Global environmental changes in the high tropical Andes

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General Discussion

Impacts of global environmental change stressors on high Andean ecosystems across space and time: key issues and advances
I. Introduction

1.1 Overarching rationale

The high tropical Andes constitute a natural laboratory for the study of the effects of climate and land use change (Dangles et al., 2017). High Andean ecosystems are sensitive to ongoing climate change because many ecological processes and characteristics, such as biomass productivity, species distribution, and plant community composition are strongly linked to the elevation-temperature gradient (Körner, 2003) and precipitation patterns (Sklenár & Balslev, 2005). Furthermore, humans transformed a large proportion of the high Andean landscapes, particularly at lower elevations (Josse et al., 2011; Duchicela et al., 2019). This transformation is due to the long legacy of occupation (c. 12,000 years; Rademaker et al. (2014)), the long-lasting cultivation of annual crops such as Andean tubers (c. c. 2200 years; Léon (1977), and the herding of camelids (c. 1000 years; Postigo (2012)). The twofold pressures of climate and land use change form significant challenges to the conservation and management of high tropical Andean ecosystems. Understanding the nature of these pressures and how negative impacts can be mitigated are the main topics in the research presented in this thesis. Here I briefly summarize the challenges by climate and land use change, and the scientific approach I have used to address these challenges.

1.1.1 Climate change in the high tropical Andes

Tropical high Andean ecosystems have been identified as highly vulnerable to climate change, because of the narrow ecotones, where significant abiotic changes occur over short distances (Von Humboldt, 1807; Cleef, 1981), and to the prevalence of narrow-range species, which have limited thermal tolerances (Ramirez-Villegas et al., 2014). Indeed, the high Andean landscapes have been observed to change at a decadal rate due to the combined effect of climate change and glacier retreat dynamics (Seimon et al., 2017; Vuille et al., 2018). Changes in environmental conditions, particularly mean annual air temperatures, combined with ongoing glacier retreat are forcing alpine species to migrate upward (Seimon et al., 2007; Feeley et al., 2011; Morueta-Holme et al., 2015), and are already altering species alpha diversity and plant community composition along environmental gradients (Carilla et al., 2018). However, the likely nature and direction of ecosystem functions, vegetation changes, and species responses under future climate scenarios remain uncertain due to the lack of basic understanding of ecosystem functioning, long-term (multi-decadal)
vegetation and climate data, and data on species/community distribution and composition across the high tropical Andes.

To better understand the long-term effects of temperature changes and glacier loss on tropical alpine species and communities, improved knowledge of factors controlling the plant community composition and the plants’ thermal niches is essential. In the context of this knowledge gap in climate change impacts in the high tropical Andes, the research presented in this thesis focused on: (i) understanding patterns and processes that influence plant community composition and species diversity in high tropical alpine ecosystems (Chapter 3), (ii) determining alpine species and communities thermal niche traits to assess the potential impacts of global warming on tropical alpine ecosystems (Chapter 4), and (iii) synthesizing the expected and observed changes in tropical high Andean landscapes due to the combined effect of climate change and glacier shrinking (Chapter 5).

1.1.2 Land use change in the high tropical Andes

Long-fallow agriculture (i.e. potatoes production) combined with cattle grazing and burning have been extensively practiced for millennia in the mountain habitats of the tropical Andes (Sarmiento et al., 2003; Young, 2009). This long-term human utilization of Andean environments has resulted in a loss of species and functional diversity (Hofstede et al., 1995b; Ramsay & Oxley, 1996; Llambi & Cuesta, 2014), as well as in ecosystem degradation (e.g. loss of productivity; Ramsay and Oxley (2001b)). Several studies reported the impacts of intensive grazing, burning, cultivation, and forestation with exotic species on the physical properties and regulation capacity of the soils (Hofstede, 1995; Podwojewski et al., 2002; Farley & Kelly, 2004; Buytaert et al., 2005). Intensive grazing and burning lead to a change in the community structure of the vegetation, which in turns causes biodiversity loss, a change in soil microclimate conditions due to lower above ground biomass (AGB), and more exposure of bare ground (Hofstede et al., 1995b; Ramsay & Oxley, 1996; Keating, 2000; Monteiro et al., 2011). Nonetheless, little is known about the resilient capacity of Andean systems to recover from land use impacts using biodiversity, carbon stocks, and biomass allocation as indicators for the ecosystem recovery. One of the major knowledge gaps resides in the identification of sensitive indicators to assess ecosystem recovery from human agricultural practices (Abreu et al., 2009). This is due to the limited empirical research aimed at quantifying biodiversity and carbon outcomes, or addressing synergies and trade-offs among biodiversity and ecosystem functionality, in conservation and sustainability programs promoted
by international cooperative initiatives (Bremer et al., 2019). This leaves open questions about whether sustainable land management practices aimed at securing provision of critical ecosystem services or preserving high Andean ecosystems are meaningfully contributing to global and national biodiversity conservation goals. This thesis contributed to this emerging research topic by assessing temporal trends in ecosystem recovery after land use practices stopped by analysing trends in vegetation cover, carbon stocks and sequestration, and plant community diversity at two sites in the highlands of Peru and Ecuador (chapter 6 and 7). Finally, in chapter 8, I examined the threats posed by GEC stressors at a regional scale and identified priority areas for biodiversity conservation in continental Ecuador, considering the short and mid-term impacts of global environmental stressors.

