Primary succession after glacial retreat: comparison between terrestrial and aquatic colonisation mechanisms in tropical Andes

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Primary succession after glacial retreat: comparison between terrestrial and aquatic colonisation mechanisms in tropical Andes

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Acknowledgements

I. Introduction

Climate change is a subject of major concern nowadays. One impact of the climate change is the acceleration of glacier retreat, with major impacts on downstream ecosystem. In addition, global warming induced upward range shifts of organisms, in particular in alpine systems, to adapt to the direct and indirect effects of warming (Gottfried et al., 2012). Alpine species are particularly affected by this upward migration since those species are often specialized species adapted to the harsh environmental conditions such as low temperature, and less competitive than more generalist species from lower elevations (Alexander, Diez, & Levine, 2015). One major concern in alpine ecology is whether high altitude organisms would have time to colonize and establish in higher zones, such as newly deglaciated terrain, before migration of more competitive species. Nevertheless, the existing time-lag on upward migration poses a major problem to species establishment as warming rate keeps accelerating while the dynamics of primary succession remain slow (Zimmer et al. 2018). Previous studies showed that tropical alpine ecosystem might be one of the most affected by global warming (Bradley et al., 2006). Indeed, Andean glaciers shrinkage is among the fastest worldwide since the late 1970's (Rabatel et al. 2013). Thus, it is particularly important to characterize the pattern of primary succession and the processes involved after glacial retreat in the Andean páramo. High altitude sites are characterized by harsh conditions where only well-adapted taxa can establish such as *Chironomidae* on the streams (Irons, Miller & Oswood, 1993) or Bryophyta on the terrestrial system (Proctor, Ligrone & Duckett, 2007). Previous studies showed that biotic interactions might be involved in the processes of primary succession, for example, as plant facilitation could promote the establishment of species towards high elevation range as certain plants, nurse plants, might provide suitable habitats. (Choler, Michalet & Callaway, 2001; le Roux, Virtanen, Heikkinen, & Luoto, 2012).

In this study we tried to characterise primary succession after glacial retreat in the Andean páramo at an altitude above 4600 m a.s.l. Four systems (aquatic invertebrates, terrestrial flora, *Carabidae* and soil DNA) were studied in four zones of different deglaciation age in order to assess primary succession patterns and compare these patterns between systems. In order to do this, a characterisation of the communities of the four systems in the four zones was done along with characterisation of filtering explaining the community compositions.

Several hypotheses were established. Our first hypothesis was that on early colonisation zones environmental filtering is a major driver of primary succession with only

well-adapted taxa to harsh environment being able to establish. Our second hypothesis was that dispersion also has a strong effect on primary colonisation where taxa with higher dispersion capacity can more easily establish in deglaciated sites. Another hypothesis was that biotic interactions such as facilitation or competition are also important drivers of primary succession.

II.   Material and Methods
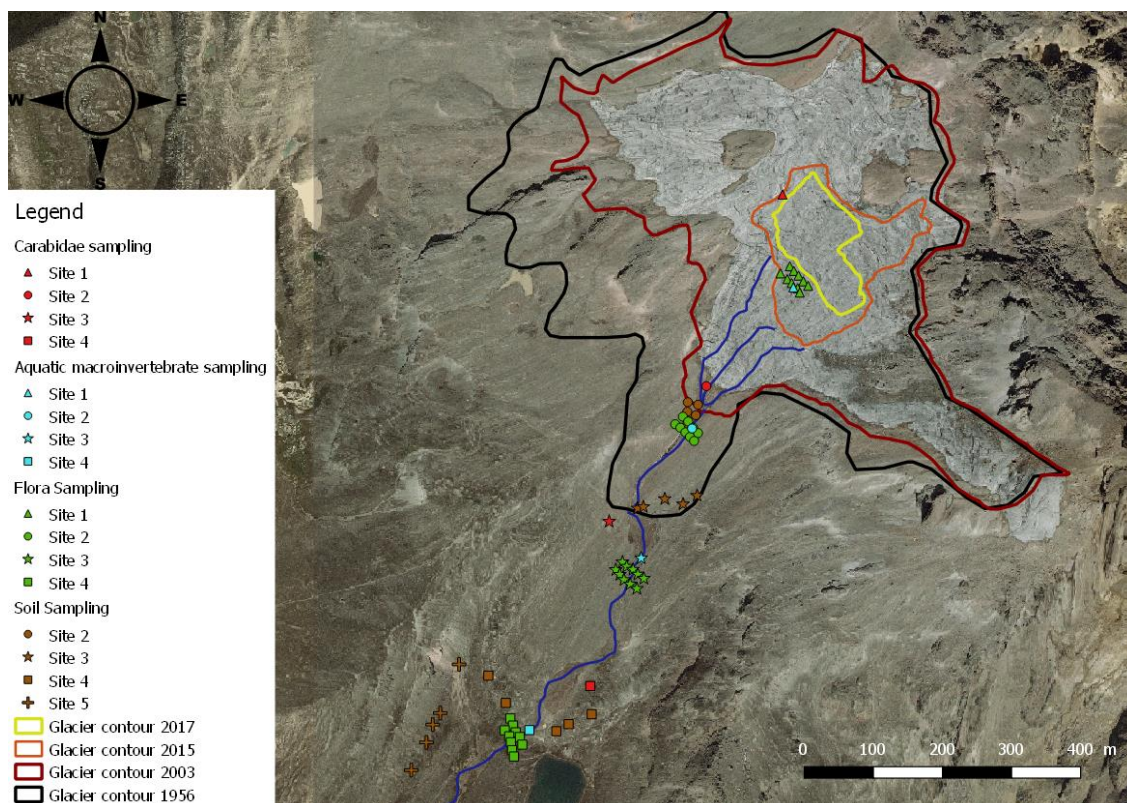
Figure 1 : Map of the Carihuairazo Mountain with the Glacier contour dating from 2017 (yellow contour), 2015 (orange contour), 2003 (red contour) and 1956 (black contour). The figures represent the sampling sites for *Carabidae* (red figures), aquatic macroinvertebrates (cyan figures), flora (green figures) and soil DNA (brown figures) each corresponding to one of the study sites (triangle, Site 1; circle, Site 2; star, Site 3; square, Site 4; cross, Site 5)

