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Community assembly in restored wetlands

PhD thesis
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Abstract:	This thesis aims to infer general rules and principles for plant species assembly in restored wetlands. The thesis reports the results from four subprojects: 1) Development of a new and simple method for modelling the responses of plant functional types along environmental gradients. 2) A test of the functional characteristics of Danish wetland species as a basis for predictive modelling of wetland assembly. 3) An experimental test of the importance of water level, fluctuations and nutrient content on species composition, species richness and above-ground biomass in wetlands. 4) A comparative study of restored and natural wetlands in order to evaluate restoration success in four restored wetlands. The studied sites are the River Brede, River Gelså, Lake Legind and Lake Spøttrup.

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Preface

The present thesis is the result of a three-year PhD-study at the Department of Wildlife Ecology and Biodiversity, National Environmental Research Institute and Department of Ecology, Evolution and Diversity, Botanical Institute, University of Copenhagen. The project was funded by the National Environmental Research Institute, the Danish Research Training Council and a grant from the World Wildlife Fund for Nature (WWF).

Acknowledgements

1 Synopsis

1.1 Introduction

1.1.1 Background

During the last 200 years, the wetland areas in Denmark have suffered a marked decline, primarily due to agricultural drainage, urban development, afforestation and water reclamation. Up to 80% of the Danish land area is affected by drainage, more than 95% of the watercourses have been channelized, and at present wet habitats such as bogs, swamps and meadows account for only 4% of land cover (Anon. 2001). Similar declines of wetland habitats have been reported from other European countries (Svensson and Glimskär 1993; Nienhuis et al. 2002), and on a global scale it has been estimated that more than 50% of the world's historic wetlands have been lost (e.g. Streever 1999).

In order to revert this development there is ongoing work to bring streams back to their old meandering courses, restore waterholes and lakes as well as the meadows connected to them. The Danish Aquatic Environment Plan II from 1998 has set as a national target to increase the wetland area with 16,000 hectares before the end of 2003 and the long-term objective is to restore 60,000 hectares of wetlands within the next two decades (Anon. 1998). However, as the restoration projects rely on voluntary support from all the landowners in a project area, the process has been delayed. Consequently, only 1,850 of the planned 16,000 hectares had actually been restored by the end of 2003 (Hoffmann et al. 2003b).

1.1.2 Restoration ecology

Around the world, restoration is increasingly used to compensate for past and planned (compensatory mitigation) wetland losses (Streever 1999). The purpose of restoration is to return an ecological system – whether conceived as an ecosystem, an ecological community or a landscape - to its original or previous condition following a period of change or disruption, usually resulting from human activities such as agriculture, development, waste disposal or mining (Jordan 1996). Restoration ecology is one of the newest and least understood areas of environmental science. However, given the continued degradation of natural and semi-natural habitats, restoration is suggested to play an increasingly important role in conservation biology (Dobson et al. 1997; Young 2000).

Setting specific goals for restoration projects, choosing appropriate restoration strategies and methods and subsequently monitoring and evaluation of the outcome is essential for improving restoration success (Fig. 1). Ecological engineering soundly based on ecological theory is most likely to succeed (Keddy 1999). This requires that ecologists are able to recommend proper restoration methods and subsequently predict the outcome of succession (Dobson et al. 1997). The

challenge is to enhance the integration of scientific knowledge of spontaneous species assemblage in communities into restoration programmes.

Figure 1. A knowledge-based decision framework for wetland restoration. I, II, III and IV indicate subjects covered by the four papers in the present thesis.
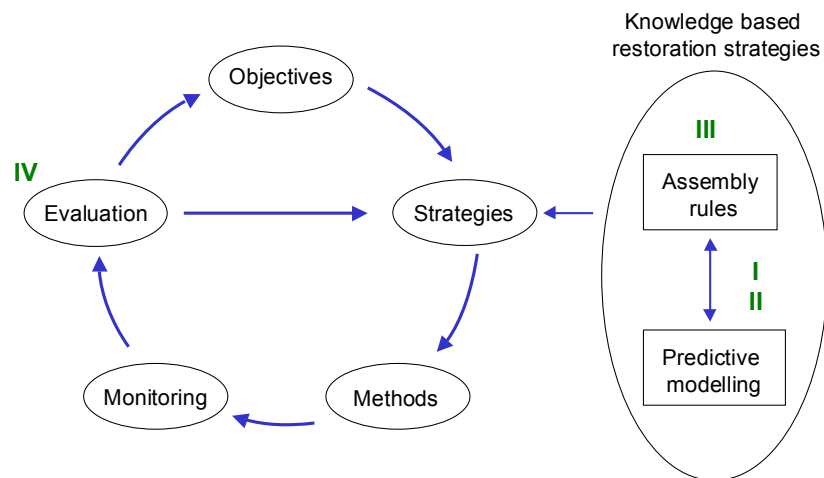
The primary motivation for wetland restoration in Denmark has been improvement of water quality and nitrogen retention. Secondary motivations include the creation of habitats for freshwater fish and water birds. Furthermore, the importance of improving overall wetland biodiversity has recently been emphasised. Despite a long-lasting recognition of the importance of clearly stated objectives (e.g. Kentula 2000; Streever et al. 1996; Streever 2000) most Danish wetland restorations have been planned and implemented without specification of what is to be accomplished by restoration.

To improve restoration strategies and methods it is necessary to closely follow and monitor ecological change. The first Danish wetland restoration project was initiated in 1989, but the first monitoring program was not implemented in the national restoration strategy before 2003 (Hoffmann et al. 2003a). Consequently, no data-driven evaluation of restoration methods, strategies and objectives has been possible. For this reason, Danish wetland restorations proceed without the vital information they could gain from completion of an evaluation phase (Fig. 1).

1.1.3 Aims

The main objective of my PhD project was to infer general rules and principles for plant species assembly in restored wetlands by analysing various data sets (see Appendix 1 for an overview).

The following projects were initiated in order to reach this objective:

- A study of methods for modelling the responses of plant functional types along environmental gradients (Article I)
- A test of response types as a basis for predictive modelling of wetland assembly (Article II)
- An experimental test of the importance of water level, fluctuations and nutrient content on species assemblage in wetlands (Article III)

- A comparative study of restored and natural wetlands (Article IV).

While the included articles report the findings from the above-mentioned projects in detail, the motivation for the synopsis was to provide a common synthesis and perspective on my results. The synopsis thus includes a synthesis of my contribution to the understanding of community assembly in wetlands, and an evaluation of its potentials for improving current wetland restoration strategies.

1.2   Approaches to assembly rule models

1.2.1   Assembly rules

Since the birth of ecology, scientists have searched for general rules explaining the distribution of species in the landscape and across geographical regions. Robert MacArthur and Edward O. Wilson´s theory of island biogeography was one of the first ecological theories based on the idea that species assemblages in communities are controlled by ecological rules (MacArthur and Wilson 1967). Hovewer, the term "assembly rule" was first presented by Jared Diamond in his paper on co-existing bird species on New Guinean islands (Diamond 1975). Since then, the assembly rules concept has been a central theme in ecology and applied to a variety of phenomena and organisms (cf. Weiher and Keddy 1999).

