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

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Summary

Over the past two decades, trait-based ecology has been a popular subdiscipline of plant ecology, which focuses on studying plant functional traits instead of species identity to understand how plants interact with the environment and other organisms. Plant functional traits are defined as the morphological, physiological and phenological attributes of organisms that impact plant fitness indirectly via their effects on the individual performance - growth, reproduction and survival. The variation of plant functional traits between organisms, also defined as plant functional diversity, is supposed to reflect community responses to abiotic and biotic conditions. Understanding why and how plants vary their traits, in the context of climate change, is of major interest to plant ecologists.

In Chapter 1, I introduced the importance of plant biodiversity, especially functional diversity, in maintaining ecosystem stability under the threats of climate change. Then, I reviewed current knowledge that has been proposed to understand functional diversity. This included the hypotheses of habitat filtering and limiting similarity which were raised to explain the mechanisms of community assembly rules. These mechanisms are presumed to culminate in trait axes such as the leaf economics spectrum (LES) which was proposed to understand plant strategies from a plant carbon management perspective. However, these theories and patterns are all based on interspecific trait variation, which only uses a mean value to represent each trait of a species. Actually, this estimation is far from representing the trait variation in reality. During the past decade, an increasing number of studies has reemphasised that intraspecific trait variation (ITV) is an important and unignorable contribution of functional diversity. This thesis focusses on knowledge gaps associated to ITV. The overarching research question is whether the patterns of ITV resemble that of interspecific variation and what the general drivers of ITV are. Therefore, this thesis aimed to investigate the global patterns and drivers of the two components of ITV, phenotypic plasticity and genetic adaptation respectively, to enhance our understanding of plant strategies in response to climate change.

In Chapter 2, I assessed whether the commonly reported trait-trait relationships between species, such as reflected in the plant economics spectrum (PES), reflect plant strategies in reality. I proposed a novel conceptual framework that allowed us to distinguish different mechanisms that lead to trait-trait relationships between species. Based on our global species' ITV database, I compared the direction and strength of intraspecific trait variation vs. interspecific trait variation. I found that

generally, compared to between species, trait–trait relationships within species were much weaker or totally disappeared. Almost only within the leaf economics spectrum (LES) traits, the between-species trait–trait relationships were translated into positive relationships within species, which suggests that they may represent plant strategies. This study deepens our understanding of general plant strategies and imply to consider the potential decoupling of those trait-trait relationships that were caused by co-varying common drivers when making model projections of ecosystem functioning in the future.

In Chapter 3, I aimed to assess the general drivers of intraspecific trait variation. In particular, I analysed whether species feature, biotic interactions, and environmental conditions are related to ITV on a global scale. I used growth form as our proxy of species feature, species alpha niche position (αi) calculated from the trait-gradient analysis as our proxy of biotic interaction, species beta niche position βi and species niche breadth Ri calculated from the trait-gradient analysis as our proxies of the environmental conditions and the position of species within the C, S, R triangle as our proxy of environment & biotic interactions. I then applied multiple statistical methods to test which proxy was related to ITV. I found that different traits had different main drivers, implying that the drivers of ITV were trait-specific. Although I did not find a general driver for ITV, I still found some order among those idiosyncratic patterns: leaf economics spectrum traits were more related to environmental conditions and leaf morphology traits were more related to biotic interactions. Size-related traits were related to both abiotic and biotic conditions. Therefore, it warrants further investigation on why certain clusters of traits seem to have similar drivers of intraspecific trait variation.

For Chapter 4, I performed a meta-analysis to investigate patterns of genetic adaptation rates and assess how these rates differ among plant species groups, growth forms and trait types, using our newly compiled genetic adaptation database of plant functional traits. This database specifically focuses on genetic adaptation independent of phenotypic plasticity. The results showed plants adapt fastest in the early years after encountering a new environment, but these rates slow down subsequently. Overall, shrubs have higher adaptation rates than trees, which confers shrubs an adaptive advantage over trees. Different adaptation rates among growth forms, life histories, phylogenetic groups and trait types suggest an important additional mechanism through which climate change may affect community composition. This study improves our understanding about how plant adapt to new environments and has important implications on the protection for the species groups with lower genetic adaptation rates.

In Chapter 5, I explored the respective and combined patterns of plasticity and adaptation for different growth forms and biomes at the global scale, based on our global species' ITV and global adaptation rate databases. I found that plasticity, adaptation and resilience differed by growth form and biome and these patterns also differed by trait. I showed that generally, herbs have lower adaptive capacity than shrubs and trees which may explain the shrub encroachment and treeline shift globally. I also observed that adaptation of biomes may be related to the humidity of climate while the plasticity within the biomes may link to continentality. I found that biomes such as the tropical savanna with dry winters and the cold semi-arid biome are facing faster changing rates of climate while they have a relatively low adaptive capacity. This implies these biomes may be most vulnerable to climate change. This is the first study quantifying the resilience among different growth forms and biomes and further studies are needed to finetune our understanding on these patterns.

In Chapter 6, I summarised our main findings and discussed their scientific implications. Our first contribution to science is we found that the plant economic spectrum (PES) detected between species did not remain within species, which suggests the PES does not represent a general plant strategy in reality. Further analysis also showed that the drivers of intraspecific variation were trait-specific, which suggests that different traits do not have strong common drivers and therefore most trait-trait relationships within species were quite weak. The disappeared trait-trait relationships within species compared to that of between species implies that these trait-trait relationships were probably driven by common environmental drivers. Therefore, they may be also decoupled between species if those environmental drivers are not related in a future climate. This may have further implications on vegetation modelling. Our second contribution is we showed that different species varied in their phenotypic plasticity and in their genetic adaptation. The respective variation of phenotypic plasticity and genetic adaptation contribute to a different adaptive capacity of species and therefore shapes the different resilience patterns among growth forms and biomes. We also qualitatively evaluated the vulnerability of different biomes to climate change and discussed its related implications on nature conservation. Thereafter, I pointed out possible directions for future research. I proposed a potential way to fully disentangle phenotypic plasticity and genetic adaptation within the overall intraspecific trait variation at a species

level. This could provide a first step to finally predict which plant species will be the winners and losers in the face of climate change. Altogether, I believe that our findings deepen our understanding of general plant strategies and have important implications on vegetation modelling and nature conservation.