1.1.3 Challenges and questions for conservation and management in the high tropical Andes

The combined effects of both stressors - climate and land use change - may strongly alter ecosystem functionality and community composition, and augment biodiversity loss (Buytaert et al., 2011). Therefore, understanding the resilience of mountain ecosystems in the high tropical Andes is paramount given the critical role these ecosystems play in providing ecosystem services, such as water regulation, for some of the most densely populated high mountain regions in the world (Buytaert & De Bièvre, 2012). A few studies have focused on how tropical alpine ecosystems recover after agricultural land use ceased (Sarmiento & Bottner, 2002; Abreu et al., 2009; Vargas Ríos, 2011), but our understanding of how these ecosystems recover as a whole is still limited. To my knowledge there are no published studies analysing and linking carbon uptake, vegetation cover, and plant community diversity as has been documented previously for grassland systems of higher latitudes (Tilman & Downing, 1994; Tilman et al., 2014) or for tropical rain forests (Finegan et al., 2015; Poorter et al., 2015). Finally, the fast rate of habitat loss and the expected impacts of climate change over the tropical Andes (Jantz et al., 2015), requires the identification of critical areas where conservation actions can be prioritized.

Following from these challenges, in this thesis I addressed six specific research questions related to ecological variation in space and time, and to ecosystem management:

*Patterns (space)*
Chapter 9

I. What are the patterns and processes that influence plant community composition, species abundances and richness, and their relation with the environmental gradients that characterize high tropical alpine ecosystems? (Chapter 3)

II. What is the effect of latitudinal and elevation gradients in shaping species and community niche traits across the high tropical Andes? (Chapters 4).

Trends (time)

I. How do high Andean landscapes change due to glacier retreat and climate warming? (Chapter 5).

II. To what extent and at which rate do ecosystems in the high Andes recover from human disturbance in terms of their carbon storage, biomass productivity, and species richness? (Chapter 6-7).

Actions (conservation, restoration/rehabilitation)

I. What indicators are sensitive enough to assess the extent of ecosystem recovery upon previous human disturbance in the high tropical Andes? (Chapter 7).

II. What are the most important areas for biodiversity conservation in mainland Ecuador, considering the various drivers of environmental change? (Chapter 8).

1.2 Scientific approach

In this thesis, the structure and functioning of high Andean ecosystems, and the associated dynamics in space and time, were evaluated in terms of plant cover and diversity, as well as of stocks and flows of carbon. I used a combination of comparative gradient analyses and diachronic studies of vegetation dynamics by means of permanent vegetation study plots. These plots were distributed along latitudinal and environmental gradients (Chapter 3-5). The distribution and number of replicates of the permanent plots allowed me to up-scale plot analyses to the landscape and regional scale, and to consider different underlying mechanisms that drive biota assemblages and ecosystem functions operating at different spatial scales (Körner, 2012). Further, long-fallow systems and areas where land use practices were suppressed provided me a unique opportunity to study the regeneration of vegetation and carbon stocks using a chronosequence
approach (Sarmiento et al., 2003; Bueno et al., 2015). Finally, I used snapshot datasets, to analyse glacial retreat and identify conservation priority areas for mainland Ecuador.

In this final chapter (chapter 9), I synthesize the results of this thesis and compare these with those from other related studies, addressing each of my specific research questions. These relate to spatial patterns (section 2), trends in time (section 3), and ecosystem management actions (section 4). I will also discuss the limitations of my research (section 5) and the need for an interdisciplinary long-term research agenda to develop a more comprehensive understanding of the links and complex feedbacks between global environmental change (GEC) stressors, biodiversity, ecosystem services, and socio-economic development across the high tropical Andes (section 6). I argue that an improved understanding of these linkages will be a key contribution to the conservation and management of these dynamic landscapes and to the design of better strategies for increasing ecosystem resilient capacity to absorb climate and land use change impacts.

2. Spatial patterns and environmental gradients that shape vegetation on mountain summits in the high tropical Andes

This thesis section dealt with two main questions: (i) What are the patterns and processes that influence plant community composition, species abundances and species richness, and their relation with the environmental gradients that characterize high tropical alpine ecosystems? (Chapter 3), and (ii) What is the effect of latitudinal and elevation gradients in shaping species and community niche traits across the high tropical Andes? (Chapter 4). Based on the research presented here, and on evidence in the literature, I concluded that: (i) annual precipitation and maximum air temperatures are the key abiotic factors driving plant community patterns combined with local spatial heterogeneity and geographic isolation, and (ii) that latitude and altitude have a profound effect, shaping species and communities thermal niche traits. Reduced seasonal temperature variation at low latitudes and restricted elevation ranges are associated with narrower thermal tolerances of tropical alpine species and communities, compared to those at higher latitudes. I first briefly discuss how I reach these conclusions.
This discussion is framed in the integrated community concept (Lortie et al., 2004) that contends that plant community patterns\(^1\) are determined by non-linear interactions among: (i) stochastic biogeographical processes, (ii) the specific tolerances of species to prevailing local abiotic conditions, (iii) positive and negative feedbacks (interactions) among plants, and (iv) direct interactions with other trophic levels. In this final chapter, I have mainly focused on the specific tolerances of species to abiotic conditions because it was directly evaluated in the related chapters of this thesis (chapters 3-4).