1) Study site

This study was conducted in the Andean páramo in a glacierized catchment, at the Carihuairazo volcano (5102m a.s.l), Ecuador (01°24′25′′S, 78°45′00′′W). The study glacier (the last one in the volcano) has had a decrease in cover over the years as seen in the contours below (contours provided by INHAMI and IRD). Glacier retreat of such a small glacier at relatively low altitudes is particularly pronounced. Thus, this glacier is expected to disappear within the next years (Rabatel et al. 2013).

The study was conducted in four different zones, separated by moraines. The four zones were located at 4770; 4738; 4660 and 4630 m a.s.l and 3, 15, 62 and around 168 years since deglaciation respectively. Thus, zones 1, 2, 3, and 4 were ice-free zones since 2015, 2003, 1956 and the end of the Little Ice Age (LIA, around 1850). One extra zone, located at approximately 800m from the glacier was added for the soil system (see below). At the four zones, we studied the aquatic community (invertebrates), terrestrial community (plants and Carabidae; zone 1-4), and soil community (zone 2-5). Altitude was extracted with GPS tracking devices. Distance was measured on QGIS (version 2.18.7) using GPS points corresponding to sampling sites.

2) Environmental and ecological measurements of the four studied systems

a) Aquatic system

At each zone (1-4), we selected one stream site of the glacial stream derived from Carihuairazo's glacier. Invertebrate community was estimated based on five Surber samples (0.05 m^2; mesh size 200µm, and preserved in 70% ethanol). This sampling was done at six different dates from May 2015 and May 2017 for sites 2-4 while site 1 was only sampled on May 2017 since the glacier was still covering this zone. In addition, at each sampling site and date, fifteen pebbles were collected in five groups of three stones, and conserved in 96% ethanol in the dark to assess chlorophyll A concentration in order to quantify the available resource.

In the laboratory, Surber samples were rinsed through a 200µm sieve and sorted thoroughly by hand in a standardized manner, without use of magnification. Macroinvertebrates were identified under a microscope at 4.5x magnification range to different taxonomic levels, mostly to family level using a dichotomous identification key of benthic invertebrates of South America (Fernandez and Dominguez, 2001). The benthic detritus left on each Surber was collected and dried in an oven for 24 hours at 80°C and then burnt to quantify the course particulate organic matter (CPOM), an additional measure of available resources for benthic macroinvertebrates. The ethanol of the stones samples were transferred to a spectrophotometer and absorption was measured at 665 and 750 nm. The ChloA (µg.cm^{-2}) was then calculated using the method proposed by Københavns Universitet (1989) that uses the absorbance, the volume of ethanol used and the pebble surface in order to calculate the ChloA. The pebbles surface was calculated according to the formula proposed by Graham et al. (1988) that uses the length (L), width (W) and height (H) of the pebbles.

