

Ecological Significance of Within-Species Leaf Trait Variability: A Test Using an Island Area Gradient

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The Ecological Significance of Within-Species Leaf Trait Variability: A Test Using an Island Area Gradient

Abstract

There is growing recognition of the need to incorporate within-species trait variability into trait-based studies to improve understanding of community assembly and how plant communities drive ecosystem processes. Given that many plant species can occupy a wide range of environmental conditions, studies that have traditionally focused solely on between-species trait variability and neglected within-species trait variability could lead to an incomplete picture of how plant traits influence community- and ecosystem-level properties. In this thesis, within-species trait variability of all component species across a well-studied system of 30 forested lake islands in the boreal zone of northern Sweden were characterized to understand how differences among individual species traits contribute to community level properties and community assembly. Collectively, the islands represent a long-term chronosequence across which there are large changes in plant community composition, diversity and above- and belowground resource availability and heterogeneity. Significant within-species trait variability was found among all dominant species that were widespread across the chronosequence. In addition, within-species trait variability was highly responsive to differences in environmental conditions among ecosystems, in a manner mostly consistent with patterns observed at the across- species level. Across contrasting environments, trait variability within species sometimes explained a greater amount of variation in overall community-level responses than did among-species variation. There was also significant within-species variation in biomass allocation patterns of co-occurring dominant dwarf shrub species across the chronosequence. This, together with directional shifts in within- and between-species functional trait diversity of both dominant and subordinate species across the gradient, provides insights on how changes in resource availability drive community trait composition, species coexistence and consequently community responses. These findings overall highlight the importance of within-species variability for understanding the responses of whole plant communities to environmental changes, and potentially to ongoing global changes. Further, given the importance of plant traits in governing ecosystem processes such as net primary productivity, carbon sequestration,

biogeochemical cycling and decomposition, knowledge of the extent and magnitude of within-species trait variability is imperative for better understanding these processes and their drivers, especially in ecosystems with low species diversity and turnover such as boreal forests.

Keywords: chronosequence, community assembly, foliar traits, functional diversity, nutrient resorption, soil heterogeneity, species diversity, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, variance partitioning

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Dedication

To my mum Grace, wife Dela and son Kekeli

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Kumordzi, B. B., Nilsson, M. C., Gundale, M. J. & Wardle, D. A. (2014) Changes in local-scale intraspecific trait variability of dominant species across contrasting island ecosystems. *Ecosphere*, 5, Article 26.
- II Kumordzi, B. B., Gundale, M. J. Nilsson, M. C. & Wardle, D. A. Shifts in aboveground biomass allocation patterns of dominant shrub species across a strong environmental gradient. *Submitted manuscript*.
- III Kumordzi, B. B., Wardle, D. A. & Freschet, G. T. (2015) Plant assemblages do not respond homogenously to local variation in environmental conditions: functional responses differ with species identity and abundance. *Journal of Vegetation Science*, 26, 32-45.
- IV Kumordzi, B.B., de Bello, F., Freschet, G.T., Le Bagousse-Pinguet Y., Lepš, J. & Wardle, D.A Linkage of plant trait space to successional age and species richness in boreal forest understory vegetation. *Journal of Ecology* (in press). doi: 10.1111/1365-2745.12458

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1 Introduction

1.1 Linking plant traits with function

Plant functional traits (PFTs) refer to morphological, physiological or phenological characteristics that impact fitness, responses to and effects on the environment (Diaz & Cabido 2001, Violle *et al.* 2007). Global studies of plant species have found consistent evidence for a trade-off between traits associated with resource acquisition (i.e. adaptation to resource-replete habitats) and those associated with resource conservation (i.e. adaptation for resource-poor habitats). As such, plants that are adapted to fertile sites often have a set of traits associated with faster growth, high nutrient acquisition and high litter quality (e.g., high specific leaf area (SLA) and leaf N and P-content and low amount of phenolic compounds) relative to those adapted to infertile sites that produce more recalcitrant organic material (Wardle 2002, Diaz *et al.* 2004, Freschet *et al.* 2010, Lagerström *et al.* 2013). This trade-off holds up across several contrasting groups of plants and at a global scale (Diaz *et al.* 2004, Wright *et al.* 2004).

Several recent studies in plant ecology have shown that plant traits can show immense variation even at local scales within plant communities (Hattenschwiler *et al.* 2008; Richardson *et al.* 2008; Jung *et al.* 2010). For instance, Cornwell *et al.* (2008) showed that at such scales, trait variation could sometimes be more important than climate in driving ecosystem processes such as plant litter decomposition. Variability in plant functional traits in response to environmental conditions can therefore be useful indicators of plant performance and fitness in contrasting environments. Understanding such trait variability may be essential for predicting patterns of community assembly (Jung *et al.* 2010; Paine *et al.* 2011; Siefert 2012) as well as for describing species contributions to ecosystem processes (Violle *et al.* 2007; Cornwell *et al.* 2008; Wardle *et al.* 2009).

1.2 Ecological importance of within-species trait variability

The vast majority of studies on plant trait variability in local communities (i.e. at scales of meters to tens of meters) have focused on between-species trait variability, because this has long been seen as the main component of plant community response to changes in environmental conditions (Garnier *et al.* 2001, McGill *et al.* 2006, Ackerly & Cornwell 2007). In such studies, trait values for each species within a community are often represented by a single mean value (e.g. Diaz *et al.* 2004, Wright *et al.* 2004), without recognition of the substantial variability that may exist within any given species. However, given that many plant species can occupy a wide range of environmental conditions, it appears that focusing solely on between-species trait variability and neglecting to consider the role of within-species trait variability could lead to an incomplete picture of the overall importance of plant traits in influencing community- and ecosystem-level properties (e.g., Albert *et al.* 2010a, Jung *et al.* 2010, Bolnick *et al.* 2011, Violle *et al.* 2011, Jackson *et al.* 2013, Kichenin *et al.* 2013). For instance, it has been suggested that high within-species trait variability may be characteristic of species that are dominant in environments with a high level of resource heterogeneity (Sultan 2000, Valladares *et al.* 2007) or in communities with low species diversity (Silvertown *et al.* 2009), for example *Metrosideros polymorpha* in the montane forests of Hawaii (Treseder & Vitousek 2001). Consequently, within-species trait variability may be an important alternative mechanism by which plant communities respond to local scale heterogeneity (Sultan 2000), and could help explain the absence of species diversity-heterogeneity relationships found in some studies (e.g., Gundale *et al.* 2011). Therefore, evaluating the magnitude and extent of local scale within-species trait variability may provide greater insights into community assembly processes in different ecosystems than is possible through considering only mean trait values for each species (Jung *et al.* 2010, Siefert 2012), and could also improve our understanding of trait-driven processes, such as plant litter decomposition and nutrient dynamics of ecosystems (Madritch & Hunter 2002, Schweitzer *et al.* 2004, Wardle *et al.* 2009, Jackson *et al.* 2013).