In plant ecology, Wilson and Gitay (1995) defined assembly rules as "restrictions on the observed patterns of species presence or abundance that are based on the presence or abundance of one or other species, or groups of species". In its strictest sense assembly rules are thus viewed as non-random patterns in community organisation caused by biotic interactions, e.g. competition, facilitation, mutualism and allelopathy (Wilson 1999). In a broader sense, as advocated e.g. by Paul Keddy, Evan Weiher and Sandra Diaz, assembly rules are defined as any kind of filter imposed on a regional species pool, including environmental conditions (Keddy 1992, Weiher and Keddy 1995a and 1999; Diaz et al. 1999). According to Keddy (1992) community assemblage can be seen as a process of deletion, in which abiotic conditions and biotic interactions act as nested sieves through which species from the regional species pool are sorted according to their niche requirements (see Fig. 2). Only species with functional characteristics that match a particular set of environmental filters will assemble in a given plant community (Keddy 1992, Weiher and Keddy 1995a, Diaz et al. 1999). In this thesis I have adopted this broad definition of assembly rules.

Figure 2. Community composition depends on a series of large- and small-scale processes. The large-scale processes (e.g. speciation, extinction and migration) determine the size of the regional and local species pools available for community assembly. At a finer spatial scale species composition (or the actual species pool) is constrained by dispersal and rules of assembly (e.g. abiotic variables and biotic interactions) that act as nested filters through which the species are sorted according to their niche requirements. After Keddy (1992), Zobel (1997) and Diaz et al. (1999).
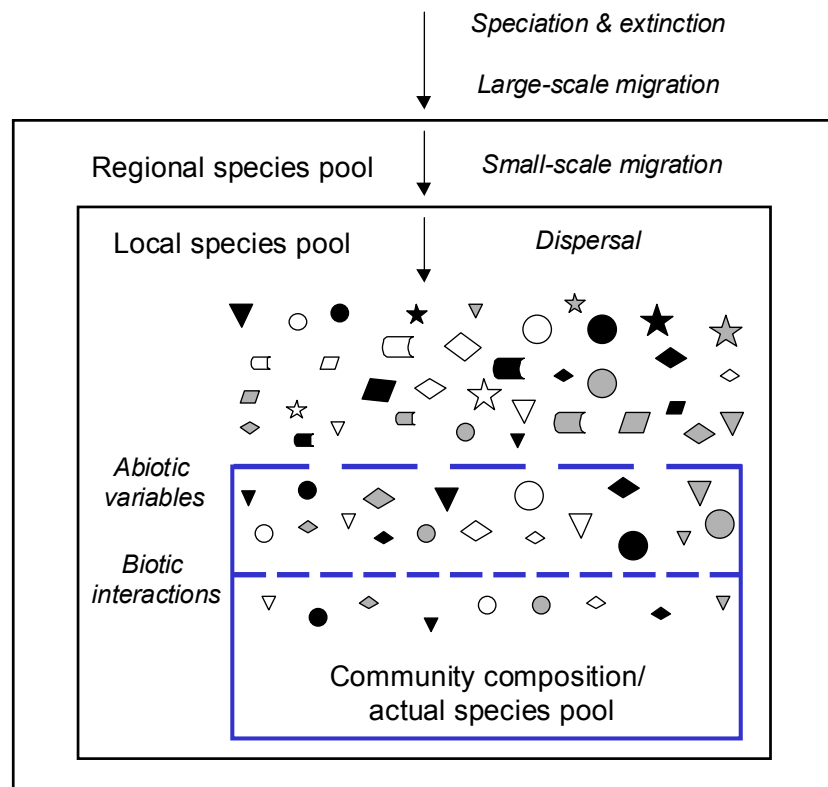
The raw material for community assemblage is the pool of species available for colonisation (Zobel 1992 and 1997; Eriksson 1993). The regional species pool is a product of the long-term, opposing processes of speciation and extinction (in evolutionary time) (MacArthur and Wilson 1967) as well as large-scale migration (in historic time) (Zobel 1997). The local species pool consists of species that are able to migrate into the community within a limited time frame (in ecological time) (Zobel 1997).

Plant community composition (or the actual species pool *sensu* Zobel 1997) is constrained by two kinds of rules that are assumed to operate simultaneously (as nested filters in Fig. 2). First, external environmental forces (e.g. climatic, edaphic or topographic conditions as well as disturbances) limit community composition according to the capability of the species from the local species pool to inhabit the site. This filter allows plants to establish and regenerate in environments to which they are adapted and ecologically similar species will be filtered into the same niche (Lavorel and Garnier 2002). This filtering process leads to under-dispersion of traits (i.e. trait dispersion of co-existing species being smaller than expected by random) within a community (Weiher et al. 1998). Second, internal biotic interactions will further constrain community composition by keeping co-existing species from being too similar (limiting similarity). This sorting mechanism leads to an over-dispersed mixture of trait values (i.e. trait dispersion of co-existing species being larger than expected by random) within a community (Weiher et al. 1998).

The vast majority of assembly rule studies have focused on limiting similarity of co-existing species. While this ecological pattern has been demonstrated in numerous animal assemblages, only very few studies have found evidence indicating that limited similarity of co-

existing species is a common pattern in plant communities. Some of the examples are the demonstration of over-dispersion of traits (Weiher et al. 1998), niche differentiation, guild proportionality and intrinsic guilds (Wilson and Roxburgh 1994) (see review in Weiher and Keddy 1995b). Many studies have demonstrated the selective actions of climate and environmental variables on plant communities, but few have been presented within the context of assembly rules (Diaz et al. 1999, but see Boutin and Keddy 1993; Weiher and Keddy 1995a). The detected patterns of community composition depend on spatial scale (Weiher et al. 1998) and the length of environmental gradients under study. At large scales and/or steep environmental gradients, as in wetlands, the impact of abiotic filters on community organisation typically overrides the effect of biotic interactions (Wilson and Roxburgh 1994).

The challenge for community ecologists is to understand which combinations of abiotic and biotic variables are responsible for determining species co-existence. Hence, assembly rules comprise the selection of environmental factors needed to understand and predict the organisation of communities (Diaz et al. 1998 and 1999). Although the complexity of natural systems makes it very difficult to find general rules of assembly, even generalisations that apply to some plant communities for a part of the time may be of great interest (Weiher et al. 1998; Booth and Larson 1999).

In order to demonstrate the existence of an assembly rule it is necessary to test it against the null hypothesis of random assembly. In my study, wetland community assembly rules have been developed and tested for three different measures of community organisation: 1) species composition, 2) derived community properties such as diversity or ecosystem functioning and 3) trait-environment linkages. The first two approaches regard community composition without consideration of functional traits, while the latter explains community assembly as the result of the meeting between traits and environment (biotic as well as abiotic).