2.1 Vegetation patterns across the high tropical Andes

In chapter 3, I assessed how environmental gradients\(^2\) in the high tropical Andes influence plant community composition, species abundances and species richness. At a continental scale, I found that the most important abiotic factors driving plant community patterns are annual precipitation and maximum air temperatures combined with substrate-type, mainly rock and scree, as reported previously for global and continental scales (Kreft & Jetz, 2007; Crous et al., 2013). I concluded that patterns in tropical alpine summit plant communities are primarily driven by local spatial heterogeneity, and that these patterns, in turn, depend on the variability of environmental conditions in the summit landscape, which will determine the number of habitat types as evidenced in the summits of Northwestern Argentina (Carilla et al., 2018). Spatial heterogeneity is related to the spatial configuration of habitats as well as to other factors such as dispersal traits (Dufour et al., 2006), and local topography (Scherrer & Körner, 2011), but I have not evaluated these effects in this thesis. Additionally, I assessed how plant community Beta diversity relates to the geographic distance across the high tropical Andes. I found that the plant community dissimilarity increased with geographic distance. Further, I found that Páramo summits exhibit a higher species turnover than Puna summits, supporting the conclusion that Beta diversity is primary controlled by geographic isolation (i.e. the continental insularity theory, Anthelme et al. (2014)). The principal observed differences in plant community composition among summits combined with the skewed taxonomic composition towards a few highly diverse genera further support the idea of a high degree

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1 In this thesis I refer to patterns in mountain summits plant community’s composition and structure, such as species richness, species abundances, and community thermal niche traits.

2 Environmental gradients in this thesis are defined as abiotic factors (e.g. annual rainfall, substrate-type) that vary along elevation and latitudinal gradients.
of recent local speciation driven by geographic isolation (Hughes & Eastwood, 2006). The reported high average net diversification rates reported for several Páramo plant lineages provides additional support for recent speciation driven by geographic isolation (Madriñán et al., 2013).

2.2 Thermal niche traits along latitudinal and elevation gradients

In chapter 4, I sought to test for the first time the Climate Variability Hypothesis (CVH; Stevens (1989)) in alpine plant communities across tropical mountain summits distributed along the Andes. I found that non-seasonal climate\(^3\) conditions on alpine summits in the equatorial tropics select for plant species with narrower thermal tolerances, compared to alpine summits exposed to increasing annual temperature seasonality at higher latitudes, which favours species with broader thermal tolerances. Further, I found a consistent trend in which species with ranges restricted to near the equator had narrower niche breadth than those with broader latitudinal distributions or occurring further from the equator. Additionally, when the species thermal niche traits were analyzed along the elevation gradient, both the thermal optimum and the niche breadth were consistently lower in species with ranges restricted to alpine environments than those with wider altitudinal range. Plant communities found on Andean summits reflected the species patterns by exhibiting a significant positive relationship between community niche breadth scores and latitude, and a negative one between altitude and community mean and minimum temperature scores. The extent of topographic isolation (Anthelme et al., 2014), changes in the alpine life zone extent during the glacial-interglacial cycles of the Pleistocene (Flantua & Hooghiemstra, 2018), and summit elevation seem to be the underlying environmental factors explaining both species and community thermal niche traits. Kessler (2002) analyzed the spatial distribution of endemic plants along elevation gradients in Ecuador and found that patterns appear to be influenced both by taxon specific ecological traits (e.g. life form, dispersal) in their specific interaction with historical processes (i.e. landscape evolution, specific evolutionary history of each taxon) and by geographical isolation.

Based on the CVH hypothesis, and Kessler’s (2002) findings, I hypothesized that narrow-range species and communities, restricted to or near equatorial latitudes, should be highly vulnerable to global warming due to a limited thermal tolerance.

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\(^3\) Non-season climate refers in this thesis as reduced seasonal air temperature throughout the year.
Using species niche breadth data and projected warming rates by the end of this century from two Representative Concentration Pathway (RCPs) scenarios, I estimated the potential vulnerability of species and communities to climate warming using the estimated proportion of species niche breadth contraction under both scenarios. I found that species particularly prone to the effects of climate warming are those with the narrowest thermal niches and are also restricted to the highest sections of mountain summits (i.e. cryophilic/cold-adapted species). Spatially restricted cryophilic species would be subject to physiological stress combined with loss of habitat suitability, due to increases in seasonal temperature variability and coupled with decreases in diurnal temperature variability due to faster night-time versus daytime warming. These findings confirm the relevance of thermal niche traits to identify species that are particularly prone to the effects of climate warming and communities with a higher risk of being subject to a warming-induced transformation of their species composition in the coming decades. Further, species niche traits are a paramount piece of information to understand community shift time lags due to disequilibrium range dynamics (Alexander et al., 2018).

3. Alpine vegetation trends (time scale)

In this section of my thesis I focused on two primary questions, linked to the two primary Global Environmental Change (GEC) stressors: (i) How high Andean landscapes are changing due to glacier retreat and climate warming? (Chapter 5), and (ii) How do temporal changes in carbon storage, biomass allocation, and species richness reflect ecosystem recovery from human disturbance in the high-Andes? (Chapters 6-7). Based on the research presented here and on evidence from the literature, I concluded that: (i) high Andean landscapes are changing at the fastest rate since the Little Ice Age (LAI) due to increased anomalies⁴ in air temperatures above 3000 m asl since the 1970’s, combined with massive loss of their glacier cover, (ii) landscape transformation has major implications for the Andean biota including alteration of hydrological dynamics in glacier-fed streams and high Andean wetlands, leading to changes in community composition, species interactions, carbon dynamics, and biodiversity loss, and (iii) high Andean ecosystems are able to recover from land use impacts based on the observed

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⁴ Temperature anomalies refers to the difference between the long-term average temperature (sometimes called a reference value) and the temperature that is actually occurring. In other words, the long-term average temperature is one that would be expected; the anomaly is the difference between what you would expect and what is happening.
high AGB sequestration rates which in turn stimulates successional vegetation
dynamics leading to an increase in species functional diversity. I now briefly
discuss how I reached these conclusions.