1.3 Variability in biomass allocation and community productivity

An important goal in global change ecology is to understand mechanisms through which environmental change affects ecosystem productivity (Thuiller *et al.* 2008). Plants allocate resources among different organs and this allocation can vary greatly among both plant species and environmental

conditions (Poorter *et al.* 2012, Freschet *et al.* 2013), however, the majority of work on allocation among plants has focused on allocation to shoots versus roots (e.g. Brouwer 1963, Iwasa & Roughgarden 1984, Kruse *et al.* 2010). Aboveground, however, plants allocate resources to organs that provide different functions, including leaves, stems and reproductive structures (Kröner 1994, Poorter & Nagel 2000, Bazzaz *et al.* 2000). As such, plants vary their investment in leaf versus stem material because there is a trade-off between allocation to leaves for maximizing light capture and thus photosynthetic gain, and allocation to stems for hydraulic conductance, supporting plant weight and resisting disturbances (Yagi 2000, Tandeia & Tateno 2004). Further, allocation patterns between vegetative (i.e. stem and leaves) and sexual reproductive organs may vary because of trade-offs between the need for carbon gain and the need to produce propagules to maintain future populations (Abrahamson 1979; Kozlowski 1992; Bazzaz *et al.* 2000). Therefore, analysing how the different fractions of aboveground shoot biomass [i.e. the proportion of total biomass produced allocated to stem (SMF), leaves (LMF) or sexual reproductive organs (RA)] varies within- and between-species, and at the community levels offers an objective way of linking plant biomass investment to different functions under contrasting environmental conditions (Poorter & Nagel 2000; Poorter *et al.* 2012). Further, assessing variations in biomass allocation patterns within- and between-species can help in predicting environmental influences on plant community and ecosystem productivity. Such knowledge is important for understanding how community assembly, trait spectra, and ecosystem processes driven by the plant community, vary across environmental gradients and among contrasting ecosystems.

1.4 Functional trait diversity, community assembly and species coexistence

Functional diversity (FD) may refer to the number of functional groups present in a community (Diaz & Cabido 1998) or the variation in the functional characteristics among species (Petchey & Gaston 2002, Mason *et al.* 2003). When trait based approaches are used, the functional diversity of plant communities can also be described in terms of functional richness, evenness and divergence (Mason *et al.* 2005, Vileger *et al.* 2008, Albert *et al.* 2011, Mason & Mouillot 2013). Generally, functional richness describes the amount of niche space coexisting species occupy and is therefore an indication of potentially used and unused niche space. Functional evenness describes the degree to which the biomass of the community is homogeneously distributed in

niche space, and functional divergence indicates the degree of resource differentiation and thus competition between coexisting species (Mason *et al.* 2005). Consequently, the components of functional diversity (i.e., richness, evenness, divergence) of a community reflects the way it uses resources, in a manner that is analogous to the functional trait of an individual reflecting the individual's resource use. Understanding how different components of functional diversity change with environmental conditions is an essential step in trait-based ecology as it helps shed light on patterns of community response and possible mechanisms that underlie species coexistence such as competition, facilitation, complementarity of resource use (Mason *et al.* 2013).

Further, recent methodological advances in trait-based ecology have provided useful frameworks to understand how functional trait diversity within- and between-species can affect community assembly (Mason *et al.* 2005, Vileger, Mason & Mouillot 2008; Ackerly 2009; Lepš *et al.* 2011, Mason *et al.* 2011) and how environmental drivers influence these functional diversity components (Le Bagousse-Pinguet *et al.* 2014). For instance, Violle *et al.* (2012) proposed a method of trait variance decomposition both within- and between-species that enables assessment of how the trait breadth of coexisting species varies across different communities. This method uses the $T_{IP/IC}$ metric, i.e. the ratio of trait variance within single species belonging to a community relative to the total trait variance of that community. Low values of $T_{IP/IC}$ generally indicate communities with low trait overlap, which in turn suggest increased niche packing between species (Violle *et al.* 2012), i.e. the tendency for coexisting species to fill available niche space along important niche dimensions. The $T_{IP/IC}$ metric is therefore advantageous in that it measures an overall overlap in functional trait space within a community, which can be related to niche-based assembly processes. A further benefit of this metric is that when it is decomposed into its components, it allows for simultaneous examination of how different components of community functional diversity (i.e., within- and between-species trait variation) respond to environmental changes or along gradients (Le Bagousse-Pinguet *et al.* 2014). Taken together, by assessing the pattern of within- and between-species functional diversity responses to variation in belowground and aboveground environmental conditions, this thesis seeks to provide insights into how these responses contribute to processes that structure plant communities across various scales (Mason *et al.* 2012; Poorter *et al.* 2012). Further, it examines the ways plant communities may respond to environmental change (Thuiller *et al.* 2008) and, ultimately, the impact that plant communities have on ecosystem processes and functions (Lavorel & Garnier 2002).

1.5 Objectives

The aim of this thesis is to understand within-species leaf trait variability and its ecological significance in community assembly and ecosystem functioning (Fig. 1). This is done using a well-characterized boreal system of 30 forest lake islands located in northern Sweden that collectively represent a long-term chronosequence across which plant community composition and diversity and above- and belowground resource availability and heterogeneity change (Figs. 2&3). Paper I characterizes changes in within-species variability of dominant species at the local scale across the chronosequence. Specifically, within-species variability in foliar, litter and nutrient resorption traits in three dominant species were quantified to assess links between within-species variability in leaf traits and spatial heterogeneity of soil resources and species diversity across the chronosequence. Paper II focusses on variability in biomass allocation and community productivity by examining changes in within- and between-species, and community-level variability in proportional aboveground shoot biomass allocation to leaves, stems and sexual reproductive organs in contrasting environments. This is done with the intention of understanding how changes in resources availability drive community trait composition and productivity. Paper III and IV focused on community assembly and species coexistence. Specifically, paper III assesses the contribution of within- and between-species variability, and their co-variation, to the response of two different components of the plant community (dominant vs. non-dominant species) to variation in local environmental conditions, whereas paper IV examines how systematic changes in within- and between-species functional diversity of co-occurring species across the chronosequence (i.e., successional age, species richness, understorey plant density and spatial heterogeneity of soil resources) contribute to species coexistence.

The central questions of each of the papers in this thesis are:

- I. Do measurements of leaf trait values within species across the chronosequence shift in predictable directions that are known to occur between species, and is this within-species leaf-trait variability greatest in communities with low species diversity and high soil resource heterogeneity? (Paper I)
- II. Does proportional biomass allocation to plant aboveground organs (stem, leaves, and fruits) differ within- and between-species and at the community level across contrasting environmental conditions? (Paper II)

- III. How important is between-species variability relative to within-species trait variability in determining community level responses to contrasting environments, and does this differ for dominant vs. non-dominant species in the plant community? (Paper III)
- IV. Are there consistent changes in both within- and between-species functional diversity that lead to a decrease in overall species trait overlap across the chronosequence, and to what extent is this impacted by changes across the gradient in species richness, understorey vegetation density and spatial heterogeneity of soil resources? (Paper VI)

By addressing this set of questions, this thesis seeks to enhance conceptual understanding of the importance of within-species trait variability and its contribution to explaining ecological processes beyond what has proven possible by focusing on only across species trait variation (Fig.1). This is particularly important for systems where species diversity is low and between-species trait variation or turnover of species among communities is likely to be limited.