1.2.2 Species composition

If the non-random patterns of community organisation, suggested by the assembly rule framework, are valid, then experimentally created environmental filters should result in the assembly of different communities from the same common species pool. In order to validate this hypothesis, a controlled wetland experiment in microcosms was carried out (see Appendix 1 and Article III). A functional analysis of the second year's data revealed a high degree of predictability of the variation in species frequency (86% explained variation) when species identity (of the 20 species) and the 12 treatments were included in the analysis (se Table 3 in Article I). Furthermore, the four combined nutrient and water level treatments resulted in a complete separation of four different species assemblages or community types in the third year of succession (see Fig. 1 in Article III). These results clearly support the assumption of environmentally mediated assembly rules, despite the fact that a very limited species pool (23 species) was available.

1.2.3 Species richness and productivity

Species richness (diversity or species density) is one of the simplest measures of community structure (Kelt and Brown 1999). Above-ground biomass (productivity or standing crop) is among the simplest measures of ecosystem properties. Consequently the relationship between species richness and above-ground biomass has been studied frequently. Some of the most widely cited theories addresing the productivity-richness relationship are the "humped back" model (Grime 1979), the "dynamic equilibrium" model (Huston 1979), and the "resource ratio" model (Tilman 1982). Although the underlying assumptions differ, all three concepts are based on the expectation that species richness generally follows a unimodal relationship with productivity (Grace 2001). Recent reviews indicate that the unimodal relationship is a widespread ecological phenomenon but other shapes are found, e.g. increasing, decreasing, U-shaped or no relationship (Grace 1999, Waide et al. 1999, Gross et al. 2000, Mittelbach et al. 2001). In the experimental microcosms I found evidence for a unimodal relationship between above ground biomass and species richness (see Fig. 2 in Article III).

In order to predict the effects of nutrient enrichment on species richness and to determine thresholds for no-effect-scenarios, it is important to know the biomass level beyond which species richness is negatively affected. The humped-back relationship between above-ground biomass and species richness in the microcosm experiment (se Fig. 2 in Article III) indicated that species richness in the first phases of a wetland assembly peaked at an above-ground biomass between 200 and 300 g m^{-2}. Above 300 g m^{-2} a clear decline could be observed.

1.2.4 Trait-environment linkages and Plant Functional Types

There is a long-standing tradition in plant ecology of seeking consistent associations between plant attributes (trait-environment linkages) or plant types (Plant Functional Types) and certain environmental conditions, irrespective of the species involved (Diaz et al. 1998 and 1999). An illustration of this principle can be seen in van der Valk (1981), who found that the fluctuations between flooded and dry conditions in prairie potholes acted as a strong environmental sieve determining the assemblage of plant species. One single trait, i.e. whether or not a species could germinate under water, sufficed to explain the regenerative success of the studied species. Unfortunately only few examples exist of the demonstration of such clear rules of assembly pinpointing a particular subset of traits (or functional group) for a given environment.

Although it is generally agreed that species respond individually to their environment, the complexity and diversity of natural systems makes grouping of species essential in order to derive general principles of succession and ecosystem recovery following human impact (Keddy 1992; Grime et al. 1997a; Westoby 1998). In recent years the concept of Plant Functional Types (PFT) has been developed as a potential quantitative approach to link traits and environments (e.g. Woodward and Cramer 1996; Gitay and Noble 1997; McIntyre et al. 1999; Rusch et al. 2003). A consistent objective for classification of

plant species according to function rather than phylogeny, has been to identify groups of species that share functional traits (morphological, phenological and physiological attributes) and therefore respond in similar ways to the environment (Gitay and Noble 1997).

There exists no universal functional classification of plant species (Skarpe 1996), although a few have been rather persistently used over time. Most frequently used are very simple classification of life forms (trees, shrubs, grasses, forbs, legumes, annuals, perennials etc.) but a few more sophisticated approaches have proven useful too (e.g. Raunkiær 1907, Grime 1973). In general, the relevant classification will depend on the aim of the user, the available traits, the scale of observation and the environmental factors or ecosystem processes of interest (Gitay and Noble 1997). Despite the large number of PFT studies, the results repeatedly confirm a few already well-documented relationships, e.g. that grazing favours prostate growth forms with protected buds, and that disturbance favours annuals and small-statured plants (McIntyre et al. 1999). Groupings that have long been recognised by botanists, e.g. major growth forms, often appear to be as successful for prediction as any recent classifications (see Leishman and Westoby 1992).

The present thesis includes two tests of trait-based assembly rules in wetland plant communities (Article I and II). The aim of both tests was to evaluate if individual attributes, or functional groups, consistently were associated with certain environmental conditions in Danish wetlands. The first paper consisted of a direct modelling of four PFTs and the environmental treatments from the microcosm experiment. The analysis revealed that when species and treatments were included as independent variables in the model we were able to explain 86% of the variation in species frequency in the experimental microcosms. However, substituting taxonomic species with functional types significantly decreased the ability to predict species responses to the experimental treatments (to 18% explained variation) (see Table 3 in Article I).

The second paper aimed to investigate if the biological profile of species (traits and known preferences) could be used for discrimination between observed species response groups in Danish wetland habitats. The analyses revealed that the functional discrimination of response groups were less successful than expected compared to the bright perspectives announced in the literature on the subject. The misclassification errors of the three presented tree-based model were 16% (two wetland clusters), 41% (four clusters) and 65% (eight clusters) (see Table 3 in Article II). A large number of species appear to have ecological preferences that are not easily interpretable from the generally accessible trait databases.

The comparison of a species-specific functional response model with a community-based model further revealed that species-environment linkages are much less predictable than community-environment linkages. Misclassification error was 41% when four species response groups were classified, compared to 17% for four community response groups (see Fig. 3 in Article II). This indicates that given a certain environment, we may successfully predict the mean Ellenberg

indicator values at plot (community) level. But although our classification is significantly better than random, we cannot provide reliable predictions regarding the ecological preferences of specific species in the community. I will discuss the reasons for this in further detail in section 1.3.1.3.

1.3   Predictive modelling

As a reflection of societal demands for quantitative assessments of the state of and trends in the environment and its associated biodiversity, ecological research is increasingly directed towards predictive modelling (Keddy 1992; Guisan and Zimmermann 2000; Austin 2002). The increased availability of powerful personal computers and statistical software has advanced this development further.

The non-equilibrium paradigm (Pickett 1980) suggests that successional pathways are complex and potentially unpredictable. According to this paradigm, ecological systems are probabilistic rather than deterministic. This is reflected both in species composition, successional pathways, mineral flow, energy flow and productivity (Parker and Pickett 1997). Even though some ecologists have focused their research on the stochastic nature of variables and processes, a need remains to identify the conditions under which acceptably accurate predictions of community organisation may be achieved.

1.3.1   Predictive modelling and trait-environment linkages

Trait-based assembly rule models are regarded as appropriate approaches to predictive modelling of vegetation responses to human-induced changes in the environment (Keddy 1992). In recent years PFT analyses have attracted much attention among plant ecologists, especially in relation to climate change (e.g. Chapin et al. 1996; Skarpe 1996; Woodward and Cramer 1996; Diaz and Cabido 1997), disturbance and land-use changes (Noble and Gitay 1996; Lavorel et al. 1997, 1998 and 1999a and b; Diaz et al. 1999; McIntyre et al. 1999; Rusch et al. 2003) e.g. grazing (McIntyre et al. 1995; McIntyre and Lavorel 2001) and fire regimes (Pausas 1999).