In addition, physicochemical measurements were conducted for every taxa sampling. Water temperature (°C) and pH were measured with a pH meter. Conductivity ($\mu S.cm^{-2}$) was measured using a conductivity meter. Oxygen saturation (%) and dissolved oxygen ($mg.L^{-1}$) were measured using an oxygen meter. Turbidity (NTU) was measured using a turbidity meter

b) Terrestrial system – Flora

At each zone (1-4), terrestrial plants were observed between September and October 2017 in ten quadrants ($1 m^2$) along 2 transects (five quadrants per transect). Quadrants were placed on both sides of the river for each site. Quadrants were subsampled in smaller quadrants of 10x10 cm in order to be more precise on the estimations. For each quadrant, the cover area (%) was determined for every flora taxon or substrate present. Flora was determined to a species level when possible. The total cover of each substrate for each smaller quadrant was then summed and divided by 100 in order to obtain a total cover for each quadrant.

c) Terrestrial system – Carabidae

At each zone (1-4), *Carabidae* were sampled using pitfall traps. Six pitfalls traps were placed during 12 or 14 days in three dates between 2016 and 2017 using wine vinegar as attractive solution. Taxa was then collected and preserved in ethanol. In the laboratory, *Carabidae* were identified under a microscope at 4.5x magnification rate to species level.

d) Terrestrial system – Soil DNA

Five soil sites were selected for each zone (2-5). Sampling was done using a shovel that was sterilized for every site so DNA would not mix up between sampling sites. Four soil samples were extracted per site and preserved in a sterilized container for further analysis. Total DNA was extracted using the PowerSoilVR DNA isolation kit (MoBio Laboratories) and two amplicon libraries were prepared for bacteria and eukaryotes. Libraries were sequenced on the Ion Torrent Personal Genome Machine. DNA sequences were filtered using the OBITOOLS software (http://metabarcoding.org/obitools), and were assigned to the relevant taxa using ecoTag program that finds highly similar sequence(s) in a suitable database (Ficetola et al. 2010).

e) Terrestrial system – environmental measures

At each zone (1-4), relative humidity and temperature was measured every 30 minutes using relative humidity/temperature data loggers for *Carabidae* or only temperature data

loggers for soil DNA (Hobo relative humidity and temperature loggers, Onset Computer Corp) during two pitfall sampling duration on each site and one month period for soil DNA. Data were then used to calculate minimal, maximal, mean and standard deviation temperature as well as mean relative humidity for the measurement period.

3) Data analyses

For each study site, aquatic invertebrate density (ind.m^{-2}) was calculated as the number of individuals collected in the 5 surbers divided by 5 surbers area. *Carabidae* density (taxa.pitfall^{-1}.day^{-1}) was calculated as the number of individuals collected in the 5 pitfall traps divided by the number of traps and the number of days. Relative abundance of soil DNA measured was averaged per soil sampling site in order to get the mean value of relative abundance per site. α-Diversity (local taxa richness), density (for *Carabidae* and benthic macroinvertebrates), cover (for flora), relative abundance (for soil), Shannon index (Shannon, 1948) and Pielou's evenness index (Pielou, 1966) were calculated for each system. Shannon calculation was done using *vegan* package in R.

a) Comparison between study sites

Kruskal-Wallis test was performed on the ecological indices mentioned earlier to compare community composition among zones. When we obtained a significant difference among zones, a Dunn post-hoc test was done using the R *PMCMR* package in order to identify which sites were significantly different. System taxa were compiled into higher taxonomic level to plot the percent represented by each taxon on the studied sites in order to find out the dominant taxa.

b) Beta-diversity and physicochemical/spatial measurements effects on it

β-Diversity can be defined as a variation in species composition among sites which provides a link between α-diversity (local diversity) and γ-Diversity (regional diversity) (Anderson et al. 2011). To analyse the dissimilarity among the study zones, we calculated Bray-Curtis dissimilarity index (β-Bray, based on abundance data) (Bray & Curtis, 1957) and the Sørensen dissimilarity index (β-Sør, based on presence-absence data) (Sørensen, 1948). For each system, β-Bray was used to perform a non-metric multidimensional scaling (NMDS) in order to assess dissimilarities in community composition among all the sites for each system. Physicochemical and spatial measurements were also fitted into the NMDS plots using the envfit() function of the *vegan* package in R. This function allows fitting

environmental variables onto the ordination in the form of vectors which will have the maximum possible correlation with the environmental variable used, indicating thus which environmental variable has an effect on the community variation among sites.

The variation of taxa assemblage can be partitioned into two components: dissimilarity due to turnover and dissimilarity due to nestedness where turnover represents the replacement of some species by other species and where nestedness represents the loss of species (the poorest assemblage being a subset of the richest assemblage) (Baselga, 2010). This concept of partitioning β-Diversity was first applied by Baselga (2010) on the Sørensen dissimilarity index where β-Sør$_{turn}$ represents the turnover and β-Sør$_{nest}$ represents the nestedness. It was then applied by Baselga (2013) to partition β-Bray into the *balanced variation in species abundances*, β-Bray$_{turn}$, representing a replacement of a number of individuals for the same number of individuals of another species from one site to the other; and the *abundance gradient*, β-Bray$_{nest}$ representing the loss of some individuals from one site to the other. In our study both β-Sør and β-Bray were calculated, partitioned and used to perform dissimilarity matrices between sites. These analyses were done in R (R Development Core Team 2013, version 3.3.3), using the R package *betapart*. Distance matrices were then performed for environmental and spatial variables for each system comparing all measurements done per variable with each the other measurements done. β-Sør, β-Bray and their partitions were then plotted against the differences of physicochemical and spatial variables then fitted to linear models for each system. Multiple regression of distance matrices (MRM) was used following Lichten's (2007) method in order to assess statistical significance.