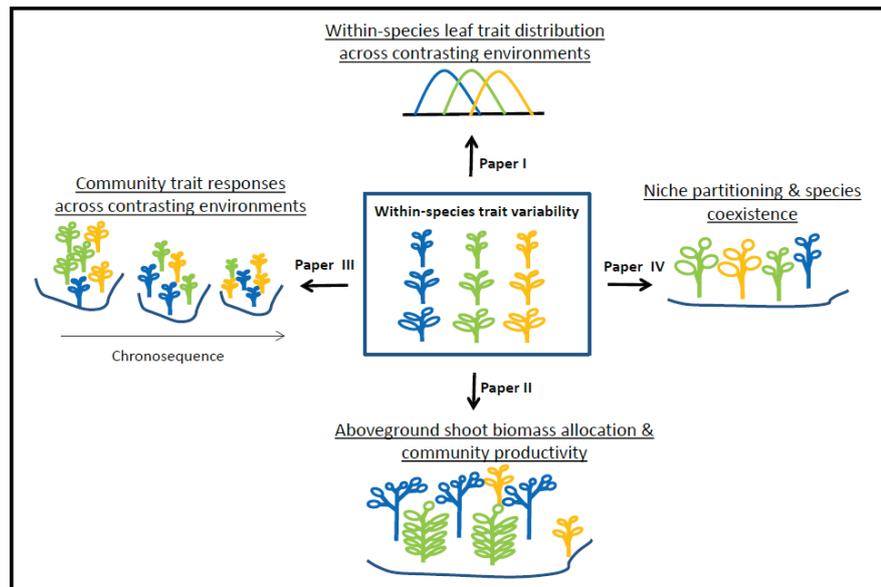


Figure 1. This thesis assesses the extent, magnitude and influence of within-species trait variability on species and community-level processes in strongly contrasting environments. Roman numerals show the different studies conducted in this thesis.

2 Study system

All the studies in this thesis were conducted in a post-fire chronosequence consisting of 30 islands located in lakes Hornavan and Uddjaure in northern Sweden (65°55'N to 66°09'N; 17°43'E to 17°55'E) (Figs. 2 & 3). The mean annual precipitation over the past 30 years is 750 mm, and the mean temperature is +13°C in July and -14°C in January. All islands were formed following the retreat of land ice about 9000 years ago. The only major extrinsic factor that varies among islands is the history of lightning-ignited wildfire, with larger islands having burned more frequently than smaller islands because of their larger area to intercept lightning (Wardle *et al.* 1997, 2003). Previous studies on these islands have shown that as they become smaller and time since fire increases, they enter a state of 'ecosystem retrogression' (Peltzer *et al.* 2010) in which there is a reduction in soil fertility (notably a reduced availability of plant-available nitrogen (N) and phosphorus (P)), plant biomass, and ecosystem productivity, and an increase in plant species diversity (Wardle *et al.* 1997, 2003, 2012, Lagerstrom *et al.* 2009; 2012).

The islands are divided into three size classes with 10 islands per class: large (> 1.0 ha), medium (0.1–1.0 ha), and small (< 0.1 ha), with a mean time since last major fire of 585, 2180, and 3250 years respectively (Wardle *et al.* 2003; 2012), these island size classes represent different stages of vegetation succession. The overstory vegetation is dominated by *Pinus sylvestris*, *Betula pubescens*, and *Picea abies*, which have their greatest relative biomass on large, medium, and small islands, respectively; these three species constitute > 99.8% of all tree individuals. The ground layer vascular vegetation is dominated by the dwarf shrubs *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum hermaphroditum*, which have their greatest relative biomass on large, medium, and small islands, respectively; these three species constitute > 97% of total shrub biomass. Other understory species present with some abundance on the islands are *Vaccinium uliginosum*, *Trientalis europaea*,

Pyrola rotundifolia, *Cornus suecica*, *Linnaea borealis*, *Melampyrum* spp,
Rubus chamaemorus and *Rhododendron tomentosum*.

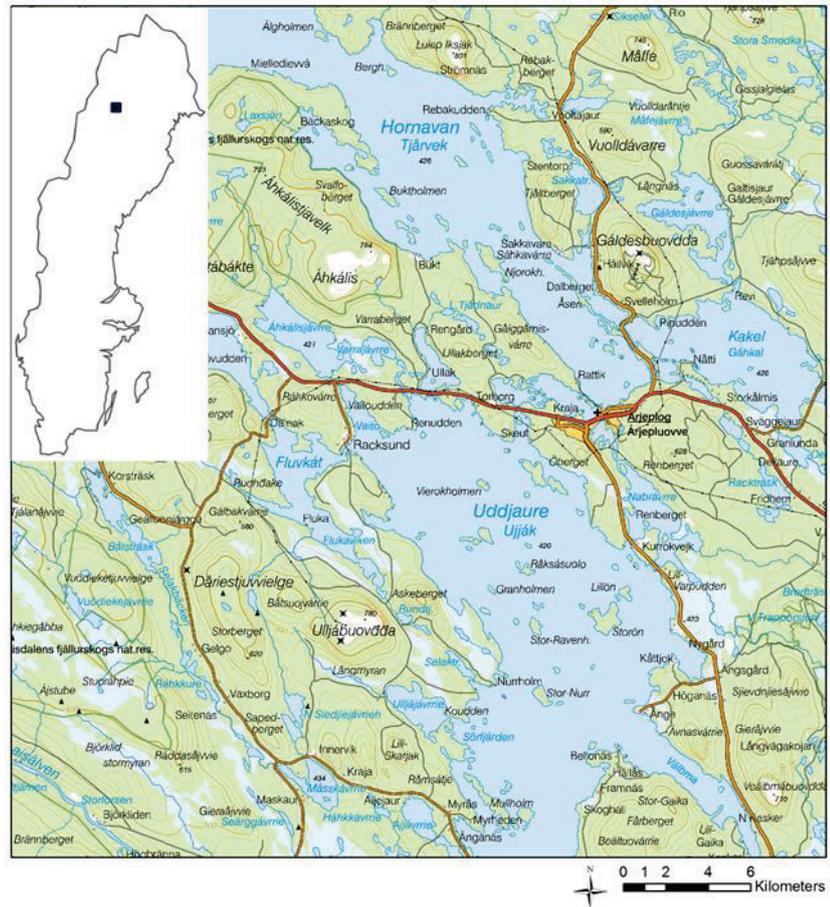


Figure 2. Location of the boreal forest island chronosequence in lakes Uddjaure and Hornavan, Arjeplog, northern Sweden.