Many approaches to functional interpretation of vegetation data have been published. These range from deductive approaches, where functional groups are determined by personal experience and autecological knowledge (e.g. Noble and Slatyer 1980; van der Valk 1981), to inductive (or data-driven sensu Gitay and Noble 1997) methods including various quantitative analyses of field observations or experimental results (Woodward and Cramer 1996). The complications associated with data-driven approaches to functional interpretation of vegetation data has been coined the "fourth corner problem" by Legendre et al. (1997) (see Fig. 3). Functional analyses will have to deal with data organised in three tables: A) species composition (species by sample matrix), B) environmental gradients (environmental conditions by sample matrix) and C) functional attributes (species by attributes matrix).

Figure 3. The fourth corner problem. The data-matrices used for functional interpretations of vegetation data include a species by sample matrix (A), an environmental condition by sample matrix (C), and a species by attributes matrix (B). In the lower right corner (the fourth corner) the functional attributes (specific to the species) are combined with environmental variables (specific to the sample) (matrix D). After Legendre et al. (1997).
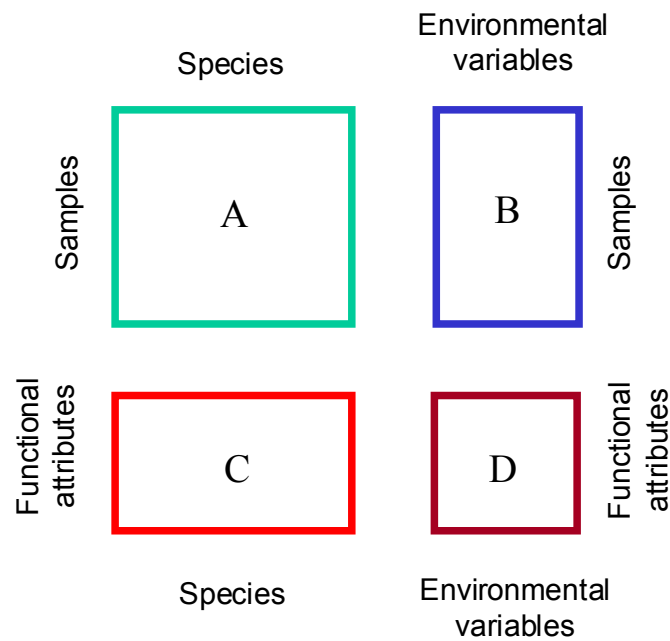
Analyses of species composition data (A) and simultaneous analysis of species composition data (A) and environmental variables (B) are commonly used approaches in community ecology e.g. various gradient analyses (Økland 1990).

1.3.1.1 Analyses of functional attributes

The most common data-driven approach (Gitay and Noble 1997) to functional analyses of vegetation data is unsupervised classification of species by attribute data sets (e.g. Boutin and Keddy 1993; Chapin et al. 1996; Henry et al. 1996; Lavorel et al. 1997; Gitay et al. 1999). This approach leads to emergent groups (or character syndromes) that reflect natural correlation patterns of biological attributes (Lavorel et al. 1997). Emergent groups are very sensitive to input data. Consequently, the result depends on which species and attributes are included in the study (Pillar 1999). Thus, inclusion of new species or attributes may change the result considerably. Although emergent groups may be correlated to environmental gradients subsequently (e.g. MacGillivray and Grime 1995; Kleyer 2002), the classification is inherently "unsupervised" in the sense that it ignores the response of species to environmental gradients. This may potentially lead to functional groups having little predictive power.

1.3.1.2 Analyses of species abundances and functional attributes

To my knowledge, Article II is the only published example of a simultaneous analysis of species composition (A) and functional attribute (C) matrices. The data used in the prediction of species co-occurrence in Danish wetlands (Article II) originated from various sources (DANVEG) and were sampled for very different purposes. Consequently, no accounts of the environmental conditions were available for analyses. We thus used groups of co-occurring species as a reflection of environmental variation. The species composition in the wetland data set (2155 samples and 527 species) was correlated with the functional attribute data set in two steps. First, an *a priori* classification of the species by sample data set was conducted in or-

der to identify groups of species with similar habitat requirements. The *a priori* classification consisted of a TWINSPAN classification followed by an Indicator Species Analysis. Subsequently, the functional attributes of the species (using both traits, strategies and ecological preferences) were used as predictor variables in a search for the species attributes that most successfully (with the lowest misclassification error) could separate the identified species groups in a supervised classification using tree-based modelling.

Rather than working with continuous gradients, clusters of wetland plots and species with affinity to these clusters form the basis for this approach to modelling of trait-environment linkages. The *a priori* classification makes it possible to compare models of increasing complexity. Different candidate models can be obtained by varying the number of clusters from the TWINSPAN analysis and thereby the number of classes in the response variable or using different criteria for inclusion of species in the modelling by varying p-values and minimum Indicator Values in the Indicator Species Analysis. Further, the functional model can be used for predictions of which group of species (the cluster membership) a new species is most likely to share habitat requirements with, given its functional "fingerprint".

1.3.1.3 A shortcut round the fourth corner

Supervised classifications that reflect the relationships between the functional characteristics of the species and the environment in which they live (trait-environment linkages sensu Diaz et al. 1998) are far more complicated. At present, no standard statistical method stands out as a widely accepted approach to the fourth corner problem (Legendre et al. 1997). Nonetheless, a number of different approaches have been published. These include simultaneous ordination of all three matrices (the co-inertia analysis by Doledec et al. 1996 used by Bornette et al. 1994; Doledec and Chessel 1994; Pautou and Arens 1994), separate multivariate ordinations (Lavorel et al. 1998; Lavorel et al. 1999a; Willby et al. 2000), matrix multiplication ("the fourth corner programme" with presence/absence data by Legendre et al. 1997) and different complex analytical procedures, e.g. multivariate analysis in combination with matrix multiplication (Diaz and Cabido 1997; Mabry et al. 2000) or generalised linear modelling (McIntyre and Lavorel 2001).

A new approach to functional interpretation of vegetation data is presented in this thesis (Article I). It is based on direct modelling of rearranged data tables. The first step is an initial merging of the three matrices (see Fig. 2) into one list file. The resulting list may be described as an abundance-environment-attributes (or functional type) list, with rows representing single observations of species in microcosms, and columns representing the frequency of the species, the environment of the microcosm (experimental treatment), and the functional attributes of the species. This way of organising data may be seen as a list file representation of the species by sample matrix, where columns have been added to represent environmental variables (specific to the sample) and functional attributes (specific to the species). With this new list, it was possible to model the success of different species as a function of environmental conditions and functional identity by the use of different Analysis of Variance models.

The functional model may subsequently be used to predict the responses of a new species to environmental change, as long as the relevant functional attributes are known. And vice-versa; the model may also suggest what kind of environmental changes that may have occurred given a reported change in species composition. We applied the method to a data set with species associated to predefined functional groups. The analysis could also have been applied directly to a list of attributes, in order to select the most appropriate set of attributes for prediction of species performance. Furthermore, the environment was represented by experimental treatments but it could just as well have been represented by field measurements of continuous environmental gradients.

