growth forms, woodiness and leaf habit were used to approximate alternative solutions. The qualitative attributes explained 8-23% of the variance within sites in leaf traits vs. soil fertility relationships. Therefore, they can potentially be used to make better predictions of global patterns of leaf traits in relation to nutrient supply. However, at a given soil fertility, the strength of the effect of each qualitative attribute was not the same for all leaf traits. The observed differences may imply a differential regulation of the leaf economy traits at a given nutrient supply, in which SLA and LPC seem to be regulated in accordance to changes in plant size and architecture while LNC seems to be primarily regulated at the leaf level by factors related to leaf longevity.

Drivers of trait variability among sites (Chapter 3) and within sites (Chapter 4), could not always be separated by using measured trait values alone. In Chapter 5, the role of resource supply and disturbance on plant trait expression was studied by combining trait gradient analysis with the CSR strategy scheme. Trait gradient analysis separates trait values into intra-site (alpha component) and inter-site (beta component) variability and CSR explicitly uses resource supply and disturbance as the main driver of trait expression. In agreement with the CSR theory, beta trait values of competitors and stress tolerators were separated only along gradients representing productivity. Ruderals, in agreement with expectations from CSR scheme, had deviating trait values (alpha values) only at the productive end of the gradient (beta values). Ruderals' patterns reflected the effects of disturbance in grasslands, floodplains and sites in early states of succession, while in old forests the ruderal classification did not allow to tease apart effects of disturbance and shade tolerance.

The use of plant traits as indicators of plant strategies and plant responses to the environmental factors is considered a promising approach to develop our understanding of ecological processes and to improve predictions of vegetation response to climate change. This thesis is the first attempt to quantify plant response to nutrient supply by using plant functional traits and to unravel the factors contributing to trait variability in this relationship. The outcomes of this study show some of the strengths and limitations of including plant traits in habitat distribution models. On one hand, plant traits can potentially be used to develop causal relationships, that are robust under climate change, for habitat distribution models. This is supported by the fact that plant response to nutrient supply could be quantified (despite the large variability); ii. the consistency of these plant responses across the globe and at a regional scale; and iii. the causal basis for these patterns, as traits have direct links to plant functioning. On the other hand, the limitations of this approach have to be considered depending on the level at which predictions of plant traits are to be made. Predicting expression of traits of species within communities is still constrained by the lack of quantitative knowledge about how shade tolerance is related to the traits under study and how to quantify disturbances. Nevertheless, even if proxies of shade tolerance, or growth forms are used, their power will probably remain only moderate (e.g. by using categorical classifications only up to 23% of the within-site variability could be explained). Therefore, within-site variability will probably remain the largest source of unexplained variability. Predicting plant traits at the level of communities seems more promising and requires: 1) The quantification of more integrative measures for characterizing nutrient supply and the quantification of disturbance regimes among sites, and 2) Increasing our knowledge on a) how different strategies are coordinated at the whole plant level, as some strategy dimensions are not independent from each other and b) which strategy components are selected under a particular suite of conditions, including nutrient supply.