3.1 Vegetation and landscape changes - Future projections

In this sub-section, I focused my research on the understanding of how high
Andean landscapes are changing due to the combined effect of glacier retreat
and climate warming in the last 40-50 years (Chapter 5). I found that these
landscapes are rapidly changing with the major transformations being related to
glacier dynamics. Since the 1970’s the tropical glaciers entered in a strong glacier
shrinkage phase which led to a loss of 20 to 50% of their cover, and some have
completely disappeared (Vuille et al., 2008; Vuille et al., 2018). Concurrently, in
the tropical Andes above 3000 m asl mean annual temperatures have increased
at a rate of approximately 0.04 °C year\(^{-1}\) in the last 30 years of the 20th century
(Vuille et al., 2003). Thus, glacier shrinkage in the tropical Andes has been more
pronounced than the global average in the last ca. 40 years, and is consistently
and robustly related to increasing temperatures (Vuille et al., 2018). Furthermore,
the glacier shrink scenarios for the Antisana and Cordillera de Vilcanota areas
(CV) suggested that by the end of the century potential glacier area losses of
72% and 60% are to be expected under a low-emission scenario (RCP 2.6) and
almost no glaciers are left in both locations (losses of 98% and 97%) under a high
emission scenario (RCP 8.5).

The projected massive loss of glacier area suggests major landscape transformations
with important ecological implications which can be summarized as: (i) formation
of new lakes and drying of existing ones as glaciers recede, (ii) alteration of
hydrological dynamics in glacier-fed streams and high Andean wetlands, leading
to vegetation modification and changes in community composition and species
interactions (e.g. on aquatic macroinvertebrates), (iii) species colonization of
new deglaciated areas along with species upward migration, (iv) shifts in the
balance between diverse cushion-dominated peat bogs and drier grass-dominated
wetlands, and (v) eventual loss of alpine biota adapted to waterlogged conditions.
Additionally, glacier shrinkage, landscape transformation, and ecosystem
modifications in the Andes can in turn affect critical ecosystem services for a
large number of rural and urban population centers (Mark et al., 2017), including
water provision and streamflow regulation (Mark, 2008), degradation of
grazing grounds for domestic cattle (particularly Andean camelids, Duchicela
et al. (2019)), and loss of carbon accumulation capacity in soils (Benavides et
Furthermore, the combined effect of climate change and reduction of stream-flow from glacier catchments on Andean wetlands has the potential to reduce their soil water regulation capacity, and to increase soil erosion and organic matter decomposition (Buytaert et al., 2011; Urbina & Benavides, 2015; Hribljan et al., 2016). The resulting changes in these ecosystem functions could threaten the carbon stability of high Andean wetlands, transforming them from a long-term sink into a source.

3.2 Vegetation recovery trends (short term)

In this sub-section of my thesis, I focused on understanding the resilience of high Andean ecosystems to land use impacts. I studied ecosystem recovery from human disturbance by means of analysing temporal changes in carbon storage, carbon uptake, and species richness in two contrasting locations of the tropical Andes. These are the humid páramos and Andean forests of the Yanacocha Reserve in Ecuador, and the mesic puna grasslands and wetlands of Huancavelica in Peru (chapters 6 and 7, respectively).

Specifically, I assessed the natural recovery of both the Andean forest (>3700 m) and páramo, 23 years after human uses ceased. I used carbon stocks and sequestration rates as a proxy to infer the recovery status of the landscape based on a synchronic approach (i.e. permanent plots dataset; chapter 6). I found that carbon stocks were lower (125.7 Mg C ha-1) than previously reported for a similar tropical mountain location, which was without human intervention (161 Mg C ha-1). The difference between both studies is probably due to the relatively lower Above Ground Biomass (AGB; 34 Mg C ha-1) and Soil Organic Contents (SOC; 64 Mg C ha-1) stocks registered in the Yanacocha Andean forest, which may reflect the different disturbance histories. Although the mountain ecosystems in Yanacocha did recover over a period of 23 years, a longer period of recovery may be needed to reach reference values for the above ground biomass. Regarding SOC stocks from the Yanacocha Reserve, I found a consistent trend of higher SOC contents in the páramo soils (112 Mg C ha-1) with respect to Andean forest soils (138.7 Mg C ha-1). Nevertheless, Zimmermann et al. (2009) did not find any significant difference in SOC stocks across a similar elevation gradient (forest-puna transition). They argued that the large spatial variability may mask the effects of elevation on strata differences. Alternatively, it is possible that the difference in SOC stock between Andean forest and páramo at Yanacocha is likely exacerbated by the historical fire events that are known to have occurred in this forest. Román-Cuesta et al. (2014) reported differences in SOC in burned and unburned Andean
forests at similar elevations in the Southern Peruvian Andes. The low SOC associated with past fire events indicates that the detrimental impact of burning on ecosystem carbon storage may have the longest legacy below ground. Aside from the importance of fire several other environmental factors are known to affect SOC (i.e. moisture, radiation, and atmospheric pressure) but these were not evaluated in this thesis (Buytaert et al., 2006; Körner, 2007; Zimmermann et al., 2009).