1.3.2 Evaluation of trait-environment linkages

The use of different methodological approaches complicates the comparison of the efficiency of the various functional classifications. Irrespective of the specific purpose of a functional classification, it is important that the generality and prediction accuracy is assessed (Gitay et al. 1999). However, very few studies have reported the statistical significance of published results. In a few cases, plant functional type models have included figures for statistical significance of univariate correlation between traits and species (Mabry et al. 2000), plant functional types (Boutin and Keddy 1993; Medail et al. 1998) or environment (Diaz et al. 1998; Lavorel et al. 1999a; Dyer et al. 2001; McIntyre and Lavorel 2001; Kahmen et al. 2002; Pywell et al. 2003). However, multivariate approaches with a measure of explained variance (e.g. r^2) of the obtained plant functional types are practically absent in literature (Doledec et al. 1996; Legendre et al. 1997, for binary data). The ability to measure explained variation is a clear advantage of the two approaches to functional interpretation of vegetation data presented in this thesis (Article I and II).

Several authors have stressed the importance of validating plant functional type models (e.g. Gitay and Noble 1997; McIntyre et al. 1999), yet very few have included a validation step in their analyses (see e.g. Kleyer 2002). An unbiased estimate of the predictive power of a model can be achieved with independent data (which has not been used to develop the model), or, when no such test data exists, with re-sampling techniques such as cross-validation (Pearce and Ferrier 2000). The models included in this study (Article I and II) were validated by cross-validation.

Although the plant functional type approach is repeatedly praised for its predictive potentials, e.g. forecasting ecosystem responses to environmental change (e.g. Diaz and Cabido 1997; Gitay and Noble 1997; McIntyre et al. 1999), very few previous methodological approaches have taken the plant functional type analyses as far as this study (Article I and II), achieving a predictive model.

1.4 Perspectives for wetland restoration

In order to successfully protect and restore wetlands, we need to understand the impact of major environmental conditions on species assembly and richness. As numerous studies have shown, various abiotic and biotic constraints may limit the restoration of wetlands (Seabloom and van der Valk 2003, Keddy 1999). The relatively poor similarity between restored and natural wetland plots revealed in the comparative study in this thesis (Article IV), may be explained by an insufficient restoration of pre-disturbance conditions.

1.4.1 Abiotic constraints

Water level, fluctuations and nutrient availability are generally considered to be among the most important abiotic variables in wetland communities and an incomplete restoration of these driving forces may act as potential constraints on the assemblage of natural plant communities in restored wetlands (Bradshaw 1997).

Eutrophication is a widespread and increasing problem for terrestrial and wetland habitats in north-western Europe. It is generally known, and has been demonstrated in numerous fertilisation experiments, that high nutrient availability leads to the dominance of productive species and low species diversity (DiTommaso and Aarssen 1991; Berendse et al. 1992; Marrs 1993). The importance of nutrient availability on wetland community organisation was documented in several papers in the present thesis. First, the major coenocline in the reference data set corresponded to a fertility gradient expressed by two attributes related to site fertility preferences (Ellenberg´s indicator value for nitrogen and Grimes stress-strategy) (see Fig. 2b in Article II). Secondly, the species composition and richness in the microcosm experiment was strongly influenced by nutrient level (see Fig. 2 in Article III). Thirdly, the majority of restored wetland plots were characterised by species with preference for nutrient-rich conditions (Article IV).

A high residual soil fertility in restored wetlands is primarily attributed to land-use history. But the high priority to nitrogen retention and denitrification in Danish wetland restoration projects, implies that the restored sites will be subjected to a continuous nutrient enrichment e.g. from agricultural run-off in addition to the airborne nitrogen deposition (on average 15 kg N ha^{-1} yr^{-1} in 1996, Bak et al. 1999). The unimodal relationship between productivity and species richness, as documented in this thesis (Fig. 2 in Article III), indicates that this could prevent the development of species-rich communities.

The hydrological regime (water level and fluctuations) is generally considered to be one of the most important variables in wetland communities (Shipley et al. 1991; Toner and Keddy 1997; Casanova and Brock 2000; Keddy 2000). The importance of water level (or moisture in general) for species assemblage in wetland plant communities has been documented in several papers in the present thesis. First, the microcosm experiment revealed a major impact of water level on species composition and richness (Fig. 1 & 2 in Article III). Secondly, the functional interpretation of the reference data set on

Danish wetland communities further revealed a moisture gradient expressed by the hydrological preferences of the species (Londo class and hydrophyte life form) (Fig. 2b in Article II).

Although numerous wetland studies have demonstrated that water level fluctuations have profound impact on community organisation (van der Valk 1981; Day et al. 1988; Weiher and Keddy 1995a; Pollock et al. 1998; Lenssen et al. 1999; Casanova and Brock 2000), the microcosm experiment failed to document any effect of the three fluctuation regimes on species composition, species richness or biomass (see Table 2-4 in Article III). While the strong impacts of nutrient and water availability on community organisation may partly explain the absent effect of the fluctuation regime, an impact of the experimental design cannot be ruled out.

An adequate restoration of the most fundamental processes in wetlands, namely the hydrological regime, is a prerequisite for development towards a natural wetland flora. In restoration of lakes and streams, effort should be put into an integration of the surrounding landscape by ensuring a hydrological interplay between the aquatic environment and the adjacent meadows. As timing and duration of flooding events are known to be of great importance for community organisation in natural wetlands (Toner and Keddy 1997, Casanova and Brock 2000) it is crucial that restoration projects allow for a dynamic hydrology to evolve. Nevertheless, improper reinstatements of a natural hydrology has occurred in several restored sites as a consequence of e.g. low position of streams (e.g. River Brede) or the design of overflow systems (e.g. Lake Legind), which prevent natural hydrological processes, like flooding, to occur.

1.4.2 Species pool constraints

The local species pools (Pärtel et al. 1996; Zobel 1992 and 1997; Eriksson 1993) available for colonisation of the restored sites are often impoverished due to depletion of soil seed banks and spatial isolation of natural wetlands preventing seeds to from reaching the restored sites. This may prevent the reestablishment of plant communities that were present prior to the degradation (Galatowitch and van der Valk 1996).

The reappearance of plant species in a restored site may depend on their persistence in the soil seed bank as a "memory" of the original plant community (Bakker et al. 1996). However, as revealed in the seed bank database by Thompson et al. (1997) many species have only transient or short-term persistent seed banks. Several studies have furthermore demonstrated that wetland drainage and cultivation seriously reduced seed bank diversity and density (Wienholdt and van der Valk 1989, Brown 1998). In the majority of restored wetlands the species will thus have to immigrate by dispersal.

In intensively managed landscapes, i.e. most North-western European countries, remnant natural wetland communities may be conceived as fragmented habitat islands in a hostile sea of agricultural fields. As suggested by the island biogeography theory by MacArthur and Wilson (1967) the farther an oceanic island is from a source of potential immigrant plants and animals, the fewer species

will be found on that island. Correspondingly, several studies have reported that distance to nearest potential seed source has a profound effect on the number of native species reaching restored wetlands (Reinartz and Warne 1993). Several studies of riparian vegetation have shown that overbank flooding promotes dispersal of seeds, diaspores, stem fragments and thereby contribute to an enhanced species richness in regularly flooded areas (Johansson and Nilsson 1996, Cellot et al. 1998, Merritt and Wohl 2002). An impaired hydrology in riparian areas may thus further restrict the potential for diverse and natural plant communities to develop.

