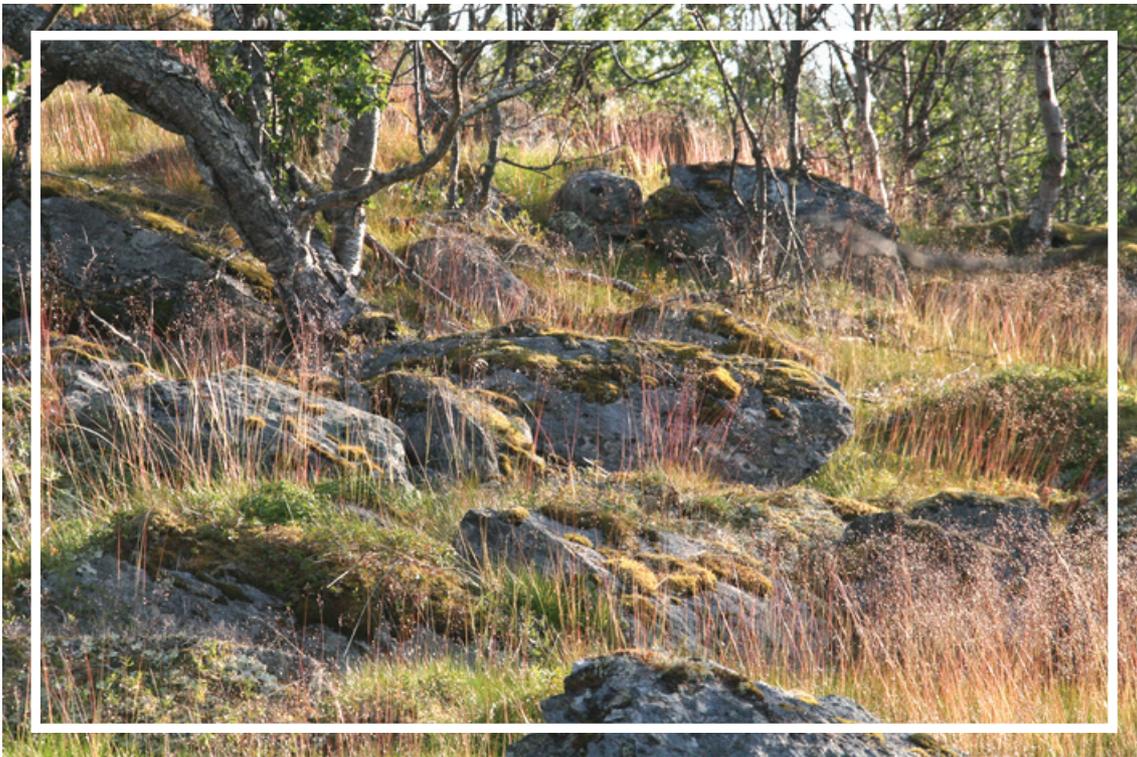




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CHAPTER 1

General introduction



Deschampsia flexuosa understorey (dry birch forest)

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PLANT FUNCTIONAL TRAITS AND THEIR USE IN ECOSYSTEM ECOLOGY

Plants, as any other living organisms, have an evolutionary background responsible for their present genotype. Geographic, topographic, climatic and biotic changes have repetitively occurred during their evolution, creating multiple evolutionary selection pressures at various time- and spatial-scales. Under these changing selective pressures, various plant genotypes have been selected, involving various ways of reproducing, dispersing, germinating, growing and resisting to a number of external abiotic and biotic factors. As a result of these dynamic evolutionary processes, each plant possesses an individual genotype. This genotype, in interaction with the environment, is expressed as a plant phenotype, i.e. a set of observable plant characteristics. These characteristics can be described as (values or categories for) ‘plant traits’.