Concerning carbon sequestration rates, I found a significant increase rate in the AGB of 2.5 Mg C ha-1 year-1 in the Andean forest, and 1.5 Mg C ha-1 year-1 in the páramo ecosystem. The carbon sequestration rate for AGB in the Andean forest was similar to those reported for recovering secondary forests in north eastern Ecuador at ca. 2.7 Mg C ha-1 (Fehse et al., 2002), while the carbon sequestration rates in the páramo were higher that found in previous studies, ca. 0.6–1.5 Mg C ha-1 year-1 (Hofstede et al., 1995a; Ramsay & Oxley, 2001a). Carbon assessments in the mountain forests of Colombia indicated that in naturally regenerating secondary montane forests carbon stocks in the above ground compartment accumulated at a rate of 4.3 Mg C ha-1 yr–1 (±0.56 SD), with stocks reaching approximately half the levels found in primary forests within 15–30 years (Gilroy et al., 2014). Since these figures concern an elevation gradient from 1,290 to 2,680 m asl, it is possible to infer that carbon accumulation rates found in Yanacocha are under the normal trend along the elevation gradient, and will probably reach the carbon stocks reference level in around 15 years from now. Further, significant positive carbon sequestration rates were also found in the Above Ground Necromass (AGN). The same gain rate was recorded for both ecosystems, i.e. 1.3 Mg C ha-1 year-1. Finally, I found no significant differences in carbon sequestration rates in the BGB between the páramo and upper montane forest. These results confirm that carbon sequestration rates in the aboveground compartments (AGB and AGN) are faster than in the belowground compartment (Below Ground Biomass; BGB) and are associated with higher elevations and high plant diversity. The observed high AGB sequestration rates in both Andean forest and páramo suggests that natural (passive) regeneration is an effective strategy for regaining AGB in degraded areas, and that interventions that stimulate successional vegetation dynamics, leading to an increase in species functional diversity, could further accelerate the process.

In chapter 7, I assessed the ecological effectiveness of seven years of long-term rehabilitation practices, which aim to increase the biomass of palatable
species to maintain the carrying capacity and sustain alpaca fibre production in the Peruvian highlands (Huancavelica). In this area, overgrazing decreased the carrying capacity of the system and led to ecosystem degradation. In this context, the Ministry of the Environment of Peru (MINAM) and the Belgian cooperation implemented rehabilitation practices in 2011-2012, including: (i) herbivory exclusion, (ii) exclusion with added irrigation, and (iii) exclusion with water collecting ditches. I found positive effects of these practices at the landscape scale. These effects include: (i) an increase in the dominance of palatable species, (ii) an augmentation of the vegetation cover of bare soil, (iii) an increase in plant species richness, but for the herbivory exclusion practice only. In the exclusion practice, the continued disturbance by alpaca browsing and trampling was eliminated, allowing less trampling-resistant species to compete. The removal of grazing might have triggered new paths for plant communities to assemble, including a progressive replacement of less-palatable short carpet grass vegetation towards a more diverse community, with higher vegetation cover and less exposed bare soil, as documented for arid systems in Australia (Witt et al., 2011). In some cases, the complete elimination of grazing and trampling is favouring specific palatable species that outcompete other lower-statured species found in non-excluded areas and eventually cause local extinctions. Consequently, and following the mid disturbance hypothesis (Grime, 1973; Connell, 1978), a season-specific rotation system (wet and dry season) is a fundamental need for herd management at the landscape scale, in order to provide an optimal balance between the dominance of palatable species and a higher species richness (Jacobo et al., 2006).

Specific differences were found between practices that just targeted grazing and trampling as a disturbance (i.e. exclusion), versus those practices that combine the elimination of grazing and trampling, plus water addition (i.e. exclusion with added irrigation). For example, the plots linked to the exclusion with added irrigation practices had a significant increase in vegetation cover in comparison to those related to herbivore exclusion solely. Further, the observed reduction in species diversity in the herbivory exclusion practice in comparison with the control sites and the other two rehabilitation practices that combine herbivore exclusion plus water addition could be related to the effect on the plant community when disturbances such as trampling are eliminated, but water stress continues to be high. Palatable species with faster recovery rates and more water-stress tolerant, such as Poaceae species that are no longer selectively grazed seems to outcompete other species with slower recovery rates. I argue that a more extended
period of exclusion will be needed to establish whether and to what extent, species diversity exhibits a positive trend in the herbivore exclusion practice, especially in a semiarid system such as the Huncavelica grasslands. Thus, the combination of exclusion with water addition seems to deliver the best short-term results.

Finally, I found significant positive changes in biomass (i.e. AGB, BGB) among the rehabilitation practices. ANOVAs tests comparing the full models and null hypothesis model showed that treatments and time are causing statistically significant differences from the control in most biomass variables, except for soil organic matter (SOM; $P = 0.28$ $P < 0.05$), with exception of the latter in the exclusion plus irrigation rehabilitation practice. The absence of a significant change in the soil carbon content might be related to the fact that in semi-arid systems, carbon pool responses to exclusion practices take long to occur. In semi-arid grazing lands in Australia, carbon benefits were recorded after 40 years of exclusion (Witt et al., 2011). Another reason for the non-significant differences in the observed biomass pools among the rehabilitation practices could be related to the fact that factors affecting plant community dynamics seem to be causing trade-offs with biomass accumulation processes, contrary to expected when removing an essential limiting factor such as water availability (Körner, 2003).