A major obstacle for conservation of wetland species is their limited seed longevity and short-range dispersal. Consequently, these species will not readily establish in restored sites (Strykstra et al. 1998; Budelsky and Galatowitsch 2000). The probability of a successful restoration is thus generally considered to be greatest on sites where the native vegetation was only recently eliminated, and where existing target vegetation types can act as a source of colonising species (Wienholdt and van der Valk 1989; Brown and Bedford 1997).

In most modern landscapes, dispersal has become a serious bottleneck in restoration management. Therefore, the "new" wetlands are formed from a limited subset of the pool of native species found in natural wetlands. The species assemblages in restored wetlands may thus reveal new, more or less stable, species combinations, e.g. the mudflat annuals community found along restored lake shores (see Article IV).

Analyses of biotic and species pool constraints on species assemblage in restored wetlands have not been an explicit aim in the present thesis. The species assemblages in the microcosm experiment were based on a common species pool and thus unaffected by potential constraints regarding dispersal and seed banks. In the field studies of restored wetlands the constraints on local species pools (e.g. distance to nearest seed source and composition of seed bank) were not quantified. In October 2000 a field experiment was set up in order to determine if species richness in a selected restored wetland (Lake Spøttrup) was restricted by environmental mediated constraints or dispersal limitation. However, an unexpected flooding event displaced the seeds and consequently the experiment was terminated (see appendix 1 for more details)

1.4.3 Biotic constraints

Many, predominantly American studies, have shown that slow succession rates could potentially lead to the establishment of persistent semi-stable states (Hobbs and Norton 1996) with dominance of competitive species with clonal growth, such as *Phalaris arundinaceae, Typha spp.* and *Lythrum salicaria,* (e.g. Platt and Weiss 1985; Galatowitsch et al. 1999; Klötzli and Grootjans 2001; Campbell et al. 2002; Seabloom and van der Valk 2003). These studies can be taken as evidence of the "initial floristic composition" by Egler (1954) and the "inhibition model" proposed by Connell and Slatyer (1977). Both studies emphasise the importance of early colonising and competitive species for the subsequent development in community composition and diversity.

In the restored wetlands studied in the present thesis I found evidence of dominance of competitive and clonal species such as *Glyceria maxima*, *Phalaris arundinacea* and *Epilobium hirsutum* in the meadows along the River Brede and the River Gelså. In Denmark documentation of the presence of "permanent" semi-stable states and knowledge about their establishment and development is rather limited (Lorenzen 1998), although they represent a potential threat to restoration and conservation of species rich wetland communities.

1.4.4   Restoration strategies

The above-mentioned constraints on community assembly in restored wetlands have lead to various restoration strategies with an increasing degree of control over the assembly process.

Since the primary goal for wetland restoration in Denmark has been improvement of water quality and nitrogen retention, the prevailing restoration strategy has been to reinstate the pre-drainage hydrological regime. As rather strong ethical objections exist against reintroduction of species when compared to many other countries (e.g. Sweden, UK and US), Danish restoration projects are traditionally initiated by spontaneous re-vegetation. This approach relies on the self-organising ability of ecosystems in which natural processes contribute to the assembly of spontaneous species reflecting local conditions (Manchester et al. 1998; Mitch et al. 1998; Prach et al. 2001). However, due to the above-mentioned potential constraints on wetland restoration in intensively managed landscapes, this approach may result in the creation of species-poor and already widespread plant communities and thus a limited enhancement of biodiversity. The comparative analyses of restored and natural wetlands supported this assumption by revealing that only 19% of the investigated plots from restored sites resembled unimproved natural wetland vegetation (se Table 3 in Article IV). The analyses further showed that the majority of these plots were sampled along restored lake shores where the vegetation prior to the restoration was characterised as natural habitats with spontaneous vegetation. This very limited success is in accordance with numerous published studies of restored wetlands (e.g. Galatowitsch and van der Valk, 1996; Mitsch and Wilson 1996; Lockwood and Pimm 1999).

The constraining effect of high residual soil fertility on the natural succession in restored wetlands has lead to the use of a different restoration strategy in the Netherlands, where eutrophication is an even larger problem than in Denmark. Here, a wide variety of measures have been implemented in order to deplete soil fertility (Marrs 1993), e.g. by top-soil removal or mowing with subsequent removal of the hay (cf. Pfadenhauer and Klötzli 1996). Such measures have not been considered in the national strategy for wetland restoration in Denmark, although such active interventions are known from Danish heathland restorations. This approach partly restrains the authenticity (the value of nature as the result of natural processes, Nygaard et al. 1999) and wildness (the value of free interplay of environmental forces and biota without human interference, Nygaard et al. 1999) of the restored site, but increases the chances of a successful restoration based on natural re-colonisation.

Yet another strategy, including an active introduction of species, has been applied to (re)create species rich communities. Important reasons for accelerating the re-vegetation by reintroduction of species are lack of sufficient seedbanks, dispersal limitations of target species and/or an intention to prevent persistent semi-stable states (Hobbs and Norton 1996). The reintroduction approach has been commonly used to boost biodiversity in restoration projects in the United States. Although an active re-vegetation strategy may lead to the desired species rich plant communities in a restoration site, this will be achieved at the expense of the authenticity and wildness of Nature (*sensu* Nygaard et al. 1999). In addition, it may be waste of resources if the reinstatement of a natural environment fails.

The complexity of species interactions means that there may be many alternative outcomes of a succession and many stable states associated with a certain species pool and set of environmental conditions. Consequently, the assembly rule theory assigns tremendous importance to the sequence in which species are introduced to or naturally colonise a community (Drake 1991). The order of arrival affects competitive interactions and may thus make the difference between communities dominated by a few competitive species and communities supporting a wide variety of rare species (Lockwood 1997). This has lead to a fourth restoration strategy, where the assembly process is guided by a slow, sequential introduction of the species known to be involved in the assembly of the desired plant community (either species by species or in groups). This approach aims to optimise the persistence of the introduced species and thus the richness of the target community.

Several studies have shown that an active introduction of species increases species richness in the first years of succession (Manchester et al. 1998). But an important prerequisite for a successful development in restored wetlands, regardless of the chosen re-vegetation strategy, is that the site conditions meet the biological requirements of the target species (e.g. natural wetland species). In a six year experimental study van Duren et al. (1998) thus showed that introduction of target species was an insufficient measure for (re)creating specific plant communities, when proper reinstatement of the relevant abiotic conditions in a degraded *Cirsio-Molinietum* fen meadow had failed. The decreasing species richness in the fertile microcosms found in the present thesis (Fig. 2 in Article III) further supports the importance of a proper restoration of the environmental conditions (e.g. nutrient content).

I recommend that scientific knowledge of potential species pool limitations and environmental constraints on plant community assembly should be an integrated part of the decision framework for wetland restoration. The objectives and strategies of wetland restoration should acknowledge the many potential end-points of natural succession and the aim should therefore not be to reassemble specific target communities. Instead restoration strategies should leave room for the authenticity and wildness of a spontaneous Nature.