The concept of traits, underpinning functional ecology, has been widely used, going back as far as Darwin’s (1859) work on species evolution or Raunkiaer’s (1934) life-form system, but its use and interpretation has strongly evolved and may nowadays hardly be captured in a single definition. The attempt to generalize this concept from organisms to communities and later ecosystems has contributed to its widespread use but has created ambiguities (Violle *et al.*, 2007). Many different categories of traits have thus been proposed to clarify and differentiate between different aspects of the ‘trait’ concept. A distinction is thus made between ‘performance traits’ defined as any trait that directly influences fitness and ‘functional traits’ as any trait which impacts fitness indirectly. The notion of ‘soft’ versus ‘hard’ traits also appeared in the literature (Hodgson *et al.*, 1999; Weiher *et al.*, 1999) with the idea that soft traits are easily measurable traits used to capture or replace the usually more informative although hardly measurable traits. Throughout this thesis, the use of ‘trait’ refers to the slightly adapted definition of Violle *et al.* (2007) as “*any [biochemical,] morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization*”.

Functional traits are getting increasing attention in ecology as they allow dissecting, quantifying and therefore comparing the way species interact with their environment (Lavorel & Garnier, 2002; Suding *et al.*, 2008). Thus, traits can express the potential response of plants to specific external biotic or abiotic factors. The state of a particular trait (qualitative trait, e.g. mycorrhizal association type) or range of trait values (quantitative trait, e.g. plant height) within a plant species potentially describes its capacity to, for instance, resist disturbance, cope with a particular stress or even adapt to ecosystem changes. On the other hand, the presence of certain trait states or values for given plant species allows predictions of the effect that these plants have on the ecosystem functions and properties (e.g. the capacity of a plant to fix atmospheric nitrogen via actinorhizal symbiosis impacts on ecosystem nitrogen availability). Traits are thus commonly referred to as either (or both) ‘response traits’ (any trait the value of which varies in response to changes in environmental conditions) or ‘effect traits’ (any trait which reflects the effects of a plant on environmental conditions; community or ecosystem properties) (Violle *et al.*, 2007).

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SPECIES ASSEMBLY RULES AS DETERMINANTS OF VEGETATION COMPOSITION

(What controls ecosystem vegetation composition?)

All over the globe, ecologists try to find consistent, predictable associations between plant species assemblages and environmental conditions (e.g. Rodwell, 1991). Similarly, a tremendous number of studies have described predictable associations between plant traits and environmental factors (Diaz, Cabido & Casanoves, 1998). These consistent associations between trait (or range of trait values) and the environment are the result of a selection process involving successive ‘constraints’ (or ‘filters’) that restrict the occurrence of certain traits and trait values in specific parts of the globe. These constraints are numerous, including abiotic, biotic and historical factors (Woodward & Diament, 1991; Keddy, 1992), and operate at different spatial (Diaz, Cabido & Casanoves, 1998) and time scales (e.g. sequential effects; Samuels & Drake, 1997). Thus, at any particular site, each filter can potentially rule out plants that do not possess the adequate trait values to establish, survive and reproduce (Keddy, 1992). Historical factors, climatic conditions, disturbance regime and biotic interactions are likely to act at successively decreasing spatial scales. This implies that only plants present within the species pool in a specific part of the globe, with a viable combination of trait values under the prevailing climatic conditions and able to resist (or being resilient to) the local disturbance regime, can potentially establish, survive and interact with other organisms (Diaz, Cabido & Casanoves, 1998). However, facilitation effects can also partly alleviate climatic and disturbance factors that would have been detrimental to the individual species (Bruno, Stachowicz & Bertness, 2003). The variety of factors that shape species assemblages, also referred to as ‘species assembly rules’ (Keddy, 1992), can thus act from global to local scales and thereby create the mosaic of biomes and communities that we know.

While the impact of these assembly rules on species assemblages may be drastic, wide ranges of plant traits are nevertheless found within local ecosystems (e.g. Cornwell & Ackerly, 2009) implying the coexistence of highly contrasting plant strategies at relatively small spatial scales (Wright *et al.*, 2004). Similarly, while some species are only adapted to very restricted environmental conditions, most species can be found in multiple environments and a large part of them is found in non-optimal environmental conditions (Lambers, Chapin & Pons, 1998).

PLANT STRATEGIES AND TRADEOFFS

(How do plants adapt to their environment?)