Though there were no significant statistical differences in the biomass pools among rehabilitation practices, there were different ecosystem responses to the different practices. For example, a decrease in belowground biomass in the irrigation and ditch treatments with respect to the exclusion and control areas could be related to a shift in plant strategies to acquire resources, with higher investment in aboveground vegetation relative to roots, due to the elimination of the two primary stressors: alpaca grazing-trampling and water shortages. Thus, these two treatments seem to favour the short-term vegetation cover at the expense of belowground biomass. The outcomes from the rehabilitation practices in terms of the trends in ratios and amounts of aboveground/belowground biomass, and in vegetation cover raise the question whether irrigation, while reducing the water stress, induces a negative feedback. Plant spacing is a crucial factor in balancing water–plant relations in semi-arid mountain environment (Körner 2003). If increased water availability results in an increase in plant cover, the accompanying modification of plant spacing may alter plant-plant interactions, shifting from a facilitation scenario towards a more competitive system (Anthelme et al., 2012; Anthelme et al., 2017). This shift might result in a reduction of resources available that end up in lower biomass production.
4. Linking ecological knowledge to informed restoration practices and conservation planning

In this final section of the thesis, I focused on two questions: (i) What indicators are sensitive enough to assess ecosystem recovery from human disturbances in the high tropical Andes? (Chapter 6-7), and (ii) What are the most critical areas for biodiversity conservation in mainland Ecuador, considering the various drivers of environmental change? (Chapter 8). Based on the research presented here and evidence in the literature, I concluded that: (i) biomass stocks (aboveground and belowground), vegetation cover, taxonomic and functional diversity, together with species evenness (abundance proportions) are useful indicators to detect ecosystem responses (trends) to passive and active restoration actions in relatively short timeframes. (ii) Ecuador requires to increase its national protected area system in 2.46 million ha to cover significant conservation shortfalls, with particular emphasis on the central and southern Andes, central Amazonia, and the central and southern portions of the coastal plain. I now briefly discuss how I reached these conclusions.

4.1 Indicators for assessing ecosystem restoration

I assessed the effect of passive and active restoration practices in two different locations with two different objectives. In the first case (chapter 6), the objective of the passive restoration practice was to restore the original high Andean ecosystems contained inside the Yanacocha Reserve, whereas in the second case the objective of the active restoration practices (named rehabilitation hereafter) was to restore vital ecological functions (i.e. biomass allocation) and ecosystem services (i.e. grassland palatability) in support of sustainable alpaca fibre production (chapter 7).

The combined outcomes of both studies allow me to identify and validate the applicability and sensitivity of ecosystem-based indicators to assess the effects of restoration practices in High Andean ecosystems. I assessed these effects using six indicators: (i) vegetation cover, (ii) species richness, (iii) Shannon-Weiner Diversity Index, (iv) below and aboveground biomass, and (vi) soil organic matter/soil organic carbon.

I found the majority of these indicators to be suited for detecting ecosystem responses (trends) to passive and active restoration actions within relative short (3-5 years) and medium (23 years) timeframes. The indicators used were sensitive
enough to detect changes in (i) biomass stocks, particularly in the AGB pool; (ii) increase in vegetation cover by excluding grazing, trampling, and burning events; (iii) increases in AGB and AGN, which were positively related to higher plant functional diversity; (iv) plant species richness, which increased although the observed trend was not always consistent. Based on my results, I argue that taxonomic and functional diversity, together with species evenness (abundance proportions) are both useful indicators of palatability for alpaca grazing.

Defining goals is an essential element in designing restoration actions that are effectively oriented toward achieving the desired outcomes (e.g. conservation vs sustainable use). Therefore, to assess the relevance and sensitivity of the indicators for restoration practices, it is of primary importance to accurately define the objectives as well as to understand the nonlinear dynamic nature of ecosystems. The resulting variability means that specific short- and long-term outcomes of restoration practices might not be adequately assessed through indicators that compare the current state of the ecosystem to a former state. Additionally, specific indicators provided different kinds of insights concerning the timing and success of rehabilitation processes. Indicators for assessing restoration outcomes should, therefore, take the desired future characteristics of the ecosystems in question as the point of reference (Cuesta, 2017).

4.2 Conserving tropical high Andean biota in a time of change

In chapter 8, I focused on a country-scale analysis through defining the most critical areas for biodiversity conservation in mainland Ecuador, considering multiple drivers of environmental change and distinctive land management objectives. By means of a reserve selection algorithm (i.e. Marxan, Ball et al. (2009)), I generated a priority areas conservation scenario that included 24% (3.64 million ha) of Ecuador’s remnant vegetation, of which 65% (2.46 million ha) is outside the current national protected area system (PANE) Significant conservation shortfalls of the PANE were concentrated in the central and southern Andes, central Amazonia, and the central and southern portions of the coastal plain. I also found that the endemic and threatened species are poorly represented in the current national protected areas system. For example, only four species of the 106 endemic or restricted range species are contained in the PANE. These results have implications for the strategies needed to cover the identified gaps, particularly those of endangered and endemic species which have a high priority at global (Stattersfield et al., 2005) and national level (MAE, 2015). Covering these gaps cannot be achieved by a linear increase in areas under conservation
since patterns in biodiversity distribution are not homogeneous in space (Gentry, 1992; Kreft & Jetz, 2007). As such, restricted range species reflect aggregate patterns in specific regions, resulting from current environmental conditions and past biogeographical and geological events (Madriñán et al., 2013; Pérez-Escobar et al., 2017). Thus, priority should be given to preserving the endemism centres where these species occur (Venter et al., 2014).