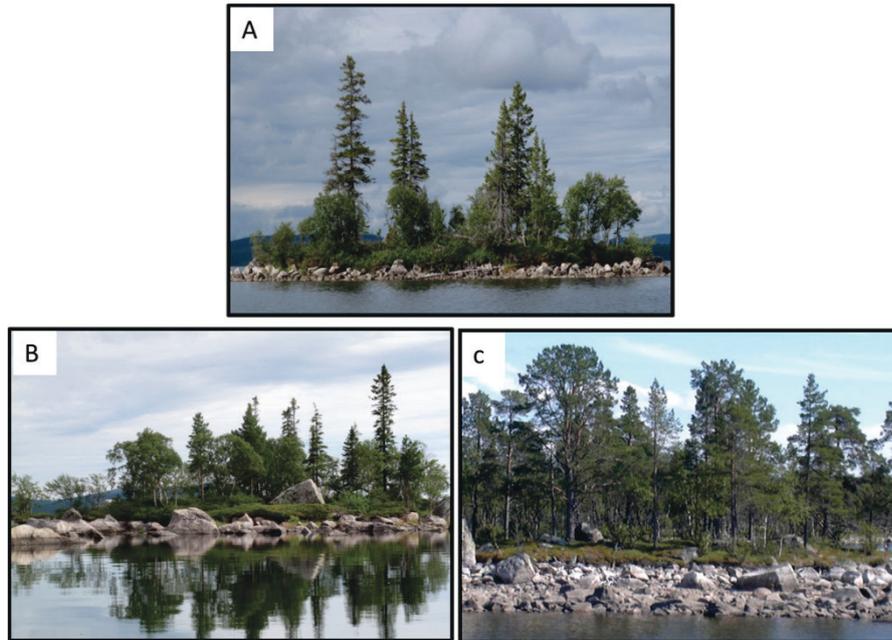


Figure 3. Different island size classes across the boreal forest chronosequence. (A) small (< 0.1 ha), (B) medium ($>0.1 < 1.0$ ha) and (C) large (>1.0 ha) sized islands. Photographs by David Wardle.

2.1 Field sampling, leaf traits and biomass measurements

All studies in this thesis focused on vascular species that occur in the understory (with the exception of one tree species in paper 1) of the 30 islands (Fig. 3). The understory layer is responsible for over half of total net primary productivity (NPP) in the system (Wardle *et al.* 2012) and plays an important role in community and ecosystem processes in boreal forests (Nilsson & Wardle 2005). For each of the 30 islands, a 10 m radius plot was established directly adjacent to a set of pre-existing experimental plots used for previous studies on that island (see, Wardle *et al.* 2003, Wardle & Zackrisson 2005, Gundale *et al.* 2011). The plots were located at similar distances from the shore regardless of island size to prevent edge and microclimatic effects from confounding the results (Wardle *et al.* 1997; 2003). Papers I, III and IV, which are focused on foliar characteristics, involve measurement of leaf (papers I, III, IV) and litter traits (paper I) of species present in the 10m radius plot established on each of the 30 islands.

For Papers III and IV, all understory species present in each plot were used, while for Paper I only three species present in the system were used. This is because in paper I, the goal was to study within-species variability of representative individual species rather than the whole community. Paper I therefore focused on three species that occurred commonly on all islands and differ greatly in their leaf chemistry (Lagerström *et al.* 2013) and life form, i.e., *B. pubescens* (a deciduous tree), *V. myrtillus* (a deciduous understory dwarf shrub) and *V. vitis-idaea* (an evergreen dwarf shrub). Paper III & IV considered the foliar traits of all understory species present (including both shrubs and herbs, and dominants vs. non-dominants) that occurred on each plot to understand pattern of community response to environmental forces and mechanisms that underlie community assembly and species coexistence.

Within each plot on each island, 10 individuals (at least 4 m apart) of each selected plant species were sampled (Fig. 4). For each individual, at least 20 fresh, fully expanded current-year leaves were collected in July 2011 (for use in all three Papers) and a similar number of freshly senesced leaves for three species (*V. myrtillus*, *V. vitis-idaea*, and *B. pubescens*) was collected from the same plant individuals as used for leaf collection in September 2011 (for use in Paper I).

For each foliar sample (i.e., from each individual plant), leaf area and fresh weight was determined for a total of 20–35 fresh leaves immediately after sampling; these samples were then oven dried to constant mass for 48 h and weighed again (Cornelissen *et al.* 2003). These values were used to calculate leaf dry matter content as the ratio of dry weight to fresh weight (LDMC; mg g^{-1}) and specific leaf area as the ratio of leaf area to dry weight (SLA; $\text{m}^2 \text{kg}^{-1}$). Similarly, for each litter sample a total of 20–35 leaves per individual for each of the three species were air-dried to determine mean senesced leaf weight. Subsamples of each plant foliar and litter sample were then ground using a ball mill (Retsch, MM 301) and analyzed for concentrations of total carbon (hereafter [C]), and nitrogen (hereafter [N]) using a LECO TruSpec CN Furnace (LECO Corporation, 2008). Concentrations of P (hereafter [P]) were obtained through acid digestion of the samples (with perchloric and nitric acid) and subsequent analysis via inductively couple plasmography (Zarcinas *et al.* 1987). From these measurements, ratios of C:N, C:P and N:P were derived for foliar and litter samples.

For each of the 10 samples (foliar and litter traits) of each species collected within each island, nutrient resorption efficiency was calculated as the percentage resorption of C, N and P during leaf senescence (Killingbeck 1996). Because substantial leaf mass loss can occur during senescence, which needs to be corrected for when values of resorption efficiency are calculated

(Killingbeck 1996; van Heerwaarden *et al.* 2003; Freschet *et al.* 2010), the measurements of mean live leaf mass and mean senesced leaf mass for each sample were used to provide this correction (van Heerwaarden *et al.* 2003; Freschet *et al.* 2010). As such, percent resorption efficiency for each of C, N and P was calculated as:

$$100 \times ((\text{MLM} \times \text{CL}) - (\text{MSM} \times \text{CM})) / (\text{MLM} \times \text{CM})$$

where MLM is mean live leaf mass, MSM is mean senescent leaf mass, CL is the concentration of the element (C, N or P) in live leaves, and CM is the concentration of the element in senesced leaves.

For paper II, measurements of the standing aboveground biomass of each of the three dominant understory species (i.e., *V. myrtillus*, *V. vitis-idaea*, and *E. hermaphroditum*) within each 10 m radius plot were made for each of two years at the end of the growing season (i.e., over 15-26 August 2012 and 12-22 August 2013), using the methods described in Wardle *et al.* (2003). Briefly, on each plot on each island and for each year, 20 individual vegetative shoots (i.e., leaves + stems) of each of the three dominant understory species (*V. myrtillus*, *V. vitis-idaea*, and *E. hermaphroditum*) were sampled. These individual shoots of each species were at least four meters apart and sourced from different clones. For each of the three species, the shoots were cut at ground level and the portion of the shoot produced in that growing season (i.e., new growth occurring between May and July) was separated from shoot material produced during preceding growing seasons. Shoot material produced during the current growing season was further separated into leaves and stems. Similarly, all ripe fruits (berries) produced in the same growing season from twenty separate shoots of each of *V. myrtillus* and *E. hermaphroditum* (collected over 12 - 26 August in 2012 and 12-22 August 2013) and *V. vitis-idaea* (collected over September 8-12 2012 and September 8-12 2013) were collected. The later collection for *V. vitis-idaea* is because this species produces fruits later in the season than do the other two species. The oven-dry weight (60°C, 72 hrs) of all collected vegetative shoot and berry material were then determined. These together with measures of relative abundance of different species provided data for the proportion of total aboveground material that has been produced during the current year, and the proportion of the current year production allocated to leaf, stem and berry material.