Plants, in the course of their evolution, during their ontogenesis and during their life, are permanently confronted with conflicting environmental demands. One major dilemma they are facing is, for instance, the one between growth and defence, or in other words between carbon and nutrient acquisition and conservation (Grime, 1979; Berendse & Aerts, 1987; Herms & Mattson, 1992; Reich, Walters & Ellsworth, 1997). Similarly, plants protect themselves against a wide range of disturbances and invest in several types of defences (Atsatt & Dowd, 1976; Vicari & Bazely, 1993; Agrawal & Fishbein, 2006) or invest carbon and nutrients differentially toward the acquisition of various resources, such as light, nutrients and water. This selective investment in

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allocation, involving plant specialisation, is commonly referred to as ‘tradeoff’. Here I follow Grime’s (2001) view of a tradeoff as “*an evolutionary dilemma whereby genetic change conferring increased fitness in one circumstance inescapably involves sacrifice of fitness in another*”. The sum of these plant adaptations and their tradeoffs represents plant strategy. As such, plant strategies do not involve single widespread adaptations among plants but rather a myriad of adaptations, used in combination and at variable intensities (Herms & Mattson, 1992). The adaptations towards acquisitive or conservative strategies, for instance, should thus be seen as a continuum (Wright *et al.*, 2004).

However, a plant is not a uniform entity. It possesses distinct organs which perform both distinct (e.g. photosynthesis vs. nutrient and water absorption) and similar (e.g. transport) functions. Consequently, plant tradeoffs are likely to occur both within and across organs. Indeed, within any environment, plant species can be ranked, based on their leaf traits, along a continuum ranging from (carbon and nutrient) acquisitive to conservative strategies (Wright *et al.*, 2004). Some studies have suggested that such a continuum in plant strategies should also occur in conductive and supportive organs such as woody stems (Chave *et al.*, 2009) or absorptive roots (Wahl & Ryser, 2000). As a consequence of potential selective investment of plants toward a particularly limiting resource (e.g. water, light), strong tradeoffs could be expected between organs. However, there is increasing evidence that plant strategies are to some extent coordinated across organs (Tjoelker *et al.*, 2005; Withington *et al.*, 2006; Reich *et al.*, 2008; Liu *et al.*, 2010), probably due to evolutionary and physiological constraints (Reich *et al.*, 2003; Kerkhoff *et al.*, 2006). In other words, while tradeoffs might exist between the distinct organs of plants, there is some evidence that these tradeoffs should be rather constrained, as a result of a necessary coordination between, for instance, leaf photosynthesis and root water uptake capacities.

Thus, the way plants have adapted to multiple external (abiotic and biotic) influences is regulated by numerous tradeoffs restricting the range of viable plant strategies. These axes of plant variation across multiple species can be parallel (partly coupled), such as plant size and woodiness, or orthogonal (i.e. largely decoupled), such as between carbon and nutrient economics, plant size or reproductive investment (Westoby, 1998).

THE ‘AFTER-LIFE EFFECTS’ OF PLANT STRATEGIES

(How does vegetation composition drive carbon and nutrient cycling?)

The functioning of an ecosystem in terms of matter pools and cycling can be summarized by considering three different subsystems (Fig. 1; Swift, Heal & Anderson, 1979). Primary producers, possessing photosynthetic organs, assimilate atmospheric carbon and incorporate it into their biomass and thus constitute the base of the cycle. Primary consumers, by feeding on primary producers, and secondary consumers, feeding on the former, extend this cycle to a much more complex pattern. Decomposers, feeding on dead organic matter, recycle it progressively into simple organic compounds and inorganic compounds that may be used by primary producers, closing thus the complex circle of matter fluxes and transformations (Fig. 1).

Primary producers are at the basis of the food chain of most terrestrial and aquatic ecosystems. Thereby, they exert a strong control on organic matter fate and therefore on

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carbon and nutrient cycles. Although plant organic matter can be redirected to other trophic levels through the influence of herbivory, a large part of their carbon and nutrients are directly returned to the decomposition subsystem after organ senescence (Cebrian & Lartigue, 2004). The decomposition subsystem is vital to the cycling of matter and energy in ecosystems for it fulfils two key functions: the degradation and mineralisation of dead organic matter and soil formation (Swift, Heal & Anderson, 1979). These functions determine to a great extent the habitat and available resource for primary producers and consumers (Swift, Heal & Anderson, 1979; Horner, Gosz & Cates, 1988).

