Trait-based studies of páramo vegetation in the northern Andes

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Chapter 6

Synthesis

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The present study is among the first attempts to systematically collect quantitative information of functional plants traits in the páramo of Colombia. This understanding is necessary, as in spite of the essential role of páramo ecosystems in social and biological contexts, human activities in the páramo put at risk the maintenance of ecological functions and the provision of ecosystem services of páramo (Vuille et al. 2003, Bradley et al. 2006, Andrade et al. 2010). I collected functional plant trait information from almost 160 native plant species belonging to páramo ecosystems. Examining functional traits and environmental conditions (e.g., soil variables) will contribute to establish a baseline for the functional structure of páramo plant communities under semi-natural conditions. In the following sections I will discuss the principal findings of my study and future research options.

Non-destructive methods to assess the biomass of páramo vegetation

Severely degraded páramo typically features a low aboveground biomass (Hofstede 1995, Verweij 1995, Vargas 1996), which recovers only slowly if the páramo is protected against further human impact. Our allometric methods to estimate plot biomass in a non-destructive way (Chapter 2), opened many opportunities to monitor quantitative information regarding biomass recovery of páramo vegetation in different scenarios, for example in areas selected for environmental restoration (Ramírez et al. 2015). As indicated in Chapter 2, allometric modelling approaches have been used in the tropical Andes, but only for biomass estimates of particular growth forms, such as tussocks (Verweij et al. 2003, Oliveras et al. 2014) or caulirosettes (Torres et al. 2012). Instead, our estimation method involved all vascular species in the plots, and therefore yielded an optimal approximation of biomass production of paramo vegetation (Körner 2003). Besides, these allometric models also allowed to efficiently estimate the belowground biomass of which the importance has repeatedly been emphasized (Scurlock and Hall 1998, Ma et al. 2008). Knowledge of the different components in carbon allocation patterns can in this way, underpin estimations of local and global carbon budgets (Flombaum and Sala 2007). Information generated at plot level of páramo plant biomass is also important for estimating primary productivity using vegetation models and remote sensing techniques (Minaya et al. 2016). On the downside, it must be realized that considerable efforts may be required to reduce the uncertainties of the biomass estimates obtained by allometric methods to acceptable levels, especially in case the species composition of the targeted paramo vegetation is quite distinct from that recorded in our study.

Páramo plant community structure related to trait information

I consider as main findings of this study, which also act as a general answer to the research questions formulated in the introduction and in Chapters 3-5, that the community structure and successional patterns of the páramo vegetation showed significant relationships with the mean and variability of specific leaf area (SLA) and plant height. In part, these findings were not unexpected: plant community structure has earlier been found to correlate with SLA and plant height (Weiher et al. 1999, Choler 2005, Diaz et al. 2016, Blonder et al. 2018). However, in the context of páramo new insights were obtained of which the most important ones can be reiterated and synthesized as follows:

1) Aboveground plant biomass in páramo ecosystems is influenced by the interplay between plant-traits, soil variables and plant species composition. In path models these three variables

explained almost 50% of the biomass variation, as shown in Chapter 3. The framework formulated in functional ecology approaches emphasizes the interrelationship between plant traits, environmental factors (biotic and abiotic), and ecosystem attributes (Diaz et al. 2007). Path analysis and structural equation models have been adopted as an alternative to test the contribution of multiple variables (e.g., plant traits, environmental factors) to explain ecosystem properties (e.g., green biomass, total soil C) (Shipley 2000, Grace 2006, Lavorel and Grigulis 2012, Becknell and Power 2014, Sande et al. 2017). This approach is encouraging to evaluate the interactions that occur in nature, by integrating the effects of different factors in one analysis. On the other hand, conceptual models using environmental components can be tested to disentangle the contribution of differences factors to ecosystem processes. For example, in our study, community values of SLA showed a negative relationship with aboveground biomass while plant height showed a positive relationship. From this, we could confirm the hypothesis that páramo vegetation is functionally structured by plant traits. Our results also showed that species composition, as biotic factor, explained most of the variation in the aboveground biomass, and essentially cancelled out the effect of SLA on biomass. Therefore, the effect of SLA on biomass seemed mostly interspecific, i.e., a consequence of the between-plot differences in species composition. From the effects of the soil variables we inferred that soil acidity and soil bulk density acted as key soil variables driving the aboveground biomass in semi-natural areas of páramo vegetation. This information may contribute to a better understanding of the underlying mechanisms that maintain páramo biomass. Aboveground plant biomass in páramo ecosystem is essential to maintain ecosystem services (e.g., water regulation). Testing simultaneously key environmental factors like soil temperature and humidity, microbial activity, should be extended in high Andean grasslands to better comprehend the functioning of páramo ecosystems.

2) Vascular plant species with a higher interspecific variability of SLA and plant height showed a higher local and regional abundance in our páramo plots. The latitudinal extent of these species was only related to the interspecific variability of SLA and not to that of plant height. These findings are the among the first to report ecological differentiation in trait variability between páramo plant species that occur in higher and lower abundances at local and regional levels, and between species with different patterns of latitudinal distribution. At local and regional scales, páramo plant communities reveal the general pattern found elsewhere, in which the majority of the species occur in the lower tail of abundance distributions (Brown et al. 1996, Walker et al. 1999, Gaston 2011). Previous research in páramo plant communities from different perspectives has shown the association between plant communities and environmental factors (Cleef 1979, 1981, Monasterio 1980, Rangel-Ch 2000, Rangel-Ch and Sánchez 2005, Cleef et al. 2005, Arellano-P and Rangel-Ch 2008, Moscol-Olivera and Cleef 2009, Rangel-Ch 2018). Páramo ecosystems are characterized by a high variability in topography, soil and environmental conditions. It seems that a higher variability in SLA and plant height confers to the species the ability to cope with the environmental variability of the páramo ecosystem. Intraspecific variability in SLA was consistently positively related to the latitudinal distribution of the species. However, plant height did not show a relationship with the distribution of plant species. Although SLA and plant height correlate with soil resource availability, light variability

(Lambers and Poorter 1992, Poorter et al. 2009) and biotic interactions (De la Riva et al. 2016, Moles et al. 2009), they may represent different plant strategies that lead to some extent to divergent patterns at local and regional scale.