c) Interactions between studied systems

Because available data from the studied systems did not have the same length, simulations were done for the systems with less data to test the effect of biotic system between each other. All data was then fit to linear models where the factor was the studied site and the linear response corresponded to every possible combination of α-Diversity and taxa count (density, cover, relative abundance; depending on the system) from each system. An anova was then performed to the models in order to assess possible interactions between the biological systems and also to assess if interaction between the site and the variable had a role in the response. Combinations of variables having a significant p-value in the anova test were then plotted.

All analyses and figures produced were done in R (R Development Core Team 2013, version 3.3.3) using packages *vegan*, *PMCMR*, *betapart*, *cowplot* and *ecodist*Site differences on α-Diversity, abundance, Shannon and Pielou's evenness per system.

III.   Results

1) Site differences on α-Diversity, abundance, Shannon and Pielou's evenness per system.

Figure 2 : α-Diversity, abundance index (varying for each system), Shannon index and Pielou's evenness index for benthic macroinvertebrates (a), flora (b), *Carabidae* (c) and Soil DNA (d) per deglaciation period site.

Site 1 showed to have the lowest diversity and taxa abundance overall the sites, and appears to be also characterized by strong dominance for the flora and benthic macroinvertebrates (Fig. 3a, c). Overall, *Carabidae* didn't show any significant differences on diversity across sites but the *Carabidae* density showed to be different from one zone to another (Fig 2.c). Site 2 appeared to have slightly more taxa diversity and abundance compared to site 1 but remained nevertheless low. New taxa appeared to have colonized this site compared to site 1 but the dominance of a single taxon remained strong. Soil DNA sampled on sites 2-5 seemed to be more heterogenous in terms of α-Diversity but with apparent differences in relative abundance between sites 2-3 and sites 4-5. Site 3 appeared to be characterized by the colonization of new taxa families for benthic macroinvertebrates and

and flora. Dominance of a single taxon remained but seemed to be lowered for benthic macroinvertebrates. Site 4 presents the highest taxa diversity and abundance overall, even more new taxa appear to have colonized this site (Fig. 2 & 3). Kruskal-wallis showed no
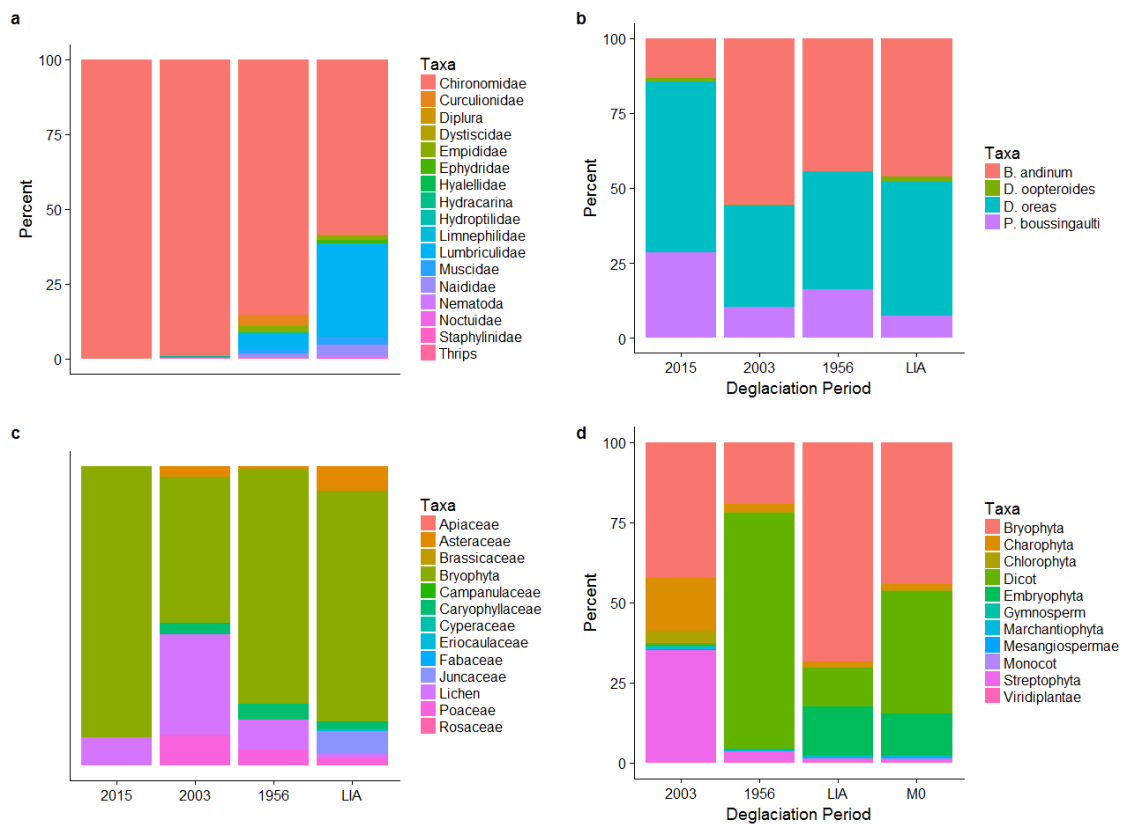
Figure 3 : Taxa percentage bar plot for benthic macroinvertebrates (a), flora (b), *Carabidae* (c) and Soil Viridiplantae DNA (d) per deglaciation period site.

