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Phenotypic plasticity and genetic adaptation of plant functional traits on global scales
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CHAPTER 6

General discussion

This thesis aimed to investigate the global patterns and drivers of intraspecific trait variation (ITV) – phenotypic plasticity and genetic adaptation – of plant functional traits, to enhance our understanding of plant strategies to respond to climate change. To achieve these goals, I first compiled two relatively comprehensive global databases: the species' ITV database (with 2064 species and 11 functional traits across 19 studies) and the genetic adaptation rate database (with 72 species and 35 functional traits from 74 studies). Then, I applied trait-based approaches to compare the global patterns of trait variation within and between species (**Chapter 2**), explored the general drivers of phenotypic plasticity and genetic adaptation respectively (**Chapters 3 & 4**) and assessed the resilience of vegetation with different growth forms and from different biomes to climate change (**Chapter 5**).

In this chapter, I first synthesise the main findings of this PhD study (section **6.1**) and then discuss the scientific implications resulting from this thesis (section **6.2**) and provide potential directions for future research (section **6.3**). I finalise this chapter with my main conclusions (section **6.4**).

6.1 General overview

In the first study of this thesis, we examined whether the so-called plant economics spectrum (PES) reflects plant strategies in reality: if the PES reflects plant strategies, the trait relationships assumed to reflect plant strategies in the PES should also be expressed in trait relationships within species. To investigate, we provided a novel

framework that enabled us to distinguish different mechanisms that may have caused the trait-trait relationships between species. By comparing the direction and strength of trait-trait relationships within and between species in on our newly compiled global species' ITV trait database, we found that except for some leaf economics spectrum (LES) traits, most trait-trait relationships between species disappeared within species. Therefore, we concluded that except for LES, the PES did not generally represent plant strategies.

To better understand why most traits were decoupled within species, we further analysed the drivers of ITV in our second study. We expected environmental conditions, biotic interactions or species features would correlate to ITV, but we found that none of them generically explained the variation of ITV. Particularly, we showed that LES and size-related traits were more related to environmental conditions while leaf morphology traits were more related to biotic interactions. Also, the drivers of ITV strongly deviated from those of species mean trait values. Therefore, we concluded that the drivers of ITV were trait-specific. We expect that the different drivers between the ITV of different traits also strongly affect the trait-trait relationships within species.

Since ITV includes both phenotypic plasticity and genetic adaptation, the latter can help plants adapt to environmental changes beyond their current genetic constraints and potentially produce future generations which are more adaptive to climate change. In our third study, we hence focused on the drivers of genetic adaptation of plant functional traits. To investigate this, we first compiled a global genetic adaptation rate database, of which the variation of plant functional traits was solely induced by genetic adaptation based on common garden experiments. We then analysed how annual and generational genetic adaptation rates changed with elapsed time and tested whether these rates were related to plant history, growth form, phylogeny and trait type. We found that both annual and generational genetic adaptation rates were highest at the beginning when the plants encountered new environments and these rates gradually decreased after they had adapted and established in these environmental conditions. Our results also suggested that shrubs may be more adaptive than trees. These results have important implications regarding plant adaptation to new environments and will improve the prediction of vegetation responses and ecosystem functioning upon climate change.

Our fourth study is the first to evaluate how phenotypic plasticity and genetic adaptation, respectively, differed between growth forms and biomes and how these

two components of ITV simultaneously contributed to the adaptive capacity of different growth forms and the resilience of different biomes. We revealed that herbs had lower adaptive capacity than shrubs and trees and some biomes such as tropical savannas with dry winters and cold semi-arid regions may have the lowest resilience to climate change. Recognising these findings rely on a small sample size, they point towards divergences in resilience between species groups, which has potential implications for how to manage different biomes and associated growth forms in the face of changing environmental conditions.