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2   Articles in thesis

I.   A shortcut round the fourth corner - a new approach to functional interpretation of vegetation data

Nygaard, B. & Ejrnæs, R.
Accepted for publication in Journal of Vegetation Science (vol. 15)

II.   Can species occurrences in Danish wetlands be predicted form functional attributes and indicator values?

Nygaard, B. & Ejrnæs, R.
Submitted to Journal of Vegetation Science (16.10.2003).

III.   The impact of hydrology and nutrients on wetland assembly and diversity – evidence from a 3-year microcosm experiment

Nygaard, B.
Submitted to Oikos (11.12.2003)

IV.   A comparative analysis of restored and natural wetland vegetation

Nygaard, B. & Baatrup-Pedersen, A.
Planned to Biological Conservation.

A shortcut round the fourth corner - a new approach to functional interpretation of vegetation data

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Abstract. In this paper we present a new approach to the simultaneous analysis of a species composition data set, an environmental gradients data set and a functional attributes data set. We demonstrate its advantages in terms of statistical modelling including model development and assessment as well as subsequent prediction. Our method is applied to a set of case data deriving from experimental wetland microcosms including 20 species, 12 treatment combinations and a classification of species into functional groups. Acknowledging that lack of independence between samples and over-interpretation of data may lead to overly optimistic assessment of model performance, we use cross-validation with different subsets of data to obtain realistic model performance measures. It is shown that although the outcome of the wetland experiment is predictable in terms of experimental treatments and taxonomic species, the functional groups cannot be used to explain the variation in species frequencies in the experiment. We compare the method with recently published approaches to the functional analysis of vegetation data, and discuss its applied perspectives.

Keywords. Cross-validation; Functional classification; Plant functional type; Statistical modelling; Assembly rules; Trait-environment linkage; Predictive ecology.

Nomenclature. Tutin et al. (1964-1980).

Can species occurrences in Danish wetlands be predicted from functional attributes and indicator values?

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Abstract. This study investigates to what extent species-specific information on biological traits, strategies and ecological preferences can be used for identification of species response groups in Danish wetland habitats. A large data set was collected from the literature, including plots with species and species with attributes. A TWINSPAN clustering of vegetation plots followed by an Indicator Species Analysis was used to identify groups of species with similar habitat requirements. These species-clusters formed the basis for tree-based classification models attempting to predict species-cluster from species traits, strategies and ecological preferences.

Our analyses revealed that available information on ecological preferences was more useful for prediction than information on species traits related to e.g. growth form, life form, life history, leaf phenology and seed weight. Cross-validation revealed the optimal classification trees to be small-sized leading to only three to four response groups discriminated mainly by their known ecological preferences. Although these models were all highly significant in their discrimination of species, the misclassification error of the models was found to be considerable.

Our results indicate that the classification of functional response groups for prediction of the occurrence of single species may be less rewarding than generally claimed in the literature on the subject. Perspectives for future research are discussed.

Keywords. Functional classification; Functional response types; Statistical modelling; Wetland communities; Trait-environment linkage; Predictive ecology.

Nomenclature. Tutin et al. (1964-1980).

Article III

The impact of hydrology and nutrients on wetland assembly and diversity - evidence from a 3-year microcosm experiment

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Abstract. Protection of biodiversity and restoration of species-rich plant communities depend on an adequate understanding of how diversity is regulated. After 25 years of research there is still disagreement about the relationship between productivity and richness as well as its underlying mechanisms. In this paper I report from a three-year study of species diversity patterns and community assembly in a synthesised wetland succession. The treatments applied to the experimental microcosms included factorial combinations of two nutrient levels, two water levels and three water level fluctuation regimes. A standard seed mixture of 23 wetland species representing a wide range of plant functional types was sown in each microcosm.

I found strong and consistent effects of water and nutrient level on species composition, species richness and biomass but no clear effect of water level fluctuations. The observed relationship between biomass and species richness provided empirical evidence for a positive relationship in the infertile range (16 to 204 g m^{-2}) and a negative relationship in the fertile range (372 to 1156 g m^{-2}). This pattern is consistent with the "humped-back model", with a maximum species richness at an above ground biomass between 200 and 300 g m^{-2}. The increasing species richness with biomass at low fertility could partly be explained by variation in water logging causing a variation in seedling establishment and hence biomass and richness. I interpret the decreasing species richness at high fertility as an indirect effect of treatments on competitive intensity mediated through above ground biomass. Finally, I discuss the results in the light of current theory on the mechanisms behind diversity in wetlands.

A comparative analysis of restored and natural wetland vegetation

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Abstract. The restoration of wet meadow communities along two restored lakes and two restored streams of varying age (six to 11 years) and land-use history was evaluated through comparison with a large reference data set. 199 plots with restored wetland vegetation were assigned to four *a priori* classes. Two classes consisted of restored lake shores with 1) improved and 2) "natural" vegetation, the other two of stream border communities with 3) moist and 4) wet conditions. The 1530 reference plots were assigned to eight *a priori* classes based on the degree of human impact ("naturalness") and their weighted averages of Ellenbergs indicator values for nitrogen and moisture.

These 12 *a priori* classes were used as response variables in a quadratic discriminant analysis along with the plot scores of a joint ordination. The predicted classes were used to evaluate if natural wetland vegetation had developed in the four restored wetlands. Half the restored wetland plots had a floristic composition that was unique for the restored sites, e.g. a pioneer community with mudflat annuals and sites under transition from wet meadow vegetation to a lake shore reed belt. 31% of the restored plots resembled the already widespread improved communities and primarily those from nutrient rich, moist and wet sites that have a limited conservation value. And only 19% of the restored plots resembled natural plant communities. The relatively poor similarity with natural wetland vegetation is discussed and recommendations for future restoration projects are given.

Keywords. Wetland restoration; restoration success; reference wetlands; supervised classification; natural re-colonisation.

Appendix 1- Available data

Data available for the papers in this thesis are listed below.

Data source	Article I	Article II	Article III	Article IV
Functional attributes	x	x		(Ellenberg values)
DANVEG				
Habitat variation		Oligo- to eutrophic		Meso- to eutrophic
Number of samples		2155		1530
Number of species		527		390
Sampling in restored wetlands				x
Microcosm experiment	2. year		3. year	
Species composition	x		x	
Species richness			x	
Above ground biomass			x	
Field experiment				

Functional attributes of wetland plant species

Screening for functional attributes was pioneered by Grime (Grime 1973 and 1979; Grime et al. 1997b) for the Sheffield flora in England. Since then an intense effort has been put on selecting traits relevant for functional analysis (Weiher et al. 1999), producing protocols for their measurement (e.g. Cornelissen et al 2003) and constructions of databases e.g. ECOFLORA (Fitter and Peat 1994) and LEDA - A database on the life history of the Northwest European flora (see www.leda-traitbase.org). Measurements of functional traits, in the field or experimentally, is extremely time consuming and most published studies of functional traits thus rely partly (Leishman and Westoby 1992; Bornette et al.1994; Pautou and Arens 1994; Lavorel et al. 1999a) or solely (e.g. Kleyer 1999; Pywell et al. 2003) on readily available traits.