2.2 Species abundance and environmental explanatory variables

Species abundance data of understory vegetation was obtained on each 10m radius plot (one per island) using the point intercept (or point quadrat) method (Goodall 1952), where the total number of times the vegetation of each species was intercepted by a total of 200 downwardly projected points were determined (Wardle *et al.* 2003). Estimate of total understory vegetation density for each island was calculated as the total number of times that plant material was hit by the 200 points (Fig. 4). This relative measure of plant density among islands was used as a measure of the level of competition that may occur in the understory (Tilman 1988; Weigelt & Jolliffe 2003).

Net primary productivity (NPP) of the total understory vegetation on each plot was determined by using the approach described by Wardle *et al.* (2003). Briefly, this involved, for each of the three dominant dwarf shrub species, multiplying its total aboveground biomass (obtained by converting our point intercept data to biomass using allometric equations; see Wardle *et al.* 2003) by the proportion of that biomass which was produced in the current year of measurement. For each of the two years of measurement on each plot, this value was summed for the three species to provide a measure of NPP and mean of the NPP values for each of 2012 and 2013.

Data on the percentage of ambient photosynthetic photon flux density passing through the forest canopy (hereafter 'light transmission') were obtained from data collected by Wardle *et al.* (2003), using measurements obtained from Licor quantum sensors (LI-COR, USA). For each island, fifty point measurements were made in a grid of 20 x 20 m under the tree canopy and about 20 cm above the dwarf shrub layer vegetation in the vicinity of the existing experimental plots. Fifty measurements were simultaneously made in the open (away from the island) and paired with the under canopy measurements to give percentage transmission values. Measurements were performed only on 3 overcast days. These measures of percentage light transmission were used as a measure of aboveground resource availability for the understory vegetation of that island community (Poorter & Arets 2003; Coomes *et al.* 2009).

Data on nutrient availability for each island were obtained from data collected by Gundale *et al.* (2011). Briefly, these data include measurements of soil total N and P on soil samples collected to 5-cm humus depth on each island and soil mineral N (extractable NH_4^+ + NO_3^-) and P (PO_4^-) made at 49 positions within each of the 10 m radius plots established on each island. These measurements were averaged to provide a single value for each island and used as measures of belowground resource availability (Mokany *et al.* 2006).



Figure 4. Species abundance measurements using the point intercept method and leaf sample collection on the islands. In photographs, David Wardle and Andy Siegenthaler (left) and a very happy looking Bright Kumordzi (right). Photographs by Bright Kumordzi and Morgan Karlsson.

2.3 Calculations and data analyses

2.3.1 Community-level trait response measures

For each island (paper II & III) and each year (paper II), the abundance-weighted community average values of each of the response variables (i.e., traits) that we measured were estimated to understand community-level changes in the measured response variables across the island gradient. These calculations were performed as described by Garnier *et al.* (2004) i.e.,

$$\text{Community weighted trait response} = \sum_{i=1}^n (P_i * RV_i)$$

where P_i is the proportion of total biomass (or total pin intercepts per 200hits) represented by species i , and RV_i is the estimated value for the response variable of species i . In paper II, community weighted measures were made for biomass allocation variables (i.e., RA, LMF and SMF) estimated for each island for each of the two years. Meanwhile, in paper III, community weighted measures were determined for each measured trait for each island; this was done three times, i.e., for all understory vegetation, for dominant species only, and for non-dominant species (see Grime *et al.* 1998; Wardle *et al.* 2003).

2.3.2 Species trait variability and community functional diversity measures

In paper I, for each measured trait (LDMC, SLA, litter and foliar C, N, P, C:N, C:P and N:P, and resorption efficiency of C, N and P) for *Vaccinium myrtillus*, *V. vitis-idaea*, and *Betula pubescens* on each of the 30 plots (one per island), a mean trait value (hereafter ‘within-island mean’) and coefficient of variation for that mean value (CV or standard deviation divided by mean; hereafter ‘within-island CV’) based on the ten separate foliar or litter samples from that island was calculated. The within-island CV was used as a measure of within-island variability of that trait (see Albert *et al.* 2010b, Fajardo and Piper 2011, Gundale *et al.* 2011).

In paper III, a variance decomposition technique was used to assess the relative contribution of within- and between-species trait variability to community-level responses separately for dominant species and non-dominant species across the island system. Briefly, this involved the decomposition of the total sum of squares (SS_{specific}) of the plot-level trait variance related to specific environmental variables (i.e. island size, light transmission, understory vegetation density and soil mineral N and P) into ‘Between’ ($SS_{\text{between-species}}$), ‘Within-species’ ($SS_{\text{within-species}}$) and ‘covariation’ (SS_{cov}) components, so that $SS_{\text{specific}} = SS_{\text{between-species}} + SS_{\text{within-species}} + SS_{\text{cov}}$. For each trait (i.e., SLA, LDMC, LNC and LPC) on each island, ‘specific’ community-average trait values were calculated using species trait values as measured on that island (which includes both within- and between species effects), while ‘fixed’ community-average trait values were determined using species trait values averaged over all 30 islands (which removes the within-species variability effect) (Kichenin *et al.* 2013). A set of R codes developed by Lepš *et al.* (2011) was then used to estimate the proportion of total trait variance that is explained by a specific environmental variable as well as the relative contribution of within-and between-species trait variability and their covariation.

Further, in Paper IV, the total community functional diversity (based on 10 individuals per species present; numbers of species ranges from 3 to 14) was estimated for a 10 m radius plot on each of the 30 islands. For each island, the total community functional diversity was then partitioned into ‘within-species’ and ‘between-species’ components following de Bello *et al.* (2011) to understand how environmental variables simultaneously influence within- and between-species functional diversity across different communities. The within-species functional diversity was calculated as the variance of trait values within each species (i.e., within-species variance) whereas between-species functional diversity was calculated as the difference between total community and within-species trait diversity. Finally, species trait overlap ($T_{P/C}$), calculated as the

ratio of within-species variance to total community variance, was used to understand how coexisting species fill available niche spaces along important niche dimensions (Violle *et al.* 2012).

2.4 Statistical analyses

Multivariate analysis of variance (MANOVA) and univariate analysis of variance (ANOVA), and correlation and regression analyses were used to test specific questions presented in each of the papers in this thesis. In all ANOVA analyses (treated as mixed effect models), island size class was used as the main plot factor and species as the subplot factor, with individual islands as the units of replication; using island size classes and ANOVA in this manner enables formal testing of the interactive effect of island size with species, and therefore whether species show contrasting responses to island size (Wardle *et al.* 2003, Wardle & Zackrisson 2005).

In paper I, split plot MANOVA (Gardner & Tremblay 2006) was used to test for the overall effect of island size, species and island size \times species interaction on all response variables (i.e., traits). Separate MANOVAs were performed for within island means (with each within-island mean as a separate data point) and within-island CVs (with each within-island CV as a separate data point) for each of the three sets of traits: leaf traits, litter traits, and resorption traits. When MANOVAs indicated significant main or interaction effects, univariate split plot ANOVAs were then performed for each trait separately. In Paper II, biomass allocation response variables (RA, LMF, SMF) and their community-level measures were analysed using a Repeated Measures split plot ANOVA to test for the effect of island size class, species, year and their interactive effects. When interactions between species or island size and year were significant, data were then analysed separately for each year using split plot ANOVA. For Papers I and II, whenever appropriate, one-way ANOVAs were then used to test for effects of island size and species on the response variables separately and when these effects were significant, means were then compared by post-hoc comparisons (Tukey's test) at $P \leq 0.05$. In all cases, where necessary, the data were transformed to satisfy assumptions for ANOVA.

