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Phenotypic plasticity and genetic adaptation of plant functional traits on global scales

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CHAPTER 1

General Introduction

1.1 Importance of biodiversity for ecosystem stability in the face of climate change

Due to human activities, we are facing an unprecedented climate change crisis this century. Climate change is characterised by the continuously increasing global mean surface-air temperature and shifts in precipitation patterns. It is also associated with more frequent extreme weather events such as heat waves, frosts, heavy storms and droughts (Stott, 2016). Such climatic changes have profoundly impacted the survival and existence of species on Earth and ecosystem functioning. The major impacts include increasing species extinction (Habibullah *et al.*, 2022), altered species' ranges (Thomas, 2010), shift of vegetation (Cazzolla Gatti *et al.*, 2019; Lu *et al.*, 2021) and changes of biogeochemical and biogeophysical processes (Dawson *et al.*, 2011; Peñuelas *et al.*, 2013; Flower *et al.*, 2019). The observed increasing tree mortality (even occurring in ecosystems which have been considered quite resistant) caused by extreme climatic conditions recently (Hartmann *et al.*, 2022), raises concerns about whether and how plants will cope with future climatic conditions.

Plants are the backbone of ecosystems and play a vital role in ecosystem functioning and associated services, such as biomass production and nutrient cycling. As the main producers, plants use the energy from captured sunlight to convert carbon dioxide into carbohydrates through photosynthesis. These organic matters are the source of direct and indirect food (energy) for many other organisms such as insects,

birds and mammals. Plants do not only provide food provisioning, but also shelter for many animals (Schulze *et al.*, 2004). The by-product of photosynthesis, oxygen, is also essential for the survival of most living organisms. As plants can absorb carbon dioxide from the atmosphere through photosynthesis, they are important to the carbon cycling of ecosystems and have the potential to counteract climate change by reducing the carbon dioxide concentration of the atmosphere. Besides, plants are also important to water cycling as they absorb soil water and release water vapor into the atmosphere through transpiration, a process essential to allow carbon dioxide to diffuse into the plant. Next to affecting the water cycle, transpiration also regulates climate through the energy exchange involved (Katul *et al.*, 2012). Finally, the cycling of nutrients such as nitrogen and phosphorus is also significantly influenced by plant soil nutrient uptake and litter decomposition (Ordoñez *et al.*, 2009; Austin & Ballaré, 2010).

After two decades of biodiversity-ecosystem function research, there is consensus that the loss of plant biodiversity will result in the deterioration of the ecosystem functions and related services (Knapp, 2019). A global analysis of 147 grassland plant species from 17 biodiversity experiments showed that high plant diversity is needed to maintain the multiple ecosystem functions at multiple times and places in changing environments (Isbell *et al.*, 2011). A massive global natural experiment in 224 dryland ecosystems also showed that plant species richness was positively related to 14 ecosystem functions such as carbon sequestration, carbon cycling and nutrient cycling (Maestre *et al.*, 2012). Another 12-year experiment that manipulated multiple environmental changes also suggested the loss of plant species numbers led to a decrease in the stability of ecosystem productivity (Hautier *et al.*, 2015).

However, to understand the impact of biodiversity loss on the breakdown or transformation of ecosystems, we should not only focus on the loss of plant identities, but also look at the functional features of the plants involved, which reflect the roles and effects of organisms in their ecosystems. Functional features help us to identify how different organisms contribute to the processes and services that ecosystems provide, such as nutrient cycling, carbon sequestration, pollination, water purification, and climate regulation (Dussault, 2019). By looking at the functional features of organisms, we can also identify which organisms are more important or unique in their functions, and which ones are more vulnerable or resilient to environmental changes. For example, to understand why some species or individuals survive when hit by extreme heat or drought while others do not, we

need to study the functional facets of organisms as expressed by their genetic, physiological and structural characteristics that contribute to their fitness and therefore help maintain ecosystem functioning (Mahecha *et al.*, 2022).