6.2 Scientific Implications

6.2.1 Advantages of estimating intraspecific trait variation across communities by trait-gradient analysis

In this thesis, we estimated intraspecific trait variation using the trait-gradient analysis (Ackerly & Cornwell, 2007), because of two major advantages of this method. The first advantage is that this method has an increased accuracy of the ITV estimate, since magnitude of ITV evaluated in this way is less influenced by the length of environmental gradients, compared with other approaches. Commonly adopted variance partitioning approaches (Messier *et al.*, 2010; de Bello *et al.*, 2011; Lepš *et al.*, 2011; Siefert *et al.*, 2015; Umaña & Swenson, 2019) express ITV magnitude as a variance component (a proportion of total trait variance among communities), but the trait variance of both within species and across communities largely depend on the environmental range over which the species are sampled. Also, it is hard to know whether the sampled environmental range covered the entire range of possible intraspecific trait variation. Therefore, the magnitude of ITV based on variance partitioning approaches might be over- or underestimated. Instead, the trait-gradient analysis uses observed trait gradients to normalise the environmental gradients and to express the magnitude of trait variation of each species (ITV) and the magnitude of trait variation across communities as slopes. Even if the trait gradients did not cover the full range of environmental variation, the ITV can still be quantified as the trait variation in the community is normalised to 1 (see more details in section **2.2.2** of **Chapter 2**). Therefore, in this way, the estimate of ITV is less sensitive to the length of environmental gradients.

In addition to increasing the accuracy of ITV estimates, another advantage of the trait-gradient approach is that the ITV estimate of each species can be regarded as a species' property, as it indicates the plasticity of each species (we assumed that the ITVs in our database were mainly contributed by phenotypic plasticity, see section

5.2.1 of **Chapter 5**). Therefore, it provides the opportunity to further test whether ITV is related to other drivers such as phylogenetic relatedness or climate. In **Chapter 3**, we tested whether ITV was related to eco-evolutionary drivers such as the environmental conditions, prevailing biotic interactions and species features. We observed that those relationships were quite weak. Therefore, evolutionary drivers such as phylogenetic relatedness might be another potential mechanism which could better explain the variation of ITV to some extent. Although we did not find phylogenetic clustering in the trait-trait relationships within species (Fig. S5-9, **Chapter 2**), further detailed investigations should test whether phylogenetic relatedness is another underlying mechanism of trait covariation within species.

6.2.2 Weaker trait-trait relationships within species suggest the importance of alternative strategies co-occurring in local communities

A major contribution to science in **Chapter 2** is that we provided a conceptual framework to distinguish different mechanisms that lead to trait-trait relationships between species by comparing the strength and direction of these relationships within and between species. As the key component of the framework, our trait-trait relationships within species were expressed by ITV-ITV relationships rather than by trait-trait values themselves. If trait-trait relationships truly represent a plant strategy driven by physiological or eco-evolutionary constraints, both traits are expected to change simultaneously, also within species. This pattern should express itself as a positive ITV-ITV relationship for those two traits. Furthermore, using species' ITVs makes the number of data observations for the comparison of trait-trait relationships within and between species the same, as each species only has one ITV and one mean value for each trait. Therefore, it also made the comparison more direct and eliminated the potential bias in statistics caused by different sample sizes.

An interesting pattern we observed in our study was that the strength of trait-trait relationships within species was much weaker than that of between species (R^2 0.024-0.568 for between species, and 0.025-0.202 for within species, Table S3 in **Chapter 2**) This relatively weaker trait correlation within species indicated that more than 80% variation of one trait was decoupled from the variation of other traits. To better understand this variation, we further investigated the drivers of ITV and found that the drivers of ITV were trait-specific (**Chapter 3**). This result explained the decoupling of trait-trait relationships within species to some extent, as the ITV of each trait was caused by different drivers. Previous study has also found inconsistent trait correlations at different taxonomic levels for LES traits. They