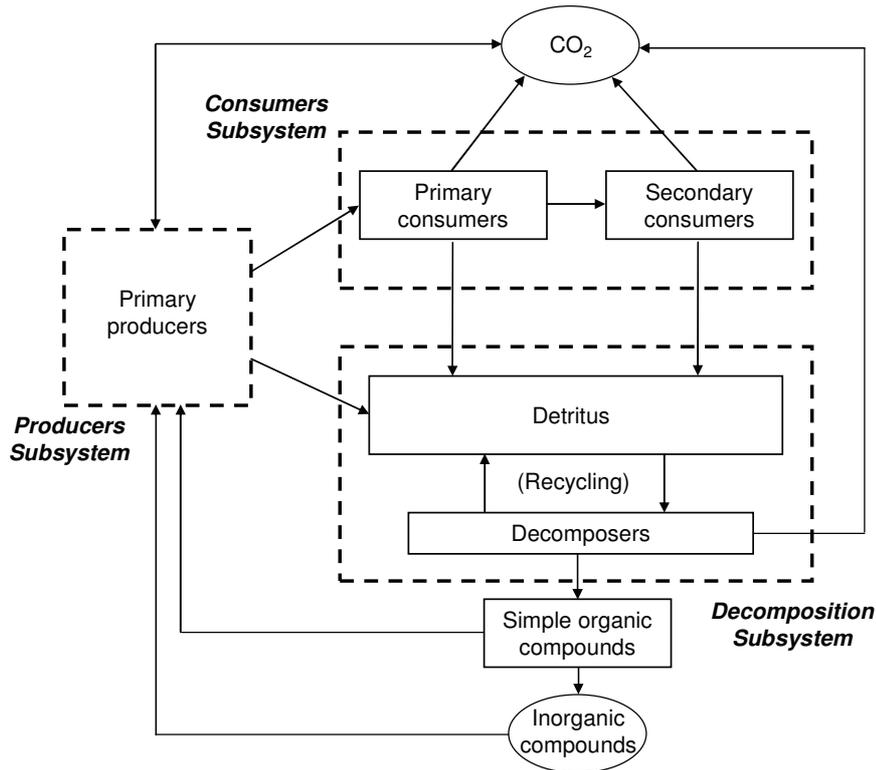


Fig 1. Model of ecosystem structure. Rectangles and ovals represent respectively organic and inorganic matter pools. Arrows represent major matter fluxes. Redrawn from Swift, Heal & Anderson (1979).

Plant growth in natural terrestrial ecosystems is generally N or P limited (Güsewell, 2004). To grow and persist under these regimes of nutrient limitation, plants have developed two main strategies: optimising nutrient acquisition or reducing their losses. Nutrient leaching resistance and nutrient resorption are two important strategies to avoid losses. *Nutrient resorption* is a dynamic, highly regulated process involving exchanges of nutrients and metabolites from organ to organ (Killingbeck, 1986; Aerts, 1996). It potentially occurs all year round, especially in evergreens, but is most pronounced during periods of organ senescence leading to plant dormancy such as in winter in cold climates, and concerns all senescing plant parts (e.g. Aerts & De Caluwe, 1989; Gordon & Jackson, 2000). The resorption process is of great adaptive significance because the resorbed nutrients are directly available for further use (e.g. seed filling, bud growth, storage; Simpson, Lambers & Dalling, 1983; Milla *et al.*, 2005), thereby decreasing a species' dependence on nutrient uptake (Aerts and Chapin 2000). In spring, remobilisation of nutrients from storage organs can lead to (competitive) early regrowth