In the present thesis the functional attributes were initially assembled for as many Danish wetland species as possible, but complete records were only available for a limited number of attributes and species. The used functional attributes were in most cases easily measured features of plants acting as surrogates for the underlying physiological adaptations (Weiher et al. 1999; McIntyre et al. 1999). Furthermore, all available characteristics (biological attributes, strategies and indicator values) have been included in the analyses. This approach sacrifices the mechanistic understanding in order to improve the predictive ability of the functional models (se Article II).

The specific biological attributes readily available for Danish wetland plant species include seed weight (Hodgson et al. 1995), propagule longevity (data from Thompson et al. 1997 and index calculated from Bekker et al. 1998), dispersal mode (Frank et al. 1990), growth form (Hansen 1981), life history (Hansen 1981, Hodgson et al. 1995), canopy height (Hansen 1981), canopy structure (Hodgson et al. 1995),

lateral spread (Hodgson et al. 1995), life form (Hansen 1981, Ellenberg et al. 1991, Hodgson et al. 1995), ability to vegetative reproduction (Hodgson et al. 1995), onset of flowering (Hansen 1981) and leaf phenology (Ellenberg et al. 1991, Hodgson et al. 1995).

These biological attributes were supplemented with one classification of species according to strategy (functional syndromes): Grimes CSR-strategies (Grime 1979; Hodgson et al. 1995) and two sets of indicator values reflecting species preferences along environmental gradients: Ellenberg indicator values for nitrogen, moisture, light and soil acidity (Ellenberg et al. 1991) and Londo´s phraetophyte classification of plant species according to hydrological preferences (Londo 1988).

Finally, field measurements of Specific Leaf Area (SLA), canopy height and biomass was conducted on the 23 species in the experimental species pool, but these data have not been used in any of the four papers in this thesis.

DANVEG – a database on DANish VEGetation types

DANVEG is a database of published and unpublished accounts of natural and semi-natural plant communities in Denmark (Nygaard et al. 1999). The first version of the database was developed at the National Environmental Research Institute, Department of Landscape Ecology (now Department of Wildlife Ecology and Biodiversity) in 1999, but it is under continuous improvement (see www.danveg.dk).

The wetland data in DANVEG was collected in the period 1910-1997 and comprises 2155 samples and 527 species. The database covers a wide range of wet and moist terrestrial habitats from nutrient-rich swamps and reed beds over mesotrophic meadows and fens to oligotrophic bogs and mires. Further, the data set encompasses a gradient in human impact ranging from natural habitats with spontaneous vegetation (e.g. bogs, mires and flushes) to culturally improved meadows and pastures. Only plots collected from homogeneous stands of a limited size (max. 100 m^2) were included in the database. Species abundances were originally recorded by either frequency or cover scales but in the analyses the measures were transformed into a common numeric scale from 0 to 100 in order to keep species abundances. The origin of the 2155 samples are shown in the appendix of Article II.

Sampling in restored wetlands

Originally, the present study aimed to rely the search for key factors in the early successional stages of restored wetlands on data from the monitoring program of the Danish Aquatic Environmental Plan II (Hoffmann et al. 2003a). Due to the postponed initiation of the restoration projects the first monitoring data were not available until September 2003. Consequently, I have based the analyses on my own studies of two re-established shallow lakes in north-western Jutland (Lake Spøttrup near Rødding and Lake Legind near Nykøbing Mors) and two middle-sized streams in southern Jutland (River Brede near

Tønder and River Gelså at Bevtoft). These data were supplemented with data from the master theses by Stine Cortsen and Bent Albæk (se Article IV for more details).

Microcosm experiment

By simplifying the complexity of natural environmental conditions experimental microcosms have proved to be a useful approach to test hypothesis regarding complex ecological relationships (Fraser and Keddy 1997). An outdoor controlled wetland experiment in microcosms was set up in April 2000 as a factorial design with combinations of two nutrient levels (nutrient-poor versus nutrient-rich), two water levels (water level 10 cm below versus 30 cm below soil surface) and three water level fluctuation regimes (water table constant, water table raised above the soil surface from October to March and water table raised above the soil surface four days every three weeks). The 12 treatments were replicated six times for a total of 72 microcosms and a standardised seed mixture of 23 wetland species was applied to each microcosm (consult Article III for more details). The species were chosen to represent four different functional types in Danish wetlands (consult Article I for more details).

Frequencies of the 23 species were assessed in August 2000, August 2001 and September 2002 in sixteen 10 x 10 cm subplots in each microcosm. The total above ground biomass was harvested immediately after the last sampling. Frequency data per species in each microcosm from August 2001 was used in the predictive models in Article I. Data on species composition, richness and above ground biomass from September 2002 was used in Article III.

Field experiment

In order to study the colonisation potential of 14 native wetland species a field experiment was set up in October 2000 in a former agricultural field along the shore of the restored Lake Spøttrup. The experiment was established in a 20 by 50 m area that had been grazed by cattle since 1994. The experiment included 14 species, two two-level treatments (ploughing and cutting) and three replicates (n=168). 12 of the 14 native wetland species were choosen from the species pool of the microcosm experiment: *Agrostis stolonifera*, *Alopecurus geniculatus*, *Bidens tripartita*, *Caltha palustris*, *Carex nigra*, *Cirsium palustre*, *Deschampsia cespitosa*, *Epilobium hirsutum*, *Hypericum tetrapterum*, *Juncus conglomeratus*, *Lotus pedunculatus* and *Phalaris arundinacea* along with two rare species *Lathyrus palustris* and *Trollius europaeus.* Initially the experimental area was divided into six compartments of which three were ploughed to a depth of 30 to 40 cm and three remained undisturbed with a rather dense and low vegetation cover. Further, each compartment was divided in two blocks of which one was subjected to cutting every two weeks. 14 50 by 50 cm plots were established in each of the 12 blocks and 100 seeds from one of the 14 native wetland species were spread evenly over the soil surface in each plot. Finally, the experimental area was fenced to avoid disturbance from the cattle.

The experiment was planned to run for two years. However, in the winter 2000-2001 an exceptionally high water level in Lake Spøttrup combined with a strong breeze resulted in flooding of the experimental area. The flooding event resulted in a displacement of the seeds and the experiment was consequently terminated.

National Environmental Research Institute

The National Environmental Research Institute, NERI, is a research institute of the Ministry of the Environment.
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This thesis aims to infer general rules and principles for plant species assembly in restored wetlands. The thesis reports the results from four subprojects:
1) Development of a new and simple method for modelling the responses of plant functional types along environmental gradients.
2) A test of the functional characteristics of Danish wetland species as a basis for predictive modelling of wetland assembly.
3) An experimental test of the importance of water level, fluctuations and nutrient content on species composition, species richness and above-ground biomass in wetlands.
4) A comparative study of restored and natural wetlands in order to evaluate restoration success in four restored wetlands. The studied sites are the River Brede, River Gelså, Lake Legind and Lake Spøttrup.

Community assembly in restored wetlands