found that some species expressed opposite trait correlations within *vs.* across species (Fig. 3 in Anderegg *et al.*, 2018). Similar idiosyncratic trait correlation patterns across environmental gradients at the species level were also observed in another study (Fig. 4 in Umaña & Swenson, 2019). These findings may explain why the strength of trait covariation within species was weaker than that of between species. These results also imply that a particular trait correlation cannot be regarded as a universally optimal strategy for all plant species to adapt to a given environment and suggest the existence of alternative strategies within communities. In this sense, different plant species may have different trait expressions to deal with the same environmental pressure, which results in multiple trait combinations with similar fitness for the species co-occurring in the local community (Marks & Lechowicz, 2006; Umaña & Swenson, 2019). This implication may explain why the observed trait convergence within species according to the habitat filtering theory was usually weaker than that of between species and hardly more than 50% of the intraspecific trait variation could be explained by trait-environmental relationships. It also explains why most trait-environment relationships show a large amount of unexplained variance within communities (*e.g.* Fig. 1 in Ordoñez *et al.*, 2010). Therefore, alternative strategies may be more dominant within communities or at a small ecological scale than between communities.

For larger ecological scales, such as between communities, the importance of alternative strategies may be reduced, since the relative importance of environmental differences increases. Consequently, at this scale, the trait convergence can be quite strong, such as observed for the plant economic spectrum (PES), which indicates trait variation is associated with environmental conditions. However, as we found that PES was mostly absent within species, it indicates that these covaried trait-trait relationships between species cannot be regarded as true coordination or trade-offs which are physiologically or eco-evolutionary linked. Instead, we argued that this covariation might be caused by common drivers which simultaneously but independently affect these traits (**Chapter 2**). It means that those two traits could be, for example, independently selected for by two coupled environmental drivers which leads to the observed trait-trait relationship. as we conclude that the PES does not truly represent a plant strategy (*i.e.* a true coordination or trade-off), it implies that if those environmental drivers will become correlated differently *e.g.* because of climate change, the PES we observed currently may be strengthened or weakened in the future. In section **6.3.2** below, we also

discuss how this change may have important implications for global vegetation modelling.

6.2.3 Importance of disentangling the two components of intraspecific trait variation

Phenotypic plasticity and genetic adaptation are the two main mechanisms that cause observable trait changes in species. However, it is difficult to distinguish to which extent changes of trait expression are induced by phenotypic plasticity or genetic adaptation as these two mechanisms usually work simultaneously in natural conditions. This difficulty has resulted in a lack of attempts to disentangle the respective contribution of phenotypic plasticity and genetic adaptation to ITV in field studies on a global scale.

However, to separate their contribution is important, as they play different roles in adapting to changing environments. Phenotypic plasticity can respond to environmental change in a faster way than genetic adaptation, but the phenotypic change through plasticity can hardly be inherited by future generations. While it takes a longer time scale to induce phenotypic change through genetic adaptation, this change is inheritable. Also, since phenotypic plasticity is sometimes non-adaptive (Vinton *et al.*, 2022), whether phenotypic plasticity or genetic adaptation is more important to adapt to environmental change is context-dependent. For example, if the direction of environmental change is the same for a long period, then the species with higher genetic adaptation rates may survive better as their adaptive traits which have been selected by the environmental condition can be reproduced in their future generations to deal with similar environmental conditions. In contrast, if the direction of environmental change is changed more randomly and faster, then the species with higher phenotypic plasticity may be advantaged as they can respond more quickly to environmental cues. For example, dealing with a temporarily stressful condition, the current generation may plastically change its trait value even if those values are further deviated from its optimum value, as this change helps this species to survive in this stressful period (Ghalambor *et al.*, 2007). After that period, if the environments become normal, the reproduced generation does not have to inherit the non-optimum traits.

In **Chapter 4**, we attempted to separate genetic adaptation from ITV by building up another genetic adaptation database which had been compiled from data of common garden experiments about different populations of invasive species. By using data only from different populations of a species grown in the same environmental

conditions (common garden), the trait variation through phenotypic plasticity can be eliminated and the trait difference detected between populations in common garden experiments can be regarded as the result of genetic adaptation. We used populations of invasive species in particular, because this helped us to specify when those populations started to adapt to different environments (*i.e.* the divergence time, Δt, which is needed to calculate its evolutionary rate).

