

CHAPTER 7

General discussion and summary



Litterbags in a stream, near Abisko research Station

As described in Chapter 1, this thesis focuses on answering four main 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) how do these after-life effects feed back on species assemblages (Chapter 1, Fig. 2). In Chapter 3 through 6 I answered some aspects of those questions separately. Here, I summarize the main results of each previous chapter and connect them to the general research question that they address (A – D) and identify some aspects emerging from my research that would require further investigation.

HOW DO SPECIES ASSEMBLY RULES DRIVE PLANT TRAIT SPECTRA ACROSS SPATIAL SCALES AND GEOGRAPHIC AREAS?

While species assembly rules act from the global scale to the individual plant, most studies have focused on the assembly of plant communities from regional pools of species. Therefore, relatively little was known about their absolute and relative importance across different spatial scales and geographically distinct areas with different surrounding species pools (Willis *et al.*, 2010). In Chapter 2 I demonstrated that the convergence of leaf trait values occurring among species from global to regional assemblages can be twice as strong as that from regional to community assemblages, stressing thereby the need to extend species assembly study beyond its usual scope. Whether this overall convergence pattern is due to stronger mechanisms of trait convergence or weaker mechanisms of trait divergence at higher scales still needs to be resolved, as convergence and divergence add up along a continuum of interspecific trait variation.

Another important finding of Chapter 2 is the large variation observed in the relative importance of distinct drivers of major species assembly across scales and geographic areas. Thus, while trait convergence generally predominates over trait divergence from global to community scales, their outcome was highly variable across climatic zones (Chapter 1, Fig. 2 A). However, the approach I used in Chapter 2 could not disentangle the respective influences of different drivers of trait assembly. Complementary approaches are thus needed to get a stronger mechanistic understanding of convergence and divergence drivers across scales and geographic areas (e.g. Cornwell & Ackerly, 2009; Laliberté & Legendre, 2010).

Finally, a large range of leaf trait values was observed within all studied plant communities, indicating that contrasting plant strategies co-occurred within any environment type. The large and continuous range of carbon and nutrient economics strategies observed in Chapter 3 within our subarctic ‘model system’ is consistent with this general pattern in plant traits and strategies. However, while plant economic strategy may be relatively variable within most ecosystem types, species assembly rules most certainly act also upon other axes of plant specialisation (e.g. reproductive strategy, plant height; Westoby, 1998). Indeed, the worldwide observation of recurrent predictable associations between plant species assemblages and environmental conditions (e.g. Rodwell, 1991) suggests that the rather loose filtering of several orthogonal axes of plant specialisation can possibly lead to a strongly constrained assemblage of species. This still needs to be tested.

DO PLANTS HAVE AN INTEGRATED ECONOMIC STRATEGY ACROSS ORGANS?

The existence of a fundamental tradeoff among vascular plants between traits inferring rapid resource acquisition and those leading to resource conservation is now widely accepted, but is based on empirical data with a strong bias towards leaf traits, with additional focus on size descriptors and reproductive traits (Grime *et al.*, 1997; Reich, Walters & Ellsworth, 1997; Westoby, 1998; Díaz *et al.*, 2004; Wright *et al.*, 2004). In Chapter 3 I showed that within my subarctic model system each vegetative plant organ (leaves, fine stems, fine roots) seems to be constrained by the same tradeoff, owing to direct and indirect mutual dependencies between these traits (Reich *et al.*, 2003; Chave *et al.*, 2009; Elser *et al.*, 2010). While tradeoffs in leaf traits are likely to stem from (1) a necessary tradeoff between allocation to structural tissues versus liquid phase processes and (2) an evolutionary tradeoff between leaf photosynthetic rates, construction costs, and leaf longevity (Shipley *et al.*, 2006), relatively little is known on the origin of fine stem and fine root tradeoffs. It seems rather intuitive that the ‘cell volume’-‘cell wall thickness’ tradeoff identified in leaves (Shipley *et al.*, 2006) could also underpin similar tradeoffs found in fine stems and fine roots, but this still needs to be investigated empirically.