I also found that although the critical biodiversity areas provide a spatially explicit framework for focusing conservation efforts at the national level, incorporating additional criteria to prioritize conservation strategies is of utmost importance. The inclusion of environmental change stressors (e.g. climate change, population density change) and biodiversity co-benefits (e.g. carbon stocks) to the critical biodiversity areas provide valuable information for the design of more robust conservation strategies. For example, the modelling of the potential effects of climate change on the composition of biotic communities revealed that important biodiversity areas located in the eastern and southern Ecuadorian Andes-Amazon interphase. The preservation of these regions could help mitigate climate change impacts on the biodiversity by enhancing habitat connectivity and preventing local extinctions of species by facilitating upward migration and allowing species to reach suitable areas under warmer conditions. Further, forest remnants of the eastern Andean versant showed high carbon stocks but are spatially located in areas with increased risk of land use conversion. Thus, the preservation of the mountain forest of the Eastern Andes requires to design conservation strategies that address drivers of habitat conversion in the context of rapid social and economic change. These areas can become ideal candidates for mechanisms such as REDD+, which target threatened ecosystems with high potential to mitigate the emission of GHG and, at the same time, generate additional benefits through the conservation of biodiversity.

5. Limitations

In this section I describe the limitations of my research findings and first pay attention to those related to spatial patterns and then focus on temporal trends. I then go on to link these limitations to future research (section 6).

5.1 Spatial patterns and environmental gradients that shape vegetation on mountain summits in the high tropical Andes

The high level of community dissimilarity identified between tropical mountain summits could also result from the limited numbers of study sites. If a higher
number of more evenly distributed summits across the Andes could be incorporated, a more gradual change in species composition and a more representative view of vegetation patterns along summits in the tropical Andes might be obtained. Furthermore, climatic patterns explained part of the observed variation in plant community composition, but geological/edaphic heterogeneity and landscape history could also be important determinants of changes in vegetation structure along the latitudinal gradient of the Andes. Understanding past glacier dynamics of each summit since the last glacial maximum (LGM) together with soil/substrate composition could substantially improve the identification of past and present drivers of summit vegetation patterns across the Andes. Additionally, assessing productivity patterns and understanding their limiting factors could help to understand diversity patterns and community assemblages across different spatial scales.

Thermal niche trait patterns across the high tropical Andes were assessed using monthly mean temperatures during the growing season, instead of daily records. The influence of annual and daily temperature variation on species thermal ranges was documented by Chan et al. (2016) and McCain (2009) for endothermic and ectothermic vertebrates. Both studies evidenced the importance of annual and daily temperature variability to shape species niche breadths and argued that the pronounced daily temperature variation could be of a similar magnitude as the annual variability in temperature. Consequently, the estimated thermal niche traits might have been assessed by using only a limited data set on the range in daily temperature variations (Sklenář et al., 2016). Future work is needed in order to accurately assess the influence of daily temperature variation on the thermal niche traits of tropical alpine plants.

My analysis of species vulnerability to climate warming is a simple analysis of the projected thermal niche contraction based on two IPCC warming scenarios, that does not include species dispersal traits and positive plant interactions. I found that cryophilic species will be most vulnerable to warming due to their narrowest thermal niches. Most cryophilic species located in mountain summits have seeds that disperse by wind (Melcher et al., 2004; Holzinger et al., 2008; Matteodo et al., 2013), which could enhance their vulnerability due to their limited dispersal capacity. The establishment of plants towards highest areas seems to depend more on two other key factors: (i) Presence of favourable local conditions associated with rocky outcrops at the highest periglacial habitats (Suárez et al., 2015); (ii) Facilitation mechanisms provided by nurse-plants (i.e. cushion plants), that can
modify local climate and substrate conditions providing more favourable habitats for plant colonization and establishment (Anthelme et al., 2012; Cáceres et al., 2015; Anthelme et al., 2017; Hupp et al., 2017). Both dispersal strategies and post-dispersal settlement success are two processes that have been little studied in the high tropical Andes and require further research.

5.2 Alpine vegetation trends

Future and ongoing landscape transformation in the high tropical Andes is expected to have unprecedented impacts on the ecosystems and their biota. Limitations of my results are related to significant knowledge gaps concerning the ecosystem responses to climate change. These knowledge gaps are centred around four main themes: (i) vegetation and soil development in deglaciated areas; (ii) development of novel biotic communities in the available deglaciated habitats; (iii) biotic interactions (facilitation, competition) among the new species members of the novel communities; (iv) carbon and water dynamics in the new ponds and lakes as a result of glacier melt. A vital aspect of these landscape transformations is whether these new small lakes can form permanent ecosystems in the mid-term, especially when glacial fed-streams are gone, and a prolonged dry season is expected (Vuille et al., 2018). Another knowledge gap concerns the still not well understood combined effects of climate and land use change on Andean wetlands, particularly their potential to reduce soil water regulation capacity, increase soil erosion and increase organic matter decomposition that could threaten the carbon balance of high Andean wetlands (Buytaert et al., 2011; Urbina & Benavides, 2015; Hribljan et al., 2016).