3) Community weighted means of SLA values were higher in early-successional than in late-successional plots. This suggests that the most dominant species in early paramo succession are selected for their capacity to quickly acquire external resources enabling fast growth, while species in late-successional stages of paramo vegetation attain dominance through a more efficient nutrient uptake, resource conservation and an improved resistance to drought. However, evidence that mid-successional communities would be predominantly built up by species showing a larger intraspecific variability in SLA than early- or late-successional communities was not detected. As expected, late-successional communities were built up by species showing a relatively low intraspecific variability, but early-successional communities did not. In my view these results suggest that in late-successional stages, species that show a large variability in SLA are preferentially filtered out because quickly growing plants that show high SLA values cannot be replaced adequately. On the other hand, in early-successional stages, species with a high SLA plasticity are not filtered out, because slow growing plants (with associated low SLA values) can easily persist in time. In synthesis, the present study showed that SLA values of plant species determine their role in paramo succession: mean SLA values mostly relate to the dominance of a species in any successional stage, while the intraspecific SLA variability mostly affects a species' chance to avoid being filtered out from late-successional stages.

New research

Integrating reproductive and physiological traits

Without any doubt, the results of our study are strongly constrained by the fact that we only studied two plant traits. Also, it is important to realize that SLA is part of a correlative complex of many traits related to the fitness of plant species (Poorter et al. 2009). In such situations, functional trade-offs, or simply spuriousness resulting from confounding variables driving SLA values and plant fitness simultaneously, may yield a large variety among species in their SLA responses along gradients. Regarding plant height quite similar remarks can be made. For more understanding of these trade-offs, it is crucial that in new studies more trait information is collected, preferably but not exclusively concerning traits that show variation independently from that of SLA or plant height, i.e., traits that are uncorrelated to the acquisition-conservation axis and more related to life history, reproduction or clonality (Díaz et al. 2004, 2016). The following quantitative traits might be measured with relative ease and efficiency: leaf dry matter content (correlates negatively with relative growth rates and indicative for resistance to physical hazards), leaf N and leaf P concentration (correlates with maximum photosynthetic rates and also indicative for nutritional quality), resprouting capacity (resistance to burning and grazing), and proportion of annuals (mostly weedy species) to perennials which is indicative for the successional status (Grime 1979, Reich et al. 1992, 1997, Poorter and Garnier 1999, Ryser and Urbas 2000, Garnier et al. 2004, Shipley 2006). Measuring physiological traits (e.g. maximum stomatal conductance, maximum net phytosynthesis) might contribute to a better understanding of plant performance in páramo ecosystems under different environmental conditions (e.g., elevation, humidity gradients). Moreover, including a physiological dimension might help to clarify the link between morphological and structural plant traits and species performance (Belluau and Shipley 2018).

Traits in long-term monitoring programs

Secondly, more research is needed to step up from my studies that merely quantified spatial trait-environment relationships at one moment in time, to studies that allow recording spatio-temporal change, and preferably include experimental manipulation. For this, recurrent community observations are imperative, which might be facilitated, for example, by monitoring programs such as those developed in the Andes of South America that focus on paramo restoration (Cabrera and Ramirez 2014, MADS 2015), páramo responses to global change (Báez et al. 2014, Cuesta et al. 2017), and those implemented in Protected Areas. Promising new research might follow the analytical trait-based framework proposed by Suding et al. (2008) (see also Lavorel and Garnier 2002). This framework facilitates predicting engineering resilience (Holling 1996, Peterson et al. 1998) in community properties on the basis of correlations between response and effect traits (Violle et al. 2007). Furthermore, applying open top chamber techniques to experimentally raise ambient temperatures (Henry and Molau 1997, Totland and Nylehn 1998, Totland 1999, Kudernatsch et al. 2008), biomass recovery can be studied as function of climate change. More in general, such studies may contribute to test whether the biomass of páramo communities can be predicted by the functional diversity of the constituent plants, following the framework set out by Diaz et al. (2007). Long-term monitoring programs in the Andes have shown that along elevational gradients plant communities have changed in response to temperature and humidity (Carilla et al. 2018). These programs have shown shifts in the relative abundance, in composition and plant cover across 10 years of plant surveys (Carilla et al. 2018). As seen before, intraspecific variability in páramo plant species is a key factor in determining plant communities (see Chapter 3 and 4). Including in these scenarios trait information (morphological, physiological and reproductive) will increase the understanding of plant performance in response to climate, and also to plant-plant interactions (e.g., Blonder et al. 2018). Traits can be seen as a proxy to determine the intrinsic adaptive capacity of species (Dawson et al. 2011) that might play a role in the ability of species to adjust their response to abiotic and biotic factors. A long-term monitoring of plant communities combining trait information, biomass information, and environmental data may contribute to identify whether observed changes in plant communities are transient responses or whether these changes have a genetic component (Dawson et al. 2011). Patterns in community ecology respond to evolutionary processes inherent of each taxon. New insight in the evolutionary processes for Andean plant species is given by the increasing phylogenetic information of highly diverse genus (Diazgranados and Barber 2017, Vargas et al. 2017). Phylogenetic and trait information will contribute to understand current patterns of biodiversity and possible responses of plant communities in a highly changing world.