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of foliage, even before the first release of nutrients from the frozen soil (Thornton and Millard 1993, Millard 1996, Bausenwein *et al.* 2001). *Nutrient leaching* is the passive removal of substances from plants by the action of aqueous solutions, such as rain, dew, fog or surface water (Tukey, 1970). While this process can potentially occur in various plant organs, it is assumed to be stronger – and has been mostly studied – in leaves. It occurs mostly during the latest phase of leaf maturation and during leaf senescence (Tukey, 1966; Tukey, 1970; Morton, 1977). Nutrient resorption and resistance to nutrient leaching impact strongly on both the amount of nutrient returned to the soil and the quality of litter entering the detrital pathway. The quality of litter entering the decomposition subsystem has, in turn, a strong impact on the decomposition process, the general carbon and nutrient turnover and therefore soil properties and nutrient availability in an ecosystem.

The process of litter decomposition usually begins once the organic material has undergone nutrient resorption, senescence and death (Aerts, 1997b). However, there are many exceptions. Leaves of some species may indeed neither experience resorption nor senescence before being abscised (Gessner, Chauvet & Dobson, 1999). Likewise, root external parts may be attacked and decomposed while the core is still functional. Coarse wood may also be damaged and/or attacked locally but stay functional as a whole or even cure or physically protect these vulnerable areas. Although differences exist between plant parts and environments of incubation, the decomposing litter generally undergoes three interacting processes: leaching, microbial establishment and fragmentation (Gessner, Chauvet & Dobson, 1999).

The leaching process consists of passive leaching of soluble material and occurs most strongly during the first few days or weeks after abscission (Brinson, Lugo & Brown, 1981; Webster & Benfield, 1986) before declining gradually with time. *The microbial establishment* represents the process by which dead material is colonized by micro-organism communities (Webster & Benfield, 1986). The composition and relative proportion of fungal and bacterial colonizers depends mostly on litter quality and the incubation environment (Bardgett & Wardle, 2010). This microbial establishment simultaneously leads to litter degradation and its conditioning for invertebrates through processes of tissue softening or nutrient immobilization (Gessner, Chauvet & Dobson, 1999; Parton *et al.*, 2007). *The fragmentation process* consists in the mechanical breakdown of litter by detritivores as well as other animals, plants or abiotic factors. This process both promotes (e.g. by damaging litter protections, such as leaf cuticle) and is promoted by the microbial colonization process, which both softens litter material and favours the presence of ‘shredding’ invertebrates feeding preferentially on microbially transformed material.

Plant strategies (e.g. carbon and nutrient economics) and thus the sets of traits of living plants have large consequences for the decomposition pathway. Notwithstanding inter- and intra-specific variation due to nutrient resorption and processes during senescence (see above), the traits of living plant materials are generally well conserved in litter (Cornelissen, 1996) and strongly control litter decomposition rates (Couteaux, Bottner & Berg, 1995; Cornelissen *et al.*, 1999; Silver & Miya, 2001; Cornwell *et al.*, 2008). A number of chemical plant traits influence litter decay, such as nitrogen, phosphorus or calcium contents (Enríquez, Duarte & Sand-Jensen, 1993; Aerts, 1997a). The nutritional quality of plant material is of major influence on the decomposition process owing to the high nutrient requirement of decomposer organisms relative to the

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generally poor substrates on which they feed (Enríquez, Duarte & Sand-Jensen, 1993; Cebrian & Lartigue, 2004). Structure-related traits can also be important determinants of litter decomposition rates, such as lignin content (Meentemeyer, 1978), physical toughness (Gallardo & Merino, 1993; Cornelissen & Thompson, 1997), specific leaf area (SLA) or dry matter content (DMC) (Garnier *et al.*, 2004; Quedstedt *et al.*, 2007) as they generally reflect the ratio between recalcitrant and soft tissues of litters. Similarly, traits related to defence against herbivores, such as polyphenol content (Horner, Gosz & Cates, 1988; Hättenschwiler & Vitousek, 2000), palatability (Cornelissen *et al.*, 1999) and pH (Cornelissen *et al.*, 2006) also impact on the quality of litters for the decomposer community.