The few studies that had investigated trait covariation between above- and below-ground organs revealed promising but partly inconsistent relationships (e.g. Kerkhoff *et al.*, 2006; Withington *et al.*, 2006). In Chapter 3 I showed that the main vegetative ‘fine’ and relatively short-lived organs of plants (leaves, fine stems, fine roots) have largely coordinated strategies with respect to carbon and nutrient economics, as indicated by the across-organ correlations of a number of underlying traits (carbon, lignin and dry matter contents, C:N ratio, pH, nitrogen content), likely due to plant physiological, ontogenetic and allometric constraints (Niklas & Enquist, 2002; Wright *et al.*, 2006; but see Baraloto *et al.*, 2010 for decoupling of coarse wood and leaf traits among tropical trees). Thus, subarctic plants have an integrated strategy with respect to carbon and nutrient acquisition and conservation, reflecting a local ‘plant economics spectrum’ (Chapter 1, Fig. 2 B). This implies that plant species that develop strong leaf defences (for instance against herbivores) are likely to also display strong belowground defences. Similarly, efficient photosynthetic capacities may go pairwise with efficient nutrient uptake strategy. These findings thus support the view that evolution works on the entire plant rather than just on isolated organs (e.g. Reich *et al.* 2003; Kerkhoff *et al.* 2006). My work was however largely based on chemical traits whose roles as proxy for root and stem functions need yet to be clarified. Some steps need to be taken to more accurately demonstrate the link between for instance nutrient absorption capacity by roots and leaf photosynthetic capacities or between the conductance capacity of each vegetative organ (e.g. Wright *et al.*, 2006). Generally, this work still needs to be extended to other traits and further tested on other floras and biomes across the world. It also needs to be extended to coarse wood and roots of shrubs and trees, which play crucial roles in plant growth and defence that are central to the ‘plant economics spectrum’ but may well be partly orthogonal (Baraloto *et al.*, 2010) to the nutrient and carbon economics of other vegetative organs.

The functional significance of most plant traits is well established for terrestrial plants, but this is less so for freshwater plants. While the function of chemical traits such as nitrogen, phosphorus and lignin contents or C:N ratio is relatively consistent across the terrestrial-aquatic boundary (Nielsen *et al.*, 1996; Hanley *et al.*, 2007), the function of other traits, such as dry matter content, needs to be considered with caution. In Chapter 3 I showed that freshwater plants seem to be constrained by the same tradeoff as terrestrial plants both within and between organs. However, whether these consistent tradeoffs across terrestrial and freshwater plants strictly reflect the same compromise between acquisition and conservation of resources needs to be investigated further. For instance, gravitational downward forces as experienced by any terrestrial plant are at least partly offset by upward forces of the water body in the direct environment of aquatic plants, with obvious consequences for their physical design.

In contrast to these findings, I showed in Chapter 4 that one of the most efficient ways of conserving resources, nutrient resorption during senescence, was not coordinated across plant organs (Chapter 1, Fig. 2 B). Besides, organ nutrient resorption efficiency was generally uncorrelated with the main organ economic strategy axis as revealed through principal component analysis (Chapter 3). Although these findings still cannot be generalized to other floras and biomes, they shed light on a long debated question: ‘are resorption processes dependent on other plant strategic adaptations?’ (Pastor, Stillwell & Tilman, 1987; Kobe, Lepczyk & Iyer, 2005). Two factors potentially explain the strikingly poor link in the subarctic flora studied here. First, nutrient resorption is of tremendous importance in plant economics to most perennial plants, irrespective of the position on the phylogenetic tree and irrespective of the environment (Aerts, 1996; Killingbeck, 1996). Second, resorption processes are influenced in many, often counteracting ways by multiple physiological factors related to organ carbon and nutrient economics, each with their own adaptive value in evolutionary selection.

HOW DO ‘AFTER-LIFE EFFECTS’ OF PLANT ORGAN TRAITS AND STRATEGIES DRIVE CARBON AND NUTRIENT CYCLING?

While at large geographical scales leaf litter decomposition rates are strongly determined by climate (Berg *et al.*, 1993; Parton *et al.*, 2007) and community composition of soil organisms (Lavelle *et al.*, 2006), local-scale interspecific variation in litter quality (‘species identity’) is their predominant driver (Cornwell *et al.*, 2008). Indeed, structural and chemical leaf traits have ‘after-life effects’ on litter decomposability (Cornelissen *et al.*, 2004). Some evidence exists that interspecific variation in litter quality is also the predominant driver of root litter decomposition (Silver & Miya, 2001) and the huge range in wood functional trait values (Chave *et al.*, 2009) and within-site wood decomposition rates (Harmon *et al.*, 1995; van Geffen *et al.*, 2010) suggests that similar pattern may exist for plant stems too. However, owing to the lack of an appropriate method to study long-term decomposition of slowly decomposing materials such as woody stems and roots (summarised as coarse woody debris), much remains to be done in order to disentangle the respective roles of species-specific factors, interacting abiotic factors and decomposer communities on their turnover rates. In Chapter 5 I presented a new short-term method allowing for long-term estimations of decomposition rates. This new method opens up promising perspectives for comparing