significant difference among sites for benthic macroinvertebrates α-Diversity, Taxa density, Shannon index and Pielou's evenness (p-value>0.05, Annex 1). Nevertheless, we observed a tendency of increasing α-Diversity, taxa density and Shannon index while evenness showed no tendency, evenness was more homogenous in zone 3 (Fig. 2a, Annex 1). The family *Chironomidae* was dominant in all zones. However, the relative abundance of *Chironomidae* decreased with increasing deglaciation age from 100% in site 1 to 58.53% on site 4. Thus, new taxa occurred following the deglaciation age. Particularly, *Muscidae* (Diptera) as well as *Lumbriculidae* (Oligochaeta) or *Hydracarina* (Acari) appeared at site 2. In addition, *Curciolionidae*, *Empididae*, and *Hyallelidae* (Amphipods) appeared at site 3 and *Ephydridae* (Diptera), *Noctuidae* (Lepidoptera) or *Limnephilidae* (Trichoptera) at site 4 (Fig. 3a).

For the flora we observed significant differences for all indices among sites (kruskal-wallis; p-value of 3.3×10^{-6}, 1.85×10^{-7}, 3.01×10^{-6}, and 3.46×10^{-4} for α-Diversity, vegetation cover, Shannon index and Pielou's evenness respectively). Post-hoc Dunn test revealed significant differences between sites (p-value < 0.05, Annex 1) being for α-Diversity and

Shannon index between site 1 and sites 2-4 and between site 2 and site 4. For vegetation cover significant differences were observed between site 1 and sites 3 and 4 respectively (Fig. 2b, Annex 1). At site 2 we observed *Poaceae, Asteraceae and Caryophyllaceae* families. At site 3, only one new angiosperm family appeared; the *Cyperaceae* family, while at site *Apiaceae, Brassicaceae, Campanulaceae, Eriocaulaceae, Fabaceae* and *Juncaceae* occurred at site 4 (Fig. 3c). Overall we thus observed an increase in vegetation cover and Angiosperm taxa. We observed a significant difference in litter cover (kruskal-wallis test p-value $9.7x10^{-6}$) (Post-hoc dunn test p-value<0.05) between sites 1 and sites 3 and 4 and sites between 2 and 4 on litter cover for the sampled quadrats (Annex 2, Annex 3).

For *Carabidae*, Kruskal-Wallis tests showed only significant differences for taxa density among sites. We observed higher density values in sites 2 and 4 compared to sites 1 and 3.The differences between sites revealed by Dunn's test showed no significant values (Dunn test p-value <0.05) between site 1 and sites 2 and 4. For α-Diversity, Shannon index and evenness we obtained no significant differences among sites (Fig. 2c, Annex 1). The four *Carabidae* species present in the Carihuairazo community (*Bembidium andinum, Dyscolus oreas, Dyscolus oopteroides* and *Paratrechus boussingaulti*) were observed in all zones. We found no dominant species across all sites. Relative abundance of *B. andinum* was slightly higher at sites 2-4 while *D. oreas* at site 1. The proportion of *B. andinum* and *D. oreas* were similar in sites 3 and 4 while *D. oopteroides* and *P. boussingaulti* density was low in all sites (Fig. 3b).

Kruskal-Wallis tests done on soil DNA showed no significant differences among sites on all ecological indices (p-value>0.05, Annex 1). Indices at site 2 were more heterogeneous samplings on relative abundance, Shannon index and evenness than the rest of sites sampled (Fig. 2d, Annex 1). The dominant taxa revealed by the soil DNA is different in every studied site. Taking a particular look at soil plant DNA (Fig. 3d) in order to compare the present DNA with the Flora established on each site we could notice that on common sites corresponding to deglaciation periods of 2003, 1956 and LIA (Sites 2 to 4 respectively) there are shared taxa such as Dicotyledon plants and Bryophyta. An importance difference to note is that on site 3 there is a very notable dominance of Dicotyledon dominance in the soil compared to the other sites where Bryophyta remains dominant among the species that are visible to the naked eye. The presence of other type of Viridiplantae such as Algae like Charophyta on site 2 also gives us a slight glance on how primary colonisation of Viridiplantae works. Finally if we just focus on present *Enchytraeidae* measured in soil DNA we can note that there is a variation of

relative abundance between sites (Kruskal-Wallis p-value of 2.77×10^{-3}, Annex 4, Annex 5). Indeed, there will be a significant difference (Dunn's Post-hoc p-value<0.05) between sites 2 and 3 and sites 4 and 5. There will be a sharp increase in *Enchytraeidae* relative abundance according to soil DNA starting from site 4 (Annex 4, Annex 5).