Plant organs usually differ strongly in their decomposition rates. Leaves generally have the fastest decomposition rates, followed by non-woody stems, non-woody roots, woody stems and woody roots, although current evidence is based mostly on studies in which comparisons between organs were confounded with environmental drivers of decomposition rate other than organ traits (Brinson, 1977; Hobbie, 1996; Dearden *et al.*, 2006). Photosynthetic leaves and stems often display fast decay rates, owing to their generally high nutrient and low lignin and complex carbohydrate contents (Hobbie, 1996). In contrast, the decomposition of woody substrates is generally much slower owing to their highly recalcitrant structures and low nutrient content (Harmon *et al.*, 1986; Webster & Benfield, 1986; Cornwell *et al.*, 2009; Weedon *et al.*, 2009), while the low area to volume ratio (or large diameter) of coarse woody litter may also be of great importance (Scheu & Schauermaun, 1994; van Geffen *et al.*, 2010). The physical properties of woody litters, especially the coarse materials, can strongly impact on local biotic and abiotic parameters, influencing thereby the local decomposition processes of other materials (Diez *et al.*, 2002). Thus, the relative investment of plants in different organs also has large consequences for the decomposition subsystem and soil properties and ultimately feeds back on the plants themselves (see below).

Plant strategies also influence the overall plant biomass production and therefore litter production rates. Thus carbon and nutrient acquisitive species produce better quality litter but also larger amounts of litter compared to conservative species (Aerts, 1999; Wardle *et al.*, 2004). Plant strategies thus influence the decomposition pathway in two main ways: through the amount of litter produced, that is, the flux of matter entering the decomposition subsystem, and through litter quality, which largely controls nutrient release rates and overall availability.

PLANT-SOIL FEEDBACKS

(How does vegetation composition feed back on vegetation composition?)

The control of plants on the decomposition subsystem is not unidirectional. As described before (Fig.1), soil processes control, among other properties, water and nutrient availability to plants. These mutual influences between soil and plant properties are the cause of important feedbacks between the two main components of ecosystems (Aerts, 1999; Wardle *et al.*, 2004). However, these close linkages between plant and soil are not only mediated by plant litter or soil nutrient availability but through a variety of mechanisms (Bardgett & Wardle, 2010). These interactions follow both direct and indirect pathways and involve interactions with various organisms such as soil

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detritivores and herbivores as well as a variety of processes such as root exudation and mycorrhizal associations.

At the ecosystem level, these feedbacks can either lead to the stabilisation of environmental conditions or trigger progressive and profound changes that may lead to changes in vegetation composition (Aerts & van der Peijl, 1993; Berendse, 1994; Nilsson & Wardle, 2005). For instance, plants of fertile environments generally display traits promoting quick acquisition of resources, while plants living in nutrient-poor habitats mainly favour traits decreasing nutrient loss (Aerts, 1999; Díaz *et al.*, 2004), thereby both creating a positive feedback on nutrient cycling. As a consequence, litter of fertile environments usually contains more nutrient and less recalcitrant compounds than litter of less fertile environments. They are also responsible for larger organic matter inputs to the soil. Thus, in nutrient-rich habitats, higher litter input and quality generally leads to larger and quicker nutrient release for plant uptake than in nutrient-poor habitats where low litter input and quality maintain low nutrient availability.

AIMS AND OUTLINES OF THE THESIS

The main aim of this thesis is to investigate the hypothesized existence of a '*Plant economics spectrum*' (PES), which involves close relationships between the economic strategies of plants' main vegetative organs (leaves, stems and roots) and to explore the impact of such relationships on carbon and nutrient cycling in a model system (see below). The current literature on plant strategies and their ecosystem consequences is strongly based on evidence from leaf traits and reproductive traits, with generally strong bias against the contributions of non-leaf vegetative organs. This thesis aims to improve this balance by adopting an explicit whole-plant approach to carbon and nutrient dynamics of living and dead organs.

More specifically, this thesis addresses the following research questions: (A) how do species assembly rules drive plant trait spectra across widely varying spatial scales and geographic areas, (B) whether plant species have an integrated economic strategy across organs, (C) how do 'after-life effects' of those plant traits and strategies drive carbon and nutrient cycling and (D) feed back on species assemblages (Fig. 2). The general outline of the thesis, and the approach to these four questions, is as follows.