Unfortunately, separating ITV into genetic adaptation and phenotypic plasticity was not fully achieved. First, the units of ITV and genetic adaptation rate were inconsistent, which meant we could not obtain their relative magnitudes directly. In our database, the genetic adaptation rate was estimated by the method proposed by Haldane (1949) to calculate the evolutionary rate (as a (transformed) relative change in trait values per year). In contrast, the normalised ITV values did not contain any time dimension. Therefore, we could not simply obtain the magnitude of phenotypic plasticity by subtracting genetic adaptation rates from ITV values. Second, focusing on invasive species only also resulted in limited set of species that were common across our ITV and genetic adaptation databases, reducing sample size and hindering our attempt to compare relative magnitudes of phenotypic plasticity and genetic adaptation.

Despite these limitations, our genetic adaptation database is still the most comprehensive genetic adaptation rate database of plant functional traits. The observed relative higher genetic adaptation rates of plant species in the early years after encountering a new environment emphasised the important role of genetic adaptation in adapting to climate change (Fig. **4.2** in **Chapter 4**). Since we assumed the main component of each ITV estimate of our ITV database is phenotypic plasticity, we used these ITV estimates as the approximate values of phenotypic plasticity (see section **5.2.1** of **Chapter 5**). By investigating the patterns of phenotypic plasticity and genetic adaptation together for plants from different biomes, qualitative assessments suggests that phenotypic plasticity may play more important roles in adapting to temperature while genetic adaptation may be more important in adapting to moisture (**Chapter 5**). However, due to data limitations, this finding could not be comprehensively tested. If we would like to know the relative importance of phenotypic plasticity and genetic adaptation for plant species in adapting to climate change quantitatively, further research is needed to fully separate these two components of ITV. This would entail two major components: firstly, to devise methods to unify the units of ITV and genetic adaptation, and

secondly, to enlarge the current genetic adaptation database to allow comprehensive quantitative assessments.

6.2.4 There might be a trade-off between being plastic and being genetically adaptive

To understand the interaction between phenotypic plasticity and genetic adaptation, we looked at the factors that affected their variation separately. We found that different traits varied in their extent of phenotypic plasticity and genetic adaptation rates while their pattern seemed complementary (**Chapters 3** & **4**). Particularly, the phenotypic plasticity of leaf size (LS) was significantly lower than that of specific leaf area (SLA) and leaf nitrogen concentration (LNC) (Fig. S4, **Chapter 3**; with the limitations mentioned above, we regard ITVs as approximate values of phenotypic plasticity in this test). In contrast, we saw the genetic adaptation rate of LS was four to six times higher than that of SLA and LNC (**Table 5.2**, **Chapter 5**). Despite being indicative (it was not statistically tested due to the limited size of our genetic adaptation database), this suggests that there might be a trade-off between phenotypic plasticity and genetic adaptation for species in their phenotypic change. These complementary patterns thus suggest that the drivers of phenotypic plasticity and genetic adaptation may be different.

Our analysis of this trade-off is based on individual traits, and further research is needed to test if this trade-off also exists between species. If phenotypic plasticity and genetic adaptation are also negatively related between species, then the species with higher phenotypic plasticity will have lower genetic adaptation. This may have important implications for plants to adapt to climate change. Firstly, it provides indirect evidence that there are costs involved in phenotypic plasticity or genetic adaptation. If there would have been no cost involved in phenotypic plasticity or genetic adaptation, species would achieve both high phenotypic plasticity and genetic adaptation without limitation. Such costs may also limit plants to adapt to climate change as plants cannot always obtain the perfect trait expression with limited phenotypic plasticity or genetic adaptation ability to adapt to the changing environments (DeWitt *et al.*, 1998; and section **1.2.4**). Secondly, this trade-off may result in different adaptive capacities between species. While species differ in their phenotypic plasticity and genetic adaptation, it remains unknown whether phenotypic plasticity or genetic adaptation is more important for plants to counteract climate change as we discussed in section **6.2.3**. Although in **Chapter 5**, we analysed the respective and combined patterns of phenotypic plasticity and genetic