Finally, in order to achieve a more robust understanding of ecosystem responses to restoration and rehabilitation practices, studies of more extended time series (i.e. continued censuses of permanent plots) are needed. At least an extra census is required in the paramo and Andean forest to improve our understanding of the effect of passive restoration over the biomass accumulation rates, particularly on the below ground pools. In the puna of Huancavelica, the relationship between vegetation cover and the use of water ditches has been very poorly documented. I was able to see less species richness but a turn-over of species toward those more palatable. More time is needed to assess the longer-term effect of such practices on the ecosystem.
6. Future research directions

6.1 Vegetation patterns and trends

This thesis was based on the GLORIA-Andes long-term research network, which has established 17 permanent research sites across the Andes. The majority of the sites were set up between 2008-2012, and up to date at least 10 of those sites had a second census and some even already had a third census (Carilla et al., 2018). After establishing the first comprehensive continent-wide dataset for long-term permanent plots to study plant community and vegetation dynamics, the following research is now underway:

- Assessment of the role of climate and evolutionary history in shaping plant dispersal strategies on mountain summits across the tropical Andes. Within this topic, two interrelated questions will be addressed: (i) What are the dominant dispersal-related traits on Andean mountain summits? (ii) What is the role of climate vs evolutionary history in shaping dispersal strategies on Andean mountain summits? For the second question I hypothesized that environmental filtering would play a more prominent role due to the harsh climatic conditions on the summits;

- Assessment of species dispersal traits and alpine species germination rates along environmental gradients and under warming experiments. This research is based on the fact that we know that dispersal-related traits are at least influenced by minimum temperatures in the Andes (Tovar et al., 2019); thus climate change will inevitably affect plant dispersal and the capacity of plants to reach newly suitable areas. Furthermore, little is known about the germination requirements for tropical alpine plants. Therefore, knowledge generation related to plant distribution, functional traits related to dispersal and germination, and plant biodiversity responses to CC will strength the development of species distribution models to inform conservation actions.

Within the scope of the GLORIA-Andes long-term research network, three more sites were established in the last three years (one in Venezuela, one in Ecuador and one in Chile) as a way to provide for a more gradual change in species composition and a more representative view of vegetation patterns across the Andes. Complementary, based on the available re-census data and the temperature dataset collected for each summit, the following interrelated questions will
be addressed: (i) How plant communities’ composition is changing and if the observed changes can be linked to temperature anomalies across the Andes? (ii) What the influence is of daily temperature variation on the thermal niche traits of tropical alpine plants? (iii) how plant community’s composition changes are affecting species and communities’ functional traits, including thermal niches, growth forms and seed dispersal?

6.2 Indicators for assessing ecosystem restoration

Two more censuses will be carried out in the Yanacocha private reserve in order to assess variations in carbon stocks and biomass allocation along the elevation gradient. Additionally, the questions will be addressed, how changes in biomass allocation can be related to changes in taxonomic and functional diversity at the plot and landscape scale. In Huancavelica, key questions that remained unanswered are whether and to what extent the ecosystem regained its original carrying capacity and what social benefits were derived from it. Future research should focus on the following interrelated questions: (i) How many alpacas can graze in the rehabilitated grasslands (and for how long) before degrading the system again? (ii) What type of households (e.g., large/small; old/young; and number of grazing areas) would be able to rehabilitate their grasslands (what capacity at the household level is needed to engage in rehabilitation)? (iii) Does a prolonged period of exclusion combined with water provision result in a clear trend regarding species diversity and biomass allocation in the above ground and below ground compartments?

7. General Conclusions

High Andean ecosystems are major contributors to the globally significant carbon stocks and biodiversity. These ecosystems also play a fundamental role in sustaining the livelihoods of millions of people, providing essential ecosystem services such as water and food. These ecosystems and their biota are being threatened due to the combined effects of climate and land use change stressors.

In this thesis, I showed that across the Andes species distribution patterns, community assemblages, species traits, and ecosystem functions (biomass allocation) depends on abiotic conditions, particularly air temperature and annual precipitation, and their interactions. I have shown that these climatic variables, particularly annual temperature, are a vital factor to assess climate change effects on the high Andean biota along latitudinal and altitudinal gradients. Furthermore,
the projected warming scenarios showed the enormous susceptibility of high Andean landscapes to undergo profound transformations at an unprecedented speed (i.e. few decades) with significant ecological and societal implications.

This thesis has also shown our limited understanding on how these ecosystems will respond to these impacts and the need for long-term research programs upon which significant knowledge gaps could be addressed, and critical ecological thresholds identified, to support the decision-making processes. Knowledge generation can be achieved by comparative multi-scale studies across the Andes, linking glacier retreat dynamics to its consequences for biodiversity and ecosystem processes (e.g. the carbon and water balance), combined with different land use trajectories. Besides, in this thesis, I have shown the capacity of degraded high Andean ecosystems to recover from prolonged periods of land use practices. Results from my research suggest that passive restoration is a cost-effective and feasible long-term strategy that could be replicated at larger spatial scales. Restoring high Andean ecosystems is a primary strategy to increase its capacity to withstand climate change impacts. Further, carbon stocks and biomass productivity proved to be sensitive indicators for the assessment of high Andean ecosystem recovery over relatively short periods (5–20 years). However, a more extended period of continuous monitoring is required to improve the robustness of the dataset and to provide a scientific basis for restoration actions so that they can contribute to securing environmental services and mitigate climate change.
8. References


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