Also in Paper II, Pearson's correlation coefficient was used to examine the relationships of allocation variables and shoot turnover with environmental variables for each of the two years with each island treated as an independent data point; this was done both for each species singly and for the community-level measures. In Papers II-IV, general linear model (GLMs) regressions were

performed to determine relationship between the various response variables (both at the individual species and whole-community levels) and key environmental variables including island size, understory vegetation density (i.e., total number of intercepts through the point quadrat analysis), light transmission, and soil mineral N and P across the 30 islands. Multiple regression analyses were then used to determine if multiple combinations of environmental variables could best describe these response variables, with the most parsimonious model selected based on corrected Akaike information criteria (AICc) (Burnham & Anderson 2002). All data analyses in this thesis were conducted using the R-statistical software (R Development Core Team 2010).

3 Results and Discussions

3.1 Within-species trait responsiveness to the gradient

An increasing number of studies have shown that plant traits at the species-level can be highly variable in response to environmental gradients at both local and landscape scales (Cornwell & Ackerly 2009, Albert *et al.* 2010a, Kichenin *et al.* 2013). Consistent with these studies, within-species variability in foliar and litter traits (paper I) as well as biomass allocation responses of dominant understory shrubs (paper II) were found to vary considerably and were responsive to the island size classes in a similar manner to that observed at the between-species level (Wardle *et al.* 2012, Lagerström *et al.* 2013). For instance in paper I, where changes in within-island means values and within-island CVs of foliar and litter traits across the island size gradient were studied for each of three species, within-island means for SLA, foliar [N] and [P] for *B. pubescens* were least on the most nutrient limited small islands while those for LDMC were greatest, indicative of strategies relating to greater nutrient conservation on small islands and nutrient acquisition on large islands (Diaz *et al.* 2004; Wright *et al.* 2004). Similarly, within-island mean values for *V. myrtillus* litter nutrient concentrations, and resorption efficiency for all three species were responsive to island size. Further, consistent with patterns found at the species-levels across the island size classes, there was strong within-species responsiveness of shoot biomass allocation to sexual reproduction, leaves and stems (paper II). However, in both studies (papers I & II), within-species trait responsiveness was generally greater for species that are adapted for higher fertility (e.g. *V. myrtillus*) than those adapted for infertile conditions (e.g. *E. hermaphroditum*), suggesting that plasticity in these traits may constitute an integral part of the mechanism of resource acquisition in

productive environments (Crick & Grime 1987, Aerts & Chapin 2000, Cornwell & Ackerly 2009, Valladares *et al.* 2007, Kichenin *et al.* 2013).

For paper I, the prediction that trait variability would be greater on large islands because of the greater spatial heterogeneity of soil resources shown to occur on larger islands (Gundale *et al.* 2011) and their lower species diversity (Wardle *et al.* 2012) was mostly unsupported for foliar traits and gained only mixed support for litter and resorption traits. This is because within-island CVs did not respond consistently to the island size gradient but instead decreased, increased or were unresponsive to island size depending on specific trait and species considered. However, consistent with the prediction of low trait variability on small islands, within-island CVs of litter P, C:P and N:P for *V. myrtillus* and resorption efficiency of C and N for *B. pubescens* and C for *V. vitis-idaea* were found to be least on small islands, thus supporting previous findings that greater spatial variation in limiting soil resources diversifies niche space and promotes spatial variability in trait values (Schwilk & Ackerly 2005; Albert *et al.* 2011). The fact that within-island CVs of several other traits were unresponsive to the gradient (or, for some resorption traits, responded in the opposing direction) suggests that other components of spatial resource heterogeneity such as patchiness and spatial grain (i.e. spatial scale of patchiness) may be of greater importance (Hutchings & De Kroon 1994; Wijesinghe & Hutchings 1996; 1997). For example, although the total spatial variability of the most available forms of soil N (mineral N and amino N) is greatest on large islands, on those islands these nutrient forms have been shown to be spatially organized into smaller and less defined patches relative to the medium and small islands (Gundale *et al.* 2011). The unresponsiveness of within-species trait variability at the local scale level to spatial heterogeneity in more spatially variable environments may also occur because plant nutrient uptake occurs over larger scales that make fine scale resource heterogeneity unimportant.

Data collected for paper I do not support the hypothesis that variability in foliar and litter traits would be greatest for the species that dominate in the most resource-heterogeneous environments (i.e., the large islands) because of a greater range of niches and lower species diversity. *Vaccinium myrtillus* (a dominant species on large islands) had the greatest within-island CV for only one foliar trait (foliar [C]), while *B. pubescens* (dominating on medium islands) and to a lesser extent *V. vitis-idaea* (dominating on medium and small islands) often had the highest CV for both foliar and litter traits. This finding is generally inconsistent with suggestions that species adapted to more heterogeneous environments (in this case, larger islands) exhibit inherently higher variability in their trait values (Pigliucci & Hayden 2001; Callaway *et*

al. 2003). The data alternatively suggest that there may be a convergence of both litter and foliar traits at the within-species level in the most productive environments, which has previously only been shown to occur at the across-species level (Aerts 1999; Grime 2006; Shipley 2010; Mommer *et al.* 2012). In this light, *V. myrtillus* is both dominant and competitive on the most productive islands, as revealed by previous species removal experiments (Wardle & Zackrisson 2005; Wardle *et al.* 2008). It is worth noting that although one of the species used in this particular study (*B. pubescens*) is a tree species and would therefore have acquired resources at different depths and spatial scales than the two shrubs (i.e. *V. myrtillus*, and *V. vitis-idaea*), the within-island CVs for its traits and the responses of these CVs to the gradient was usually comparable to one of the shrub species (*V. vitis-idaea*), suggesting that the fact that it was a tree probably did not have a major bearing on the results.

3.2 Aboveground biomass allocation in response to changes in resource availability

Directional shifts in shoot biomass allocation among organs of dominant dwarf shrub species across the island size gradient were found at both the within-species and whole-community levels (paper II). This finding suggests that environmentally induced changes in relative shoot biomass allocation responses at the within- and between-species level can be linked to changes in plant community properties and ecosystem processes. For instance, for data collected in the 2012 growing season, within-species sexual reproductive allocation (i.e., RA) was least on small islands for *V. myrtillus* and on medium islands for *V. vitis-idaea*, and did not change with island size class for *E. hermaphroditum*. Results from correlation and multiple regression analyses suggest that at least in 2012, RA for *V. myrtillus* was most closely and positively linked to soil nutrient status, NPP and understory density. Soil fertility increases with island size, meaning that NPP and vegetation density (and hence plant competition) is high on the large islands on which *V. myrtillus* dominates (Gundale *et al.* 2012). The higher RA of this species on large islands suggests that greater investment in sexual reproductive structures may contribute to it maintaining its dominance in the most competitive environment (Wardle *et al.* 2003). In contrast, the RA of *V. vitis-idaea* was most closely related to light availability, which was least on the medium islands in which this species dominates. Instead, this species allocates most of its biomass to leaves and stems in the lowest light environment, presumably in order to maximize light capture. These contrasting results suggest that shoot allocation

patterns respond in contrasting ways for different species to the same environmental factors, in line with optimal biomass allocation theory proposing that each species should prioritize resource allocation to organs that maximises its own survival and fitness (Brouwer 1963, Poorter & Nagel 2000).