adaptation for vegetation with different growth forms and from different biomes, we were not able to analyse these patterns based on species because of the limited data in our genetic adaptation database. As both phenotypic plasticity and genetic adaptation are ways for plants to combat climate change, the combination of phenotypic plasticity and genetic adaptation can define the adaptive capacity of species to adapt to climate change. Therefore, this emphasises more research is needed to investigate the roles of phenotypic plasticity and genetic adaptation to climate change separately and in combination in the future.

6.3 Future directions

6.3.1 A potential way to separate phenotypic plasticity and genetic adaptation

As discussed above, to better understand the respective importance of phenotypic plasticity and genetic adaptation for plant species and the interaction between these two components, we need to separately quantify phenotypic plasticity and genetic adaptation. To achieve that, we may assume that plastic responses occur within a year, this may allow converting the current ITV unit into unit similar to the one for genetic adaptation, thus facilitating direct comparison. Or, we may need to find better ways to estimate genetic adaptation rates for plant functional traits which share the same unit of ITV for the same species. If we can obtain estimates in the same units, we can simply obtain the magnitude of phenotypic plasticity by the subtraction of genetic adaptation rate from ITV values.

In addition, we need to enlarge the genetic adaptation database. Our current database almost solely includes invasive species, which may lead to biased estimations of genetic adaptation rates. Invasive species may have a specific combination of traits that is not representative of all plants: compared to non-invasive species, a previous meta-analysis study showed that invasive species had higher values of performance-related traits such as higher photosynthesis and transpiration rates, higher seed numbers, higher SLA, higher shoot root ratio and higher seed germination rate and survival rate (van Kleunen *et al.*, 2010). Whether the trait space occupied by these invasive species led to overestimating their genetic adaptation rate remains unknown. For example, higher seed number, seed germination, growth and survival rates may lead to a higher adaptation rate of invasive species than non-invasive species as more generations are reproduced in a fixed period if they have similar life histories. Therefore, using the genetic adaptation rate of invasive species as a representation of all plants can lead to an overestimation. In contrast, another meta-analysis study showed that invasive species were generally more plastic than non-

invasive species, but this higher plasticity did not necessarily lead to a more adaptive provenance especially in water and nutrient-limited environments (Davidson *et al.*, 2011). In addition, if there is a trade-off between phenotypic plasticity and genetic adaptation, as we discussed in section **6.2.4**, then higher phenotypic plasticity may lead to a lower genetic adaptation rate of invasive species than that of non-invasive species. If this is the case, using the genetic adaptation rate of invasive species will underestimate the genetic adaption of all plants.

A different way to estimate the genetic adaptation rate for a species may be to collect its seeds from multiple locations with large geographic gradients (to distinguish populations) and grow them in the common garden to measure their functional traits. Then, one may use linear regression to estimate the genetic adaptation rate as the slope of the regression line by regressing the trait values of different populations *vs*. community-weighted mean trait gradients. The community-weighted mean trait gradients can be calculated in the same way as trait-gradient analysis (Ackerly & Cornwell, 2007). These trait gradients can represent the environmental gradients from which the different populations were collected. In this way, the effect of phenotypic plasticity can also be eliminated by common garden experiments and the contribution from genetic adaptation to trait variation among these populations can be considered. Moreover, as the magnitude of genetic adaptation is also defined by the slope of the regression line of each species, the unit of the genetic adaptation will be the same as the ITV value, which is unitless. Therefore, we can obtain the magnitude of phenotypic plasticity by subtraction as mentioned above. Moreover, as we do not need the divergence time (Δt) as for the method proposed by Haldane (1949) to calculate the evolutionary rate, we can apply this method for any plant species without considering the availability of Δt. Without the need of this parameter, it becomes more feasible to include non-invasive species in the genetic adaptation database. Crucially, to attain substantial common species that are both available in the ITV database and the genetic adaptation database, global collaborations are needed to collect the seeds of different populations and conduct the common garden experiments for an extensive number of species.