Question (A) was addressed in **Chapter 2** where I looked into the mechanisms of species assembly at the global scale. Specifically, I investigated the scale dependency of leaf functional diversity and tested the hypothesis that "*the impact of species assembly drivers on the leaf functional diversity of species assemblages differs across scales and across geographic areas*". To that end, I used a hierarchically structured dataset (spanning global, regional, community, species and individual scales) of two model leaf functional traits. (In a complementary study (Liu *et al.*, 2010), not included as a chapter here, we followed a whole-plant approach to a complementary question, i.e whether and how interspecific variation in aboveground (leaf) traits was coordinated with that of belowground (root) traits at different spatial scales in Northern China.)

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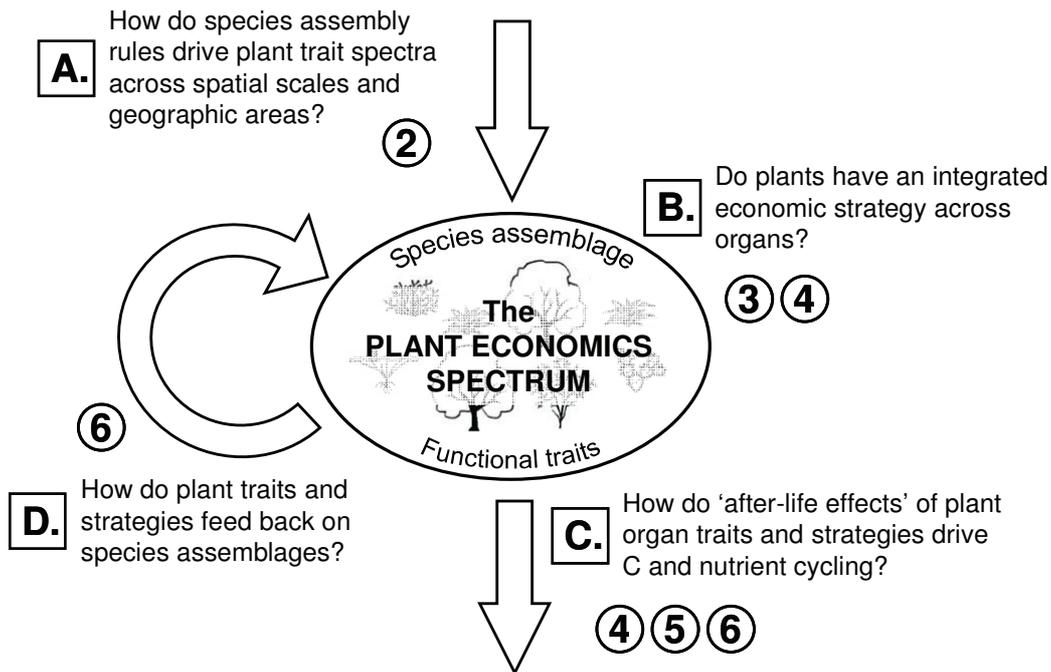


Fig. 2. Schematic representation of a plant assemblage and its local 'Plant economics spectrum' (A) under influence of 'species assembly rules', (B) where distinct plant strategies (involving coordinated strategies across vegetative organs) can coexist which (C) impact on the functioning of the system (such as carbon and nutrient cycling) through 'after-life effects' of plant organ traits and strategies drive C and nutrient cycling with (D) potential feedbacks on plant assemblage. Numbers (2-6) indicate the respective chapters of this thesis that relate to each of the four main questions (A–D).

Question (B) was specifically addressed in Chapter 3, where I studied the carbon and nutrient economic strategies of the plant's main vegetative organs, and in Chapter 4 where I investigated the nutrient dynamics during plant senescence in the same organs. In **Chapter 3** I explicitly tested the hypothesis that "*within plant species, leaf, fine stem and fine root resource economics are correlated, reflecting an integrative whole-plant economic strategy*" and enquired whether environmental features could explain a significant part of the variance in plant functional trait variations across distinct co-occurring ecosystems. For the purpose of that study I sampled living leaves, fine stems and fine roots of the dominant vascular plants of my model system and measured the same group of functional traits on each material. Each ecosystem was also measured for soil fertility and other relevant environmental parameters.