decay dynamics of slow and fast decomposing materials (e.g. Chapter 6) and distinguishing between environmental and intrinsic effects. Using this method, I showed that wood decay dynamics (and thus probably its underlying processes too) differed across species and that some structural and chemical features (lignin content, dry matter content, pH) of woody stems and roots have a strong influence on their decomposition rates (Chapter 1, Fig. 2 C). While previous studies have shown the influence of wood traits on decomposition rates, those predictions were generally based on short-term incubations or the multiple and changing interactions between species and their environment in chronosequence studies (Weedon *et al.*, 2009; van Geffen *et al.*, 2010). Besides, Chapter 5 represents the first study to accurately describe species-specific differences in wood long-term decomposition dynamics.

As seen in Chapter 4, interspecific variation in traits of living plant vegetative organs and that of organ litter tend to be strongly correlated. However, with only few studies available on interspecific variation in the decomposability of stems (Chambers *et al.*, 2000; Weedon *et al.*, 2009) and roots (Silver & Miya, 2001; Vivanco & Austin, 2006), we still did not know whether the traits underpinning decomposition rates, or their relative contributions, have the same effect across plant parts. While it seems likely that the same traits have broadly similar effects on litter decomposition of distinct plant organs, differences in the magnitude of their impact are likely. In Chapter 6 I showed that the same structural traits (lignin, carbon and dry matter content) consistently predict decomposition rates across different plant organs while the influence of chemical traits is rather variable between organs. This pattern extended over both terrestrial and freshwater plant species. Nevertheless, I observed consistent elevation shifts in the relation between decomposition rates and traits across organs, which could stem from additive effect of other traits than those commonly measured in literature but also to the changing ecological or physiological function of some traits across organs. Further studies are needed to understand the underlying causes of those shifts. Among others, the role of differences in organ structure and function should be investigated. For instance, the distribution of lignified structures throughout plant tissues or the different forms of organic nitrogen between plant organs may partly explain those shifts in decomposability. The differences in area-to-volume ratio of different fine and coarse organs may also play a role in the shifts in the elevation of trait-decomposition regressions.

As seen in Chapter 3, empirical evidence is growing that plant species possess integrated strategies across their organs with regard to carbon and nutrient economy, which are moreover robust to geographical scaling (Kerkhoff *et al.*, 2006; Liu *et al.*, 2010). In Chapter 6 I showed that a proxy for whole-plant economic strategy, as defined by the principal PCA axis determined by multiple traits of multiple subarctic species, could consistently predict interspecific differences in decomposition rates for each plant vegetative organ. Taken together, these two observations explain the coordinated interspecific variation in decomposition rates between plant vegetative organs revealed in Chapter 6, providing the first empirical evidence of a ‘plant economics spectrum of litter decomposition’. Thus, at the whole-plant level, physiological and allometric interactions between organs (e.g. Wright *et al.*, 2006; Maire *et al.*, 2009) lead to coordinated trait variation across organs (Chapter 3; Kerkhoff *et al.*, 2006) which in turn drive coordinated organ decomposabilities. The generality of such coordination in organ decomposability needs yet to be further tested on other floras. Nevertheless, these

findings constitute the first step towards a potential re-evaluation of how plants control biogeochemical cycling after organ death (Chapter 1, Fig. 2 C).