At the community level, for both 2012 and 2013 growing seasons, allocation to leaves (i.e., LMF) was greatest on medium islands. This result was reflective of the response of *V. vitis-idaea*, which is most abundant on medium islands (Wardle *et al.* 1997, 2003) and which allocated a greater proportion of its biomass to leaves on these islands. This finding highlights the contribution of within-species trait variability to observed community-level responses to environmental gradients (Kichenin *et al.* 2013). Further, the strong negative relationships observed between LMF and NPP and light availability at the community level suggest that differences in community properties (i.e. dominant species composition) linked to changes in availability of resources may exert a direct influence on community trait response (Lagerström *et al.* 2013). Together, these results suggest that species turnover and within-species variability in biomass allocation along strong contrasting environments can contribute significantly to detecting community-level patterns of response to extrinsic environmental factors (Jung *et al.* 2010, Siefert 2012, Kichenin *et al.* 2013).

Across species, contrasting patterns of allocation to shoot organs indicated distinct strategies in how two dominant and competing coexisting dwarf shrub species invest in order to access light in low-light environments. As such, the strategy for *V. vitis-idaea* (which is evergreen) is to invest heavily in long-lived leaves whereas *V. myrtilus* (which is deciduous) annually produces highly efficient photosynthetic leaves (Lagerström *et al.* 2013) while investing more in longer lived stems to support the leaves. Overall these results support recent suggestions that co-existing plant species can display highly contrasting biomass distributions to shoot organs to achieve optimum resource acquisition within a single plant community (Freschet *et al.* 2015).

3.3 Community trait response across contrasting environments

Within-species variability (and its covariation with between-species variation) was found to contribute significantly to the community-level response of several traits to local-scale environmental variation, thus highlighting the ecological importance of within-species trait variability at local scales (Albert *et al.* 2010a, Messier *et al.* 2010) (paper III). The greater contributions of within- than between-species variation to plot-level trait averages sometimes

found in our study contrasts with previous findings (e.g. Jung *et al.* 2010, Jackson *et al.* 2013). This may be because these other studies may have been conducted across larger environmental gradients with highly contrasting environmental conditions. However, congruent with the findings of Kichenin *et al.* (2013) at the regional scale, negative covariation between within- and between-species trait responses to local environmental variations sometimes occurred and these may explain the apparent lack of a community-level response to changes in environmental conditions at the local scale. Further, it was found that the influence of within- and between-species variability and their covariation appeared to vary greatly among different traits. Like in Auger & Shipley (2013), this work found that within-species trait variability contributed largely to variation in abundance-weighted plot-level SLA and LNC, indicating that measures of community-level responses of these traits may be substantially affected if within-species trait variability is ignored. Overall, these findings contribute to a growing body of evidence suggesting that the inclusion of within-species trait variability in community assembly analyses substantially improves the detection of ecological patterns and processes (Jung *et al.* 2010, Siefert 2012), particularly at local or plot-level scales (Albert *et al.* 2010, Jackson *et al.* 2013, Kichenin *et al.* 2013).

Abundance-weighted trait measures were generally responsive to variations in different environmental resources whereas non-weighted measures were not (paper III). This finding, which is contrary to the implicit assumption underpinning many community assembly studies, suggests that plant assemblages do not respond homogeneously to local variation in environmental conditions. Since abundance-weighted measures are mainly influenced by the dominant species in a community, and non-weighted measures generally reflect the importance of the many non-dominant species (Grime 1998; Thompson *et al.* 2010), these findings suggest that dominant versus non-dominant species differ in their responses to environmental variables across the island size gradient. For instance, while light transmission to the understory and soil mineral N were found to impact dominant and non-dominant species rather similarly, understory vegetation density (which is indicative of the intensity of plant competition for resources; Tilman 1988) appeared as a strong driver of the traits of only non-dominant species. This may be explained as dominant species benefitting from having higher competitive abilities due to a higher plasticity in their use of resources (Ashton *et al.* 2010, Maire *et al.* 2009). Further, in congruence with Mariotte *et al.* (2013), dominant species sometimes showed trait patterns characteristics of acquisitive plant resource strategies while non-dominant species showed strategies related to resource conservation. For instance, leaf N content (LNC) of dominant species

increased in response to higher soil mineral N while that of non-dominant species decreased. Together, these results not only make a strong case that different components of the same plant community can be under the influence of contrasting environmental variables, but also support recent findings that environmental filters are the principal drivers of dominant species abundance while niche differentiation acts strongly on non-dominant species (Maire *et al.* 2012, Garbin *et al.* 2013).

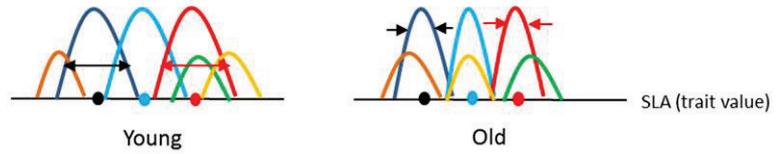
3.4 Niche partitioning and species coexistence across contrasting environments

In paper IV, significant relationships were found for within- and between-species components of functional diversity with successional age (i.e., time since fire) and species richness, but not measures of soil fertility or vegetation density, across the island chronosequence (Figs 5 & 6). This finding highlights potential mechanisms that underlie species coexistence in our studied communities. Within-species functional diversity was mainly related to the decline in species trait overlap (determined using the $T_{IP/IC}$ measure of niche packing) across communities with increasing successional age. Several earlier studies have shown that amounts of limiting plant resources such as soil nutrients decrease as succession proceeds (Connell & Slatyer 1977, Walker & del Moral 2003; Wardle *et al.* 1997; 2003). Resource limitation may therefore underlie part of the response of species niche overlap to succession (Connell & Slatyer 1977; Pickett & McDonnell 1989). Specifically, our results provide support for the view that species from late successional communities are more specialized in their resource acquisition through taking up only a specific portion of the total available resources (Bazzaz 1979; Walker & del Moral 2003; Walker *et al.* 2010). The fact that there was no significant decrease in between-species functional diversity with increasing successional age indicates that in our study system later-successional species neither occupy more trait space nor are better at occupying marginal niche spaces relative to early successional species. This contradicts a widespread idea that changes in species composition as succession proceeds leads to an increase in species functional trait diversity and therefore a progressive shift towards wider use of niche space at the interspecific level (Walker *et al.* 2010).