In **Chapter 4** I investigated the process of plant senescence in the main vegetative organs of plants. I thus compared the range of resorption efficiency/proficiency occurring in leaves, fine roots and fine stems and the relative importance of resorption and leaching on leaf nutrient losses during leaf senescence and tested the hypothesis that "*organ resorption efficiency/proficiency and leaching resistance are correlated with other organ traits related to plant nutrient economics*". To do so, I measured and related mature and shed organ nutrient contents and quantified experimentally leaf leaching resistance using both laboratory and field experiments. (In a complementary study (Lü *et al.*, 2011), not included as a chapter here, we also investigated whether micro-scale variation in soil nitrogen availability drove plasticity in plant organ nitrogen resorption in a semi-arid steppe of Northern China.)

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Question (C) was addressed in Chapters 4, 5 and 6. In **Chapters 5 and 6** I investigated the ‘after-life effects’ of plant strategies on the decomposition processes and rates of their distinct organs. In the former, I specifically tested the hypotheses that “*wood decay dynamics differ across woody debris species*” and “*woody decay rates are largely controlled by wood traits*”. In the latter, I tested the hypotheses that “*the decomposability of distinct plant organs is controlled by interspecific variation in the same functional traits*” although “*the relative influence of these traits shifts across organs*”. To that end, I incubated litter from leaves, reproductive parts, fine stems, fine roots, coarse stems and coarse roots of the dominant plants of my model system in a common environment to determine their respective decomposition rates. Long-term decomposition of coarse stems and roots was investigated by a new method that allowed long-term estimations of their decomposition dynamics and rates from short-term incubations. Some insights into question (D) are discussed in Chapter 6.

In the closing **Chapter 7** of this thesis I connect the most important results of each previous chapter to the research questions that they address (Fig. 2, A – D) and discuss their relevance with respect to the state-of-the-art in the literature.

Sub-arctic ecosystems as model system

I investigated my research questions in subarctic ecosystems of northern Sweden. Despite their remoteness, these ecosystems have the advantage that they are relatively simple and are not disturbed by human activities. The only exception is Chapter 2, which is based on the analysis of datasets from multiple floras across multiple climatic zones of the globe. Nevertheless, Chapter 2 helps to understand the different environmental filters determining the extant regional or community species (and trait) pool such as the subarctic one studied here.

For the other chapters, all plant material collection and experimental setup took place around the Abisko Research Station, North Sweden (68°21’N, 18°49’E) within the low altitude (350-400 m a.s.l.) forested area. Climatic data from the recent decade (1999-2008) showed a mean annual rainfall of 352 mm and mean January and July temperatures of -9.7 and 12.3 °C, respectively, with average daily temperatures ranging from -39.0 to 21.3 °C (meteorological data, Abisko Research Station). The forested area that I studied features Podsol soils (Sjögersten & Wookey 2002) and covers most of the landscape below 700-800 m a.s.l. except for occasional swamps and peatlands. While acknowledging the variability of natural areas and their multiple interfaces, I restricted my study to the three most contrasting ecosystem types within the chosen forests: upland dry birch forest, riparian birch forest and forest-surrounded freshwater systems (ponds and streams). Throughout the Abisko valley, forests are dominated by polycormic mountain birch trees (*Betula pubescens* Ehrh. *ssp. czerepanóvii*), whether in dry or wet areas. Four other deciduous tree species and one evergreen are nevertheless found within the area. *Pinus sylvestris* (L.) and *Populus tremula* (L.) are characteristic of the dry forest, while *Salix caprea* (L.), *Sorbus aucuparia* (L.) and *Alnus incana* (L.) are mainly found in riparian areas. Following two successive severe tree defoliations by caterpillars of the moth *Epirrita autumnata* in 1954 and 1955, which killed a large number of birch stems, the forested area of Abisko valley consist mainly of rejuvenated stands of resprouted birches of low stature (Tenow *et al.*, 2004).

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