While we know that litter traits, large scale differences in climate and the presence of particular types of soil organisms are the three strongest drivers of litter decomposition (Meentemeyer, 1978; Aerts, 1997; Silver & Miya, 2001; Cornwell *et al.*, 2008), much less is known on the relative importance of micro-climatic influences and local changes in decomposer community composition. Besides, substantial interactions might exist between litter quality and those local drivers of litter decomposition (Hunt *et al.*, 1988; Prescott *et al.*, 2000; Ayres *et al.*, 2009). Complementary to the common-garden approach used in Chapter 6, it would thus be interesting to explicitly compare decomposition rates of a wide range of litter types across my three subarctic ecosystems (dry birch forest, riparian birch forest and forest-surrounded ponds). Although not included in this thesis, I performed this set of *in-situ* decomposition experiments (Grégoire T. Freschet, Rien Aerts, Johannes H. C. Cornelissen, manuscript in preparation) and found that the role of traits as drivers of litter decay rates was consistent over terrestrial and freshwater incubation environments, suggesting strong similarities between the two contrasting types of decomposition subsystem (see Chapter 1). I also demonstrated that litter traits and the incubation matrix (including abiotic and biotic factors) had similar impacts on leaf litter decay rates. In contrast, litter traits had much stronger influence on fine stem and fine root litter decay rates than the incubation matrix. Although of relatively lower significance than the two other factors, the interaction between litter quality and incubation matrix quality had a substantial impact on leaf, fine stem and fine root litter decay rates. Thus, plant traits also have an indirect control on litter decay rates, and therefore on carbon and nutrient cycling at the ecosystem scale (Chapter 1, Fig. 2 C).

HOW DO PLANT TRAITS AND STRATEGIES FEED BACK ON SPECIES ASSEMBLAGES?

At the ecosystem level, the strong coupling between plant strategy and organ decomposability revealed in Chapter 6 yields considerable implications for plant control over soil processes. While litter decomposition is the main biotic driver of biogeochemistry at short time scales, including nutrient turnover and immobilization, soil formation, atmospheric composition and soil properties, those, in turn, have been shown to have strong feedback effects on plant performance and thus on plant community assembly (Aerts, 1999; Wardle *et al.*, 2004). The coordinated litter decomposabilities across species' organs imply a coordinated impact of plant aboveground and belowground litters on the direction and magnitude of this potential feedback loop. Thus, at the plant scale, nutrient acquisitive plants, which generally produce higher litter input and quality, should induce larger and quicker nutrient release for plant uptake not only from their leaf litter (Hobbie, 1992) but also from their stem and root litter compared to nutrient conservative plants. At the ecosystem scale such coordination in plant organ decomposability might thus promote soil fertility patchiness and promote therefore plant specific and functional diversity at small spatial scales (Chapter 1, Fig. 2 D). However, whether the impact of this whole-plant decomposability coordination is substantial with regards to soil properties still needs to be investigated. Considering the substantial differences found in organ traits (Chapter 3), organ

resorption efficiency (Chapter 4) and between organ decomposabilities (Chapter 6), both the total and the relative fluxes of litter inputs from each organ could indeed be an even stronger control on soil properties and ecosystem biogeochemistry.

CONCLUSIONS

Understanding how selection operates to create current plant assemblages adapted to the contrasting environments they are living in and how they transform their environment and trigger potential feedbacks on plant assemblages are three major aims in ecology.

In this thesis, I modestly but significantly contributed to answering these questions by studying subarctic ecosystems in a whole-plant perspective, thus looking at leaves, stems and roots simultaneously where most studies generally focused on one organ separately, principally leaves. I showed that, from global to community scales, the outcome of trait convergence and divergence mechanisms was highly variable across scales and climatic zones but consistently led to relatively large trait variance in local plant communities (Chapter 1, Fig. 2 A). Consistent with that, I identified within my 'model system' a wide range of plant carbon and nutrient economic strategies which formed a local 'plant economics spectrum', representing consistent tradeoffs in economics traits both within and across the main vegetative organs of plants (leaves, fine stems and fine roots) (Chapter 1, Fig. 2 B). Across those same species, I demonstrated that during their respective senescence phases all plant vegetative organs displayed substantial resorption rates. Despite their key role in plant nutrient economics, these rates of organ nutrient resorption were nevertheless poorly related to other important aspects of plant economics. As most living plant traits were relatively well conserved during plant senescence and generally showed a consistent impact on litter decomposability across all vegetative organs of plants, I observed a coordinated interspecific variation in decomposability of these different plant organs. This after-life effect of the local 'plant economics spectrum' has potentially large consequences for carbon and nutrient cycling at both the plant and the ecosystem scales (Chapter 1, Fig. 2 C). The impact of coordinated plant organ decomposability on soil processes may further influence plant community assemblages (Chapter 1, Fig. 2 D). The relationships underpinning the afterlife effects of the plant economics spectrum on whole-plant litter decomposability will help to improve the predictions of terrestrial carbon pools and fluxes, also in ecosystems changing in species composition, e.g. in response to natural succession, climate or land-use change. This and other advances in our understanding of vegetation composition feedbacks to soil carbon turnover are urgently needed in next-generation global models linking carbon dynamics to climate, now and in the future.

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