Further, the finding that both a decrease in within-species functional diversity and an increase in between-species functional diversity occur in response to increasing species richness (Fig. 5), supports the prediction that species trait overlap would decrease with increasing species richness. The

opposing relationships of within- and between-species functional diversity of dominant plant species with species richness suggests that dominant species shift their niche position and limit their spread around this niche position as the number of interacting species increases in a community. This finding is consistent with the niche overlap hypothesis, which suggests that co-occurring species may show systematic shifts in interspecific niche separation and intraspecific niche width along the same resource utilization axis (May 1972; Pianka 1974). The finding that between-species functional diversity increases with species richness indicates that co-occurring species show marked differences in their niche requirement in species rich communities in order to coexist (Silvertown 2004; Maire *et al.* 2012). The decrease in within-species functional diversity with increasing species richness indicates that individuals of a species tend to have similar trait values that minimize average fitness difference (Chesson 2000). This finding is in contrast to that of Le Bagousse-Pinguet *et al.* (2014) who found an increase in within-species functional diversity in plant height with increasing species richness in calcareous grassland communities. This finding emphasizes the need to measure within-species trait variability to understand patterns of species niche differentiation and coexistence. Overall, these contrasting responses of within- and between-species functional diversity with increasing species richness reveal species niche packing as an important mechanism for the maintenance of functional diversity in plant communities (MacArthur & Levins 1967; Pianka 1974).

Successional age



Species richness

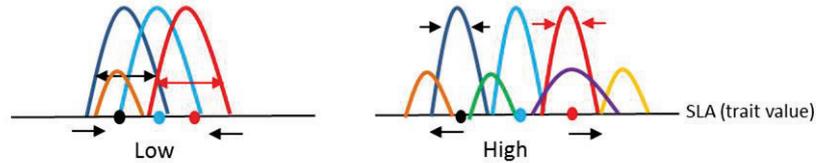


Figure 5. Summary of observed changes in dominant and subordinate species trait (SLA) variance and overlap in response to two major environmental drivers across 30 local boreal forest communities (i.e., islands). For each panel, each curve represents a different species and the area of each curve represents the relative abundance of that species in the community. Arrows above the line represent changes in within-species functional diversity while those below the line represent changes in between-species functional diversity in response to successional age and species richness. Overall, observed strong changes in community trait overlap in response to successional age and species richness are mainly driven by dominant species. Between-species functional diversity does not change with increasing successional age but does change with increasing species richness.

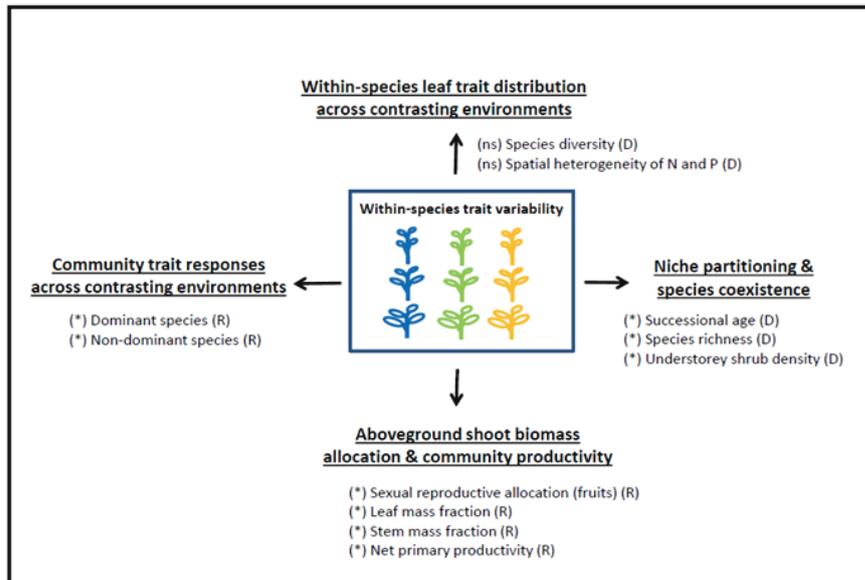


Figure 6. The importance of within-species trait variability (WSV) to ecological properties based on results obtained in papers I-IV. (*) = significant influence of WSV and (ns) = non-significance influence of WSV. (D) = Drivers of WSV and (R) = species and communities-level responses.

3.5 Conclusion and Future work

Overall, results from this thesis have several implications for understanding the ecology of within-species variability and its effects on community and ecosystem properties. First, by characterising local changes in within-species trait variability of dominant species that occur across a strong environmental gradient in northern Sweden, this study shows that significant trait variability occurs within species that are widespread in contrasting environments (Fig. 6). In addition, within-species trait variability is highly responsive to differences in environmental conditions among ecosystems, and mostly consistent with patterns observed at the species-levels. Across contrasting environments, trait variability within-species sometimes contributes more to community-level responses than does among-species variability or species turnover. This finding highlights the importance of within-species variability for understanding the response of whole communities to environmental changes at the local scale and in assessments of ecosystem processes in response to ongoing global changes (Albert *et al.* 2011, Siefert 2012). These results support recent calls to incorporate within-species trait variability into studies of community assembly (Fig. 6).

Second, accounting for the within-species trait response of plant communities to environmental factors can enhance attempts to understand the mechanisms underlying species dominance and coexistence in contrasting environments. For instance, assessment of within-species differences in biomass allocation of co-occurring dominant dwarf shrub species across the chronosequence provides insights into how changes in resources availability drive community trait composition and consequently community responses (Poorter *et al.* 2012, Freschet *et al.* 2015). Similarly, the predictable shifts in within- and between-species functional trait diversity of dominant and non-dominant species across successional and species richness gradients as demonstrated here reveals the role of niche-based processes in structuring the assembly of plant communities and promoting species coexistence (MacArthur & Wilson 1967, Chesson 2000, Mariotte *et al.* 2013).

Third, simultaneously considering within- and between-species variability in various leaf traits among dominant and non-dominant species revealed that the functional response of these two components of the plant community are controlled by different environmental factors. This implies that functional response of plant assemblages is not necessarily homogenous in the manner commonly assumed in several community assembly studies. In addition, the finding that different dominant species sometimes show contrasting responses of the same trait to the same environmental factor presents a significant challenge when using models to predict ecosystem responses from community trait values. Until current community assembly theories account for the diverse nature of species responses within plant assemblages, they are unlikely to accurately predict the consequences of changes in environmental drivers, for example global climate change (Thuiller *et al.* 2008). Further, given the importance of plant traits in governing ecosystem processes as such primary net productivity, carbon sequestration, biogeochemical cycling and decomposition, knowledge of the extent and magnitude of within-species trait variability is imperative for better understanding these processes and their drivers, especially in ecosystems with low species diversity and turnover such as boreal forests.

Finally, very few studies have characterized within-species variability of all component species within naturally occurring plant communities across contrasting environments as has been done in this thesis. This characterization is important to test how differences among individual species traits contribute to community assembly and ecosystem processes. Notably, exploring within-species trait variability using a well-studied system of independent replicated ecosystems such as done here allows assessment of the contribution of within-species trait variability to explaining ecological processes beyond what has

proven possible by focusing on only across-species trait variation. Future studies assessing the ecological significance of within-species trait variability are needed to explore the relative importance of genotypic versus phenotypic contributions to within-species variability. We also know almost nothing about the contribution of within-species root trait variability to community level root trait measures, despite growing recognition of the broad ecological significance of root traits. Finally, testing these ideas in different environments (temperate, tropical, arid, etc.) is necessary to ascertain whether the role of within-species trait variability in driving important ecological processes and functions is of general importance.

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