1.2 Variation in functional traits explain plants responses to climate change

1.2.1 Trait-based ecology and functional diversity

Over the past two decades, there has been an explosive growth of plant functional diversity studies, as ecologists started rethinking entire ecological fields from a functional perspective by applying trait-based approaches (Mammola *et al.*, 2021). Functional diversity (FD), or functional trait diversity, is an important component of biodiversity and is defined as the value and range of those species and organismal traits that influence communities and ecosystem functioning (Tilman, 2001; Petchey & Gaston, 2006). In simple words, FD is the variation of traits between organisms (Carmona *et al.*, 2016). Functional diversity is built up by variation in functional traits, which are the morphological, physiological and phenological attributes of organisms that impact fitness indirectly via their effects on the individual performance - growth, reproduction and survival (Violle *et al.*, 2007). Trait-based approach in plant ecology have been applied to understand how plant species differ in their functional traits, how these traits affect their interactions with the environment and other organisms, and how these traits influence ecosystem processes and services. The merits of using trait-based approaches in ecology relate to their capability to generalise and predict the interactions between organisms and environments/other organisms and the effects of organisms on ecosystem functioning across organisational (from individual to ecosystem) scales by looking at the functional traits rather than the taxonomy of the organisms (Mammola *et al.*, 2021). As trait values are becoming more and more available in literature (either from more literature with open-access data attached it, or from increasing datasets deposited in global databases such as TRY database (Kattge *et al.*, 2020)) and can be drawn upon for future studies, trait-based ecology is reinforcing itself as a popular subdiscipline of ecology.

1.2.2 Understanding functional diversity by community assembly rules

As a central theme of community ecology, community assembly studies the processes of how species from an available species pool colonize and coexist within ecological communities (Kraft & Ackerly, 2014). Since plant functional traits express viable strategies of an organism to deal with environmental and biotic

drivers or stressors, the phenomenon that different traits occur in different habitats shows how species are selected by environmental and biotic conditions (van Bodegom & Price, 2015). Therefore, the patterns of functional diversity can reflect the underlying mechanisms of community assembly (Spasojevic & Suding, 2012).

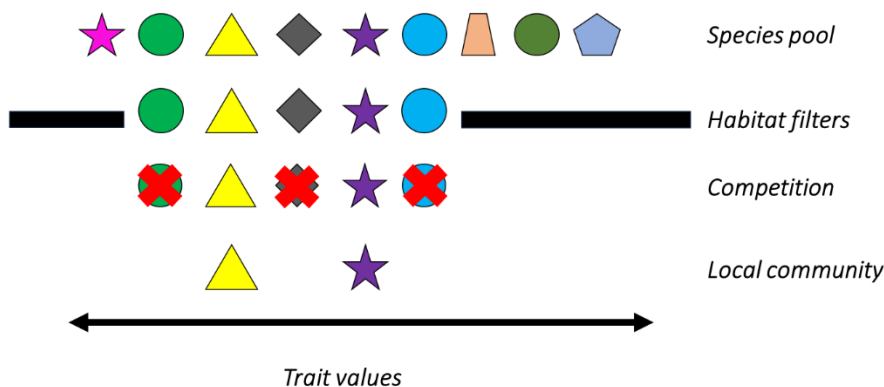


Figure 1.1 Conceptual model of two community assembly rules (habitat filtering and competition) in terms of species functional traits. Potential colonists of a local community are assumed to depend on the available species in the species pool of that region. Multiple abiotic conditions of the local community act as habitat filters to screen out the species with those trait values that cannot successfully survive and establish at the site. According to the competitive exclusion principle, resulting from the competition for resource use or requirements, co-occurring species with different traits (or trait values) that occupy different niches can finally survive and establish at the local community. (adapted from (Kraft & Ackerly, 2014).

Two main assembly rules (illustrated in **Fig. 1.1**) that hypothesise how communities are assembled have been proposed to understand functional diversity within and between communities. One is called the competitive exclusion principle (or limiting similarity), which assumes that co-occurring species tend to have different traits and occupy different niches to avoid strong competition with each other (Hardin, 1960). This mechanism usually leads to trait divergence and reflects biotic interactions within a community. The other assembly rule is called habitat filtering. It is a framework which analogies to the evolutionary process of natural selection at community level to predict species composition in certain habitats (Keddy, 1992). In this context, the habitat acts as abiotic filter to screen out those sets of trait values (for quantitative traits) or certain classes of traits (for qualitative traits) that are unsuitable for certain environments. Therefore, only those species with suitable traits or trait values can survive in this habitat. This filtering usually leads to trait

convergence at the selected set of environmental conditions, compared to the total trait variation of the species pool in the region (van Bodegom & Price, 2015). Moreover, in plant communities across global ecosystems, trait convergence, rather than divergence, is generally observed, suggesting that habitat filtering plays an important role (Freschet *et al.*, 2011; Kraft & Ackerly, 2014).

When habitat filtering is present, community mean trait values (which can reflect species composition) are expected to change along environmental gradients. Cornwell & Ackerly (2009) examined community assembly hypotheses in woody plant communities along an edaphic gradient in coastal California and found that leaf and wood traits such as leaf nitrogen concentration (LNC) and wood density (WD) were correlated with the soil water content. Others have found environmental gradients in soil fertility were related to specific leaf area (SLA) (Ordoñez *et al.*, 2009) and seed number (Fujita *et al.*, 2013). In addition, an experiment with different seed mixtures showed that trait convergence was more common than trait divergence (Fukami *et al.*, 2005). After 9-years of natural colonization and growth, while the species identities diverged, their traits were convergent in these communities (Fukami *et al.*, 2005). Similarly, others have found that plots with a similar climatic condition may have strong species turnover, but a lack trait variation between plots, indicated strong environmental-filter effects based on traits (Messier *et al.*, 2010). All of these evidences imply that the prediction of potential trait combinations by habitat filtering is promising, as long as we know the drivers that causes trait convergence (van Bodegom *et al.*, 2014). Therefore, to predict the impact of climate change on functional diversity, climate change can be regarded as a force that selects those species that can accommodate the current and future climatic conditions. Thus, upon climate change, only species with the trait combination that fit the changing environmental conditions can survive in this undergoing climate crisis.

1.2.3 Understanding plant strategy through trait dimensions

Quantitative plant functional traits vary widely among species and the ranges of variation in different traits also differ dramatically. For example, while measured values of stem specific density may differ by around 20-fold, the measurements of seed mass can vary by as much as 13 orders (Table 1 in Díaz *et al.* (2016)). Therefore, an important aim of trait-based ecology is to understand this variation. Over the past two decades, ecologists have tried to identify the key dimensions of trait variation and interpreted them as plant ecological strategies (Westoby *et al.*, 2002; Westoby

& Wright, 2006). To be specific, these dimensions represent plant eco-evolutionary trade-offs because of the costs and benefits involved in these related traits. Costs, usually referring to carbon cost, occur in trait construction or enzyme maintenances and the benefits refer to the returns of increased plant fitness from this carbon cost in certain abiotic and biotic conditions (van Bodegom & Price, 2015). Because the available carbon and energy of a plant is limited, the carbon investment in one trait implies the investment to another trait will be limited. Therefore, the balance between costs and benefits for plant species in different environments leads to the selection of interrelated trait combinations on these key dimensions.

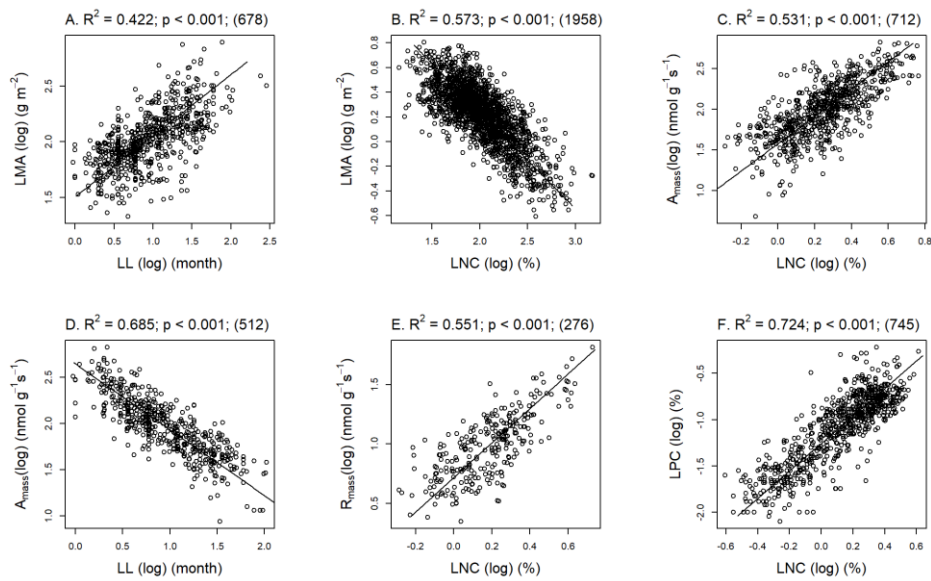


Figure 1.2 Multivariate relationships among leaf economics spectrum (LES) traits - leaf lifespan (LL), leaf mass per area (LMA), photosynthetic assimilation rates (A_{mass}), dark respiration rate (R_{mass}), leaf nitrogen concentration (LNC) and leaf phosphorus concentration (LPC): **A.** LMA vs. LL, **B.** LMA vs. LNC, **C.** A_{mass} vs. LNC, **D.** A_{mass} vs. LL, **E.** R_{mass} vs. LNC, **F.** LPC vs. LNC. If a significant relationship was found, the regression line was drawn and the R^2 was indicated above the figure, followed by the P -values. Numbers in brackets refer to the number of species included in the tests. Data is from Glopnet (Wright *et al.*, 2004).

The most famous and widely accepted dimension is the global leaf economics spectrum (LES) (Wright *et al.*, 2004). LES is defined from the leaf mass per area-leaf lifespan (LMA-LL) dimension, which represents species carbon-investment strategies, running from fast to slow return from leaf mass investment (leaf construction per unit of leaf area). That means species with high LMA (high leaf

construction investment) usually have leaves with a longer leaf lifespan to ensure a longer period to obtain photosynthesis products for growth. The LES traits include leaf mass per area (LMA), photosynthetic assimilation rates (A_{mass}), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), dark respiration rate (R_{mass}) and leaf lifespan (LL), and these six leaf traits are interrelated (**Fig. 1.2** illustrates some of their interrelationships). Later on, the concept of leaf economics spectrum was extended to other organs such as stem and root economics spectrums (Chave *et al.*, 2009; Bergmann *et al.*, 2020) and even to a whole plant economics spectrum (the Plant Economics Spectrum or PES (Freschet *et al.*, 2010; Reich, 2014)).

Another well-known trade-off dimension is the seed mass-seed output (SM-SO) dimension which represents species reproductive allocation strategies. It describes that species either produce a few large seeds or numerous small seeds. The large seeded species have higher competitive seedlings as their seeds can survive longer to ensure higher germination success while small seeded species have higher colonization ability as their small seeds can disperse longer distances to find suitable environments to germinate but their germination proportion is lower (Westoby *et al.*, 2002; Westoby & Wright, 2006; van Bodegom & Price, 2015).

With the increasing availability of global data on trait measurements as well as on climatic and soil conditions, more and more empirical patterns between trait variation and environmental conditions are being detected. Meanwhile, ecologists have proposed more eco-evolutionary theories to understand these patterns as well as above-mentioned dimensions. One prominent example is the understanding of global leaf size variation and its corresponding climatic drivers by optimality theories (Wright *et al.*, 2017). In arid areas, leaf size was negatively correlated to temperature while in humid areas, leaf size was positively related to temperature. Besides, in cold areas, leaf size was negatively related to moisture while in hot areas, leaf size was positively related correlated to moisture. The authors then proposed a leaf size model based on optimality theories to predict the geographic trends in maximum leaf size which matched the observed global leaf size variation. Similarly, a more recent study provided a mechanistic explanation for the empirical relationship between the two main LES traits, LMA and LL, based on optimality theories and successfully predicted the LMA variation trend across altitudes (Wang *et al.*, 2023).

1.2.4 From interspecific to intraspecific trait variation

Revisiting the importance of intraspecific trait variation

While the knowledge about plant functional diversity has advanced substantially, until fairly recently most trait-based analyses were based on the assumption that intraspecific trait variation can be largely ignored compared to interspecific trait variation. Therefore, the species were only represented by a mean value for each trait in this research, as were all the studies mentioned in sections 1.2.2 & 1.2.3. However, it has been long known that within a species, the traits between different individuals or populations can also vary largely to adapt to different environmental conditions. A typical example is the Hawaiian tree species *Metrosideros polymorpha* Gaud. which varied extremely in its physiological and morphological traits (Cordell *et al.*, 1998). However, only in the last decades or so, increased trait-based community research has reasserted that intraspecific trait variation (ITV), including phenotypic plasticity and genetic adaptation, is an important contribution to functional diversity and can also alter ecosystem functioning (Bolnick *et al.*, 2011; Violle *et al.*, 2012).

Many studies have shown the magnitude of ITV can be substantial, and even equal to that of interspecific trait variation. At local scales, Albert *et al.* (2010a) proposed a framework to quantify the extent, structure and source of ITV of three leaf traits within species and confirmed that there was large variation between individuals, subpopulations and populations in the alpine communities with contrasting climatic conditions. Similarly, Messier *et al.* (2010) further expanded the quantification of trait variation of tropical rainforests in Panama across larger ecological levels, including leaf, strata, tree, species, plot and sites and found that the within species trait variance was comparable to that of between species. Furthermore, three subsequent global meta-analyses also quantified the relative contribution of ITV to the total trait variation within and among communities (Siefert *et al.*, 2015) and confirmed the significant effects of ITV on the community dynamics and ecological processes (Des Roches *et al.*, 2018; Raffard *et al.*, 2019).

The extent of intraspecific trait variation differs among species

While the importance of ITV contribution to the overall community trait variation is now generally appreciated, the extent of ITV also varies between species and environments. It has been documented that plants differ in their ITV magnitude and direction in response to environmental gradients. For example, Ackerly & Cornwell

(2007) showed that 39 woody species in coastal California along a soil moisture gradient differed in their ITV magnitude (relative to the overall community trait variation) of SLA and that some of them even responded in the opposite direction of the community shift. Similar patterns have also been observed in more local studies. Kichenin *et al.* (2013) showed that the intraspecific response of five leaf traits (SLA, leaf dry matter content (LDMC), LS, LNC, LPC) to elevation differed in their strength and direction among 31 mountain species in southern New Zealand. Siefert *et al.* (2014) also found that individual trait (vegetation height, SLA, LDMC, LS) responses to environmental factors (such as soil nutrient availability, soil pH, mean annual precipitation) varied highly among species across the eastern United States. Therefore, ITV is now perceived to be an important property of plant species in response to environmental change.

Costs and limits of intraspecific trait variation

As a plant property responds to environmental cues, it has also been speculated that there are costs and limits involved in ITV (including phenotypic plasticity and genetic adaptation) processes. Compared to genetic adaptation, the costs and limits of plasticity have been more extensively discussed in literature. This research is based on the assumption that if there was no constraint (*i.e.* in relation to the energetic costs of maintaining the sensory and regulatory machinery for plasticity) for having the ability of plasticity, organisms should have infinite plasticity and express the optimum trait values in every environment. Given that this is not the case, there must be costs involved. The costs of plasticity are defined as fitness trade-offs of the organisms as associated with their plastic responses (Schneider, 2022). As a consequence, the plastic organism has a lower fitness than the non-plastic organism when producing the same mean trait value in the focal environment (DeWitt *et al.*, 1998). The limits of plasticity, on the other hand, are defined as the failure of a plastic organism to produce the optimum mean trait value while the non-plastic organism can at those conditions (DeWitt *et al.*, 1998). Such limits follow the saying that “a jack-of-all-trades is a master of none”. It has been assumed that there may be a trade-off between the developmental trait range that can be expressed across multiple habitats and the magnitude of trait expression that can be achieved within each environment (DeWitt *et al.*, 1998). Although the costs and limits of plasticity have been theoretically discussed, the empirical evidence of costs and limits of plasticity are still limited (Auld *et al.*, 2010; Schneider, 2022) and sometimes even contrasting to the hypothesis (Relyea, 2002).

With regards to genetic adaptation, natural selection is supposed to ultimately lead to the elimination of all the individuals without the improved genotype (Haldane, 1957; Darlington, 1977). However, mutations leading to the adaptation may not be possible (or present within the population of consideration) or the intermediate mutations may not be viable. Moreover, like in the case of plasticity, adaptations to a specific environment may reduce the fitness of an organism for other environments. However, empirical measurements of the costs involved in genetic adaptation are even rarer.

1.3 Knowledge gaps

While it has been recognised that intraspecific trait variation is an unignorable aspect of plant functional diversity and that the magnitude of this variation is also highly species-dependent and potentially costly (section 1.2.4), the current theories about community assembly (section 1.2.2) and plant strategies (section 1.2.3) are all based on the mean field approach (which only uses species mean trait values). Therefore, it still remains unclear whether plant functional traits within species respond to environmental gradient in the same way as those traits between species. Empirical studies observed some species responded in the opposite direction of community trait variation (Ackerly & Cornwell, 2007; Kichenin *et al.*, 2013; Siefert *et al.*, 2014), which may weaken the hypothesised environmental filtering effect based on species mean trait values. Also, the divergent responses of traits within species to environmental gradients can weaken the whole-plant economic spectrum as assessed at the interspecific level (Laughlin *et al.*, 2017). However, a global comparison of these patterns is still lacking. At the same time, the drivers of intraspecific trait variation (whether phenotypic plasticity or genetic adaptation) and their effects on plant response to climate change also still remain limited. So, understanding how plant vary their traits within species could help us predict whether species with certain characteristics are better at coping with climate change.

1.4 Research aims and questions of this thesis

Given the knowledge gaps, in this thesis, we explored the patterns of phenotypic plasticity and genetic adaptation of plant functional traits and related implications of them in response to climate change. We applied trait-based approaches to compare the patterns of intra- and interspecific trait variation and to analyse the main drivers of phenotypic plasticity and genetic adaptation, the two key components of intraspecific trait variation (ITV), based on newly compiled

databases of species' ITV and genetic adaptation rate of plant functional traits. We aimed to examine the underlying mechanisms and contributions of phenotypic plasticity and genetic adaptation to ecosystem resilience under climate change. The specific research questions addressed in this thesis are as follows:

1. Does the plant economics spectrum (PES) reflect plant strategies in reality, *i.e.* when considering intraspecific trait variation as well (**Chapter 2**)?
2. Do environmental conditions, biotic interactions and species features relate to intraspecific trait variation on a global scale (**Chapter 3**)?
3. How do genetic adaptation rates vary across plant life history, growth forms, phylogenetic groups and trait types (**Chapter 4**)?
4. Do plants with different growth forms and from different biomes vary in their resilience in term of plasticity and genetic adaptation (**Chapter 5**)?

1.5 Outline of this thesis

During my PhD study, I compiled, to our knowledge, the two most comprehensive global databases about plant intraspecific trait variation based on systematic reviews: one is the global species' ITV database including 2064 species and 11 functional traits from 19 studies; the other one is the global genetic adaptation rate database including 72 species and 35 functional traits from 74 studies. Using the global species ITV database, we first compared the patterns of global trait-trait relationships between and within species and evaluated possible mechanisms that caused this trait correlation (**Chapter 2**). We also examined if there were general drivers of ITV based on the same database (**Chapter 3**). Using the global genetic adaptation rate database of plant functional traits, we tested the potential drivers of genetic adaptation rates (**Chapter 4**). Lastly, by using both species' ITV and genetic adaptation rate databases, we tested whether the resilience patterns in terms of plasticity and adaptation differed by growth forms and biomes (**Chapter 5**).

The main content of each chapter is outlined below:

Chapter 1: General introduction

This chapter introduced the importance of biodiversity (section 1.1), especially focusing on the functional diversity, in maintaining ecosystem functioning and service (section 1.2.1) and summarized the current knowledge of understanding the functional diversity from interspecific trait variation (sections 1.2.2 & 1.2.3) and

intraspecific trait variation (section 1.2.4). The knowledge gaps, research aims and questions, and outline of this thesis were also identified in this chapter (sections 1.3 - 1.5).

Chapter 2: Global analysis of trait–trait relationships within and between species

This chapter assessed whether commonly reported trait-trait relationships between species such as plant economics spectra reflect plant strategies in reality, *i.e.* as observed within species. Firstly, a novel conceptual framework was provided that allowed us to distinguish different mechanisms that lead to trait-trait relationships between species. Then the direction and strength of 54 pair-wise intraspecific trait variation (ITV) and interspecific trait variation relationships were compared based on our newly compiled global species' ITV database. Finally, those trait-trait relationships that may truly represent plant strategies such as leaf economics spectrum (LES) were separated from those coincident trait-trait relationships which may be caused by common environmental drivers according to our framework. Its implications to model projections under climate change were discussed.

Chapter 3: Drivers of plant intraspecific variation are trait-specific

This chapter analysed whether species features, environmental conditions and biotic interactions are related to ITV on a global scale. Growth form, species alpha niche position (α_i), species beta niche position (β_i) together with species niche breadth (R_i) and species C, S, R strategies were used as our proxies of species features, biotic interactions, environmental conditions and environment and biotic interactions, respectively. In addition, multiple statistical methods were applied to test which proxy was related to ITV to assess if there is a generic driver of ITV for different traits or trait groups. The results suggest that no such generic driver exists and its implications for vegetation model predictions were discussed.

Chapter 4: Genetic adaptation rates differ by trait and plant type - a comprehensive meta-analysis

This chapter is a meta-analysis which investigated the patterns of genetic adaptation rates and assessed how these rates differ among plant species groups, growth forms and trait types. Firstly, a newly compiled genetic adaptation database of plant functional traits was compiled by systematic review. This database specifically focuses on genetic adaptation to separate this from phenotypic plasticity. Subsequently, we used generalized linear models (GLMs) to test if the plant life

history, growth form, phylogeny and trait type influence the annual and generational genetic adaptation rates. We found that shrubs overall have higher adaptation rates than trees, which confers shrubs an adaptive advantage over trees. Finally, the implications and potential vulnerability of plant groups to climate change were discussed.

Chapter 5: Global resilience of growth forms and biomes

This chapter evaluates whether growth forms or biomes differ in their resilience (the combination of plasticity and adaptation) and in these two components separately at the global scale, based on our global species' ITV and genetic adaptation rate databases. Firstly, the respective patterns of plasticity and adaptation among growth forms and biomes were tested using generalized linear models (GLMs). Then the resilience patterns among growth forms and biomes were analysed by the 2D-dimension peacock test. We discovered that herbs may have a lower adaptive capacity than shrubs and trees to environmental change and that biomes such as tropical savannas with dry winters and cold semi-arid regions have the lowest resilience while they are facing fast rates of climate change. Finally, the potential vulnerability of growth form and biomes to climate change were discussed.

Chapter 6: General discussion

This chapter discusses the main findings of this thesis by synthesising answers to the research questions and discussing the scientific implication of this thesis. It also discusses the limitations of this study and provides some future research perspectives.