2) Communities composition and physicochemical/spatial variables explaining this composition

The NMDS done had all good enough values of stress (0.17; 0.14; 0.006; 0.1 for aquatic, flora, *Carabidae* and soil DNA respectively). On each one of the systems NMDS revealed us possible differences on community compositions. As we can see for benthic macroinvertebrates (Fig. 4a), site 1 (that has a single point) community composition appears to be very distant from the rest of the sites community composition. On this system, site 2 seemingly is explained by the altitude and conductivity and is different from sites 3 and 4. Sites 3 and 4 have much more similarities than the rest of the sites and are rather explained by the temperature, the chlorophyll A content and the distance to glacier. For the flora system (Fig. 4b) we can see that site 1 remains very different from the rest of sites but unlike benthic macroinvertebrates sites 2 and 3 are more similar in terms of community composition meanwhile site 4 appears to be the much more different from these two sites. The community composition of site 2 is explained by the altitude while for site 4 community composition is explained by distance to glacier. For *Carabidae* (Fig. 4c) we can see that all sites appear to have different community composition with a slight similarity between sites 3 and 4. The composition of the community on site 1 appears to be explained by the distance to the stream. Finally, for soil DNA (Fig. 4d) we can see that all sites have different community compositions. This finding is rather interesting given the fact that on the previous section no differences were shown on calculated indices between sites. The composition of site 2 appears to be explained by altitude and max temperature while the composition of site 4 appears to be explained by distance to stream and standard deviation temperature.