6.3.2 Importance of incorporating intraspecific trait variation into global vegetation models

The patterns of trait variation within species have important implications for global models that predict the impacts of global change on vegetation dynamics, especially Dynamic Global Vegetation Models (DGVMs). Firstly, most DGVMs to date describe vegetation dynamics based on plant functional types (PFTs). Traditionally, the vegetation characteristics within each PFT were assumed to be constant in space and time (Wullschleger *et al.*, 2014), which failed to represent the observed functional diversity as there was large variation within each PFT (van Bodegom *et al.*, 2012). Later on, trait variation within each PFT was accounted for in these PFT-based DGVMs by incorporating empirical trait-environment relationships into these models (Verheijen *et al.*, 2013). Furthermore, fully trait-based models have been developed to predict trait distribution and then translate the predicted trait space into predicted PFT occurrences based on habitat filter theory (van Bodegom *et al.*, 2014). However, these models are still largely based on community mean trait values, which ignore intraspecific trait variation (ITV) within PFTs (Moran *et al.*, 2016). As ITV can be a substantial contribution to community trait variation (Siefert *et al.*, 2015) and is an important strategy for plants to adapt to climate change, incorporating ITV into these trait-based DGVMs (van Bodegom *et al.*, 2014; Verheijen *et al.*, 2016) will improve the accuracy of their prediction of global trait distribution and functional diversity.

Secondly, the decoupling of most trait-trait relationships within species indicated these trait-trait relationships between species were mainly driven by common environmental drivers (**Chapter 2**). This suggests that if those common drivers are decoupled in future climatic conditions, those trait-trait relationships between species may also fall apart. Therefore, this decoupling should be considered in DGVMs that incorporate functional trade-offs (Pavlick *et al.*, 2013; Sakschewski *et al.*, 2015; Weng *et al.*, 2017). For example, Sakschewski *et al.* (2015) developed a DVGM called LPJmL-FIT (Lund-Potsdam-Jena managed Land-flexible individual traits) which incorporated some leaf traits linked by leaf economics spectrum such as specific leaf area (SLA), leaf longevity (LL), leaf nitrogen content (N_{area}). However, we found the trait coordination between SLA and LNC was not maintained within species (**Fig. 2.5a**, **Chapter 2**). This may imply that this trait relationship may fall apart in future climatic conditions, and therefore it will influence the prediction of trait distribution by LPJmL-FIT.

Thirdly, the weaker trait-trait relationships within species and the idiosyncratic drivers of ITV for different traits also suggest the potential existence of alternative strategies as we discussed above in section **6.2.2**. Models that are based on the eco-evolutionary optimality (EEO) principle (as loosely applied in Pavlick *et al.*, 2013 and Sakschewski *et al.*, 2015) also hypothesise that the plant trait trade-offs select for one optimal solution related to plant growth and fitness for a given environment. This implies that models based on EEO approaches can be improved to make more realistic predictions by considering a series of alternative strategies (Harrison *et al.*, 2021), instead of focussing on attaining one optimal solution. For example, co-occurring species within communities may have alternative strategies (trait combinations) which result in similar fitness (or less optimal but still not easily outcompeted by the species with the optimal trait expression), allowing them to cope with the same environmental conditions in different ways. To incorporate this, EEO models can be improved by fully evaluating multiple trait combination possibilities for the same set of environmental conditions without striving for one best solution.

In addition, another aspect that we might have to rethink in the context of EEO principles is the influence of phenotypic plasticity. Since EEO principles assume that plants tend to get the best trait combination under the selective force of environments, it also suggests that any plant trait variation is adaptive. However, phenotypic plasticity encompasses both adaptive and non-adaptive plasticity, and this divergence of plasticity could influence the likelihood of adaptive evolution (Ghalambor *et al.*, 2007; Vinton *et al.*, 2022). Concerning EEO principles, if the plasticity is adaptive, then it is helpful to achieve the optimal trait trade-offs. In contrast, if the plasticity is non-adaptive, for example, the plastic responses to stressful environments may result in trait values which are further away from the favoured optimum trait value (Ghalambor *et al.*, 2007), then this non-adaptive trait combination cannot be predicted by the EEO principle. Therefore, more research is needed to understand how phenotypic plasticity may affect optimality solutions.

6.3.3 Bringing together trait-based ecology and evolutionary biology

Trait-based ecology focuses on how the environment and biotic interactions are causing the instantaneous expression of traits of species, while evolutionary biology focuses on how the environment or biotic interactions have been selecting traits through adaptation over longer time scales. Therefore, the implied mechanisms of trait expression are different in both fields. The former emphasises the instant effects of the environment or biotic interactions on species (*e.g.* through phenotypic

plasticity), whereas the latter emphasises the long-term or historical effects of the environment or biotic interactions on species through genetic changes. Those two have hardly been brought together, and remain in their different scientific fields. However, combining both the historical and the current drivers of trait expression will enable us to better understand how plants or ecosystems may change towards the future (*e.g.*, in facing climate change).

In **Chapter 5**, by looking at both phenotypic plasticity and genetic adaptation at the same time, we attempted to bring these together in one framework that evaluates whether plants could keep up with climate change through phenotypic plasticity and genetic adaptation. However, we were only able to make the evaluation qualitatively in that chapter because of the limited data in our genetic adaptation database and the difficulty of disentangling phenotypic plasticity from ITV. Therefore, to quantitatively predict the winners and losers of plant species in adapting to climate change, the first step is to unify the units of phenotypic plasticity, genetic adaptation and the needed trait variation rate for keeping up with climate change.

As we proposed above, if we can get the genetic adaptation rate with the same unit of ITV or vice versa, then we can get the phenotypic plasticity by subtracting genetic adaptation rate from ITV. Then, firstly, we can obtain the respective contribution of phenotypic plasticity and genetic adaptation in the trait variation of each species. Secondly, we may test the interactions between phenotypic plasticity and genetic adaptation of species by linear regression. Moreover, as we discussed in section **6.2.3**, the respective contribution of phenotypic plasticity and genetic adaptation to climate change depends on the directions and time scales of climate change, phenotypic plasticity and genetic adaptation. Therefore, by looking at phenotypic plasticity, genetic adaptation and their interactions together, we may also evaluate the respective importance of phenotypic plasticity and genetic adaptation for species to adapt to climate change in the future.

In addition, we can make better prediction about the winners and losers, if we can calculate the rate of change in trait values which are needed to keep up with the necessary changes in trait values given climate change. This rate can be predicted based on the relationships between climate and trait values, assuming trait convergence and by applying that relationship to future climatic conditions. By comparing this necessary change rate to the observed trait change rate for a species, we can evaluate for each species if its adaptive capacity in phenotypic plasticity and

genetic adaptation is sufficient to cope with climate change. Therefore, we may predict which species will survive or extinction in facing climate change.

Such predictions will also help further evaluate whether species turnover may happen. Although in **Chapter 5**, we focused on investigating the responses of individuals and populations to climate change, we also introduced that if phenotypic plasticity and genetic adaptation are not sufficient to counter climate change, species turnover may play its role. Since for each trait in our study, the average ITV of most species is less than one (*i.e.* lower than the magnitude of community trait change), some species turnover may happen. However, our research did not allow the quantification of species turnover. Moreover, the likelihood of species turnover is probably context-dependent. On the one hand, if for a community, the ITVs of all species are less than one and we assume this community follows the trend of community trait change as a whole, then some species turnover has to happen to fill the gap to achieve the total community trait change. Whether such species turnover will happen will also depend on the availability of the species pool in its region. On the other hand, from our analysis, we also see that some species have higher ITVs which are close to or even more than one while some species have negative ITVs. If we assume a community with those species also follows the trait change of the whole communities, those species with higher ITVs may be able to increase their abundance (possibly outcompeting species with low ITVs) and reduce the need for species turnover. Therefore, future research is needed to find out which of these situations is most likely to happen.

6.3.4 Implications of nature conservation under climate change

The evaluation and increased understanding of ITV achieved in this thesis also have some important implications for nature conservation to cope with climate change. First, we emphasised ITV is a non-negligible contribution of community trait variation under environmental change and different species varied largely in their ITV magnitudes (**Chapter 3**), which implies that ITV can help plant species to reduce the likelihood of extinction in the face of a changing climate. Moreover, different species may differ in their ability to adapt to climate change. We revealed that herbs had lower adaptive capacity than shrubs and trees, and some biomes such as tropical savannas with dry winters and cold semi-arid regions may have the lowest resilience to climate change (**Chapter 5**). This implies that some species may be more strongly at risk of extinction – due to their low ITV and genetic adaptation – than others. Accounting for this variation in adaptive capacity in nature

conservation will be essential, *e.g.* by prioritising those potentially vulnerable habitats or regions that combine high rates of climate change with species of low adaptive capacity.

Second, since ITV has seldomly been incorporated in any vegetation or land surface models to date, current estimates of species extinction rate may be overestimated (Benito Garzón *et al.*, 2019). For example, we showed that the genetic adaptation rates of plant species were relatively high in the beginning years when they had been introduced to new environments (**Fig. 4.2** in **Chapter 4**). This potential of plant species to avoid extinction to climate change has not yet been incorporated in any existing DGVMs. Besides, a recent study has shown that the acclimation of leaf dark respiration to increased temperature reduces the global plant respiration, which indicates that existing vegetation models (that do not consider plant acclimation) may overestimate the carbon release from global plant respiration (Ren *et al.*, 2023). Therefore, improving DGVMs by incorporating ITV in the future could help make more realistic prediction of species extinction and the global carbon cycle in face of climate change. This will help make better nature conservation policies about biodiversity protection and carbon neutral plans to combat the ongoing climate crisis.

Finally, as we discussed in the above sections, if we can fully disentangle plasticity and genetic adaptation by unifying their units of trait variation, enlarging our genetic adaptation database, and calculating the needed trait change rate in keeping up with climate change, we may potentially make more quantitively and accurate predictions on which plant species may or may not survive under climate change. Therefore, it will also provide valuable and specific guidance for making nature conservation policies on species protection.

6.4 Concluding remarks

With the thriving research on intraspecific trait variation (ITV) in the past decades, various studies have shown that the patterns of trait variation within species challenge our current understanding of functional diversity, as expressed in *e.g.* the assembly theory and the plant economics spectrum (PES) which are all based on species mean trait values. This project is the first comprehensive investigation of the patterns and drivers of phenotypic plasticity and genetic adaptation of plant functional traits on a global scale. One of the significant findings was that the commonly regarded PES did not maintain within species, which indicates that the PES does not represent general plant strategies. The weakened and disappearing trait correlation within species compared to that of between species suggests the

existence and dominance of alternative strategies within local communities. This also implies that most trait-trait relationships observed between species were driven by common environmental drivers and these relationships may be decoupled in a future climate. The second major finding was that species differed in their phenotypic plasticity and genetic adaptation ability. The combined difference of these two components of ITV also indicates the varied adaptive capacity of species with different growth forms and different resilience among biomes to climate change. Lastly, the large unexplained variation suggests that further research is needed to understand the drivers of phenotypic plasticity and genetic adaptation. Taken together, this study enhanced our understanding of functional diversity within species. I believe that this understanding has important implications for vegetation modelling and nature conservation under climate change. If we can solve a number of conceptual challenges and encourage the systematic and widespread capture of data relating to intraspecific trait variation and genetic adaptation, as we discussed above, we can make better predictions about species extinction and ecosystem stability in a future climate.