P-values of MRM tests with significant values (p-value <0.05, Annex 6) showed us that variation in β-Diversity (Bray-Curtis with its partitions and Sørensen with its partitions) could be explained by the variation of spatial or physicochemical measures. For benthic macroinvertebrates ΔpH affected β-Sør and β-Sør$_{nest}$. ΔTemperature (ΔT) affected on β-Bray$_{turn}$ and β-Sør. ΔChloA affected both β-Bray$_{turn}$ and β-Sør$_{turn}$. Finally, the variation of distance to the glacier ΔDistance to Glacier (ΔDG) affected both β-Sør and β-Bray (Fig. 5a).
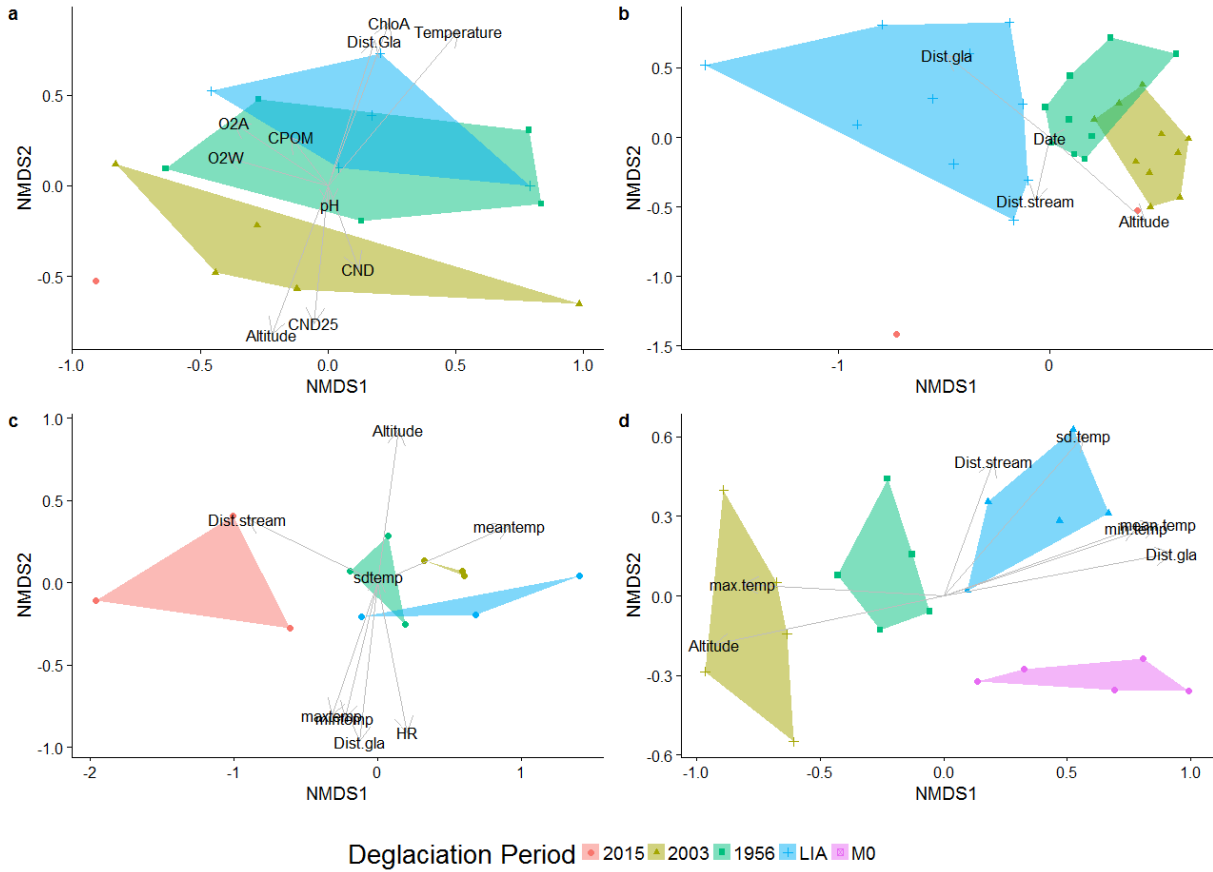
Figure 4: NMDS of Bray-Curtis β-Diversity index for benthic macroinvertebrate community (a), flora (b), *Carabidae* **(c) and soil DNA (d) per deglaciation period site showing the physicochemical and spatial variables (vectors) that contribute to the community composition.**
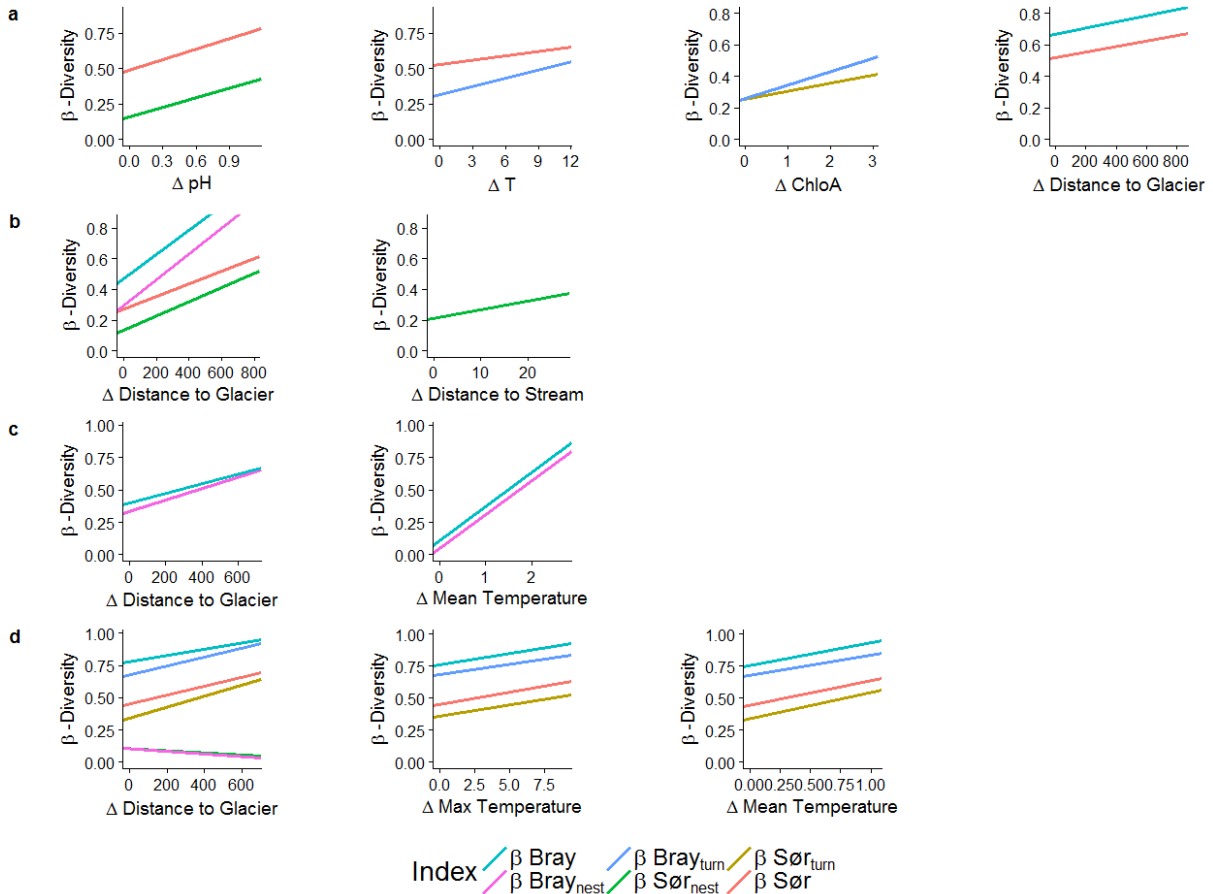
Figure 5: Multiple regressions of distance matrices of physicochemical and spatial variables fitted to β-Diversity (Sørensen with their partitions and Bray-Curtis with their partitions) for benthic macroinvertebrate (a), flora (b), *Carabidae* **(c), and Soil DNA (d).**

For flora communities' ΔDG affected β-Sør, β-Bray, β-Sør$_{nest}$ and β-Bray$_{nest}$. As distance to the stream (ΔDistance to stream or ΔDS) affected β-Sør$_{nest}$ (Fig. 5b). For *Carabidae* communities both ΔDG and ΔMT affected β-Bray$_{nest}$ and β-Bray, translated by a loss of individuals from one species to the other with varying distance to glacier and temperature. For soil DNA ΔDG affected all indices in different ways with a positive impact on the indices and on their turnover partition but a negative impact on the nestedness. Finally, ΔT affected both indices and their turnover partition in a very similar way whether we took into account the minimum temperature, the maximum temperature, the mean temperature or the standard-deviation temperature.

3) Interaction between biological systems
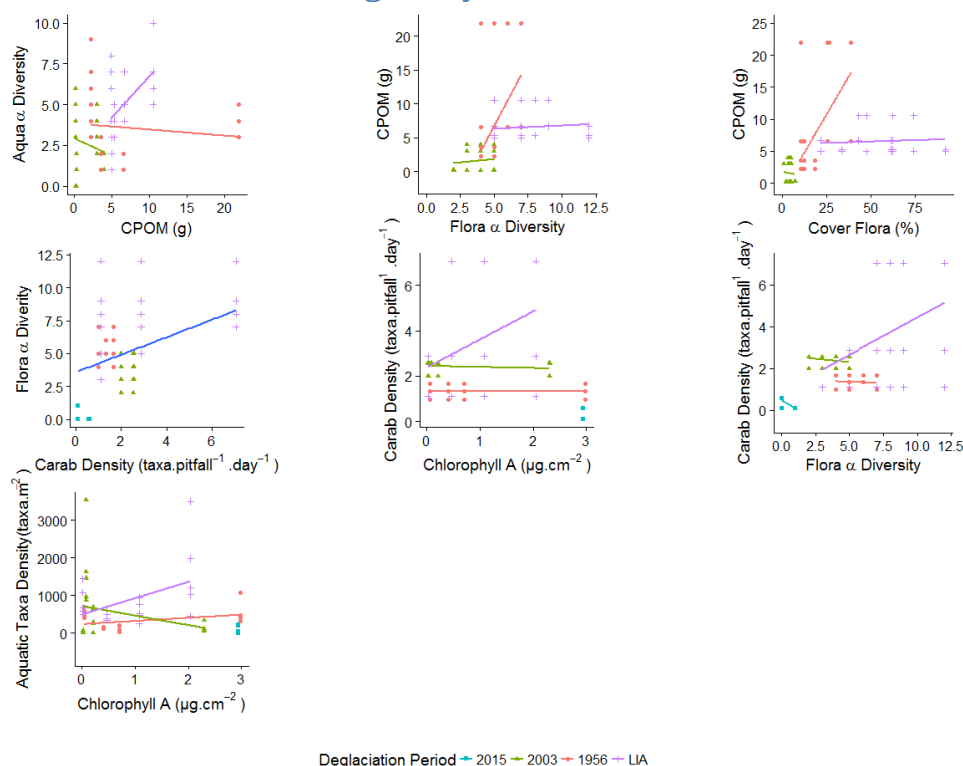
Figure 6 : ANCOVA plots of linear interactions between biological systems for each deglaciation period site. (Dark Blue line represents a linear interaction between both quantitative variables)

Interactions between the studied biological systems were likely to be found on every site taking into consideration that these interactions play a major role in the communities' structuration. We can see that across sites an existing interaction between CPOM and benthic macroinvertebrates α-Diversity that changes among sites. On earlier deglaciation period (sites 2 and 3) the increase in CPOM caused a decrease in α-Diversity opposite to site 4 with an older deglaciation age where an increase in CPOM increased α-Diversity. On the other hand

this same CPOM increased slightly in sites 2 and 4 and increased very significantly in site 3 with an increase in flora α-Diversity and flora cover. Flora α-Diversity, increased with *Carabidae* density without taking into consideration the studied sites and on the opposite, an increase in flora α-Diversity decreases slightly *Carabidae* density on sites 1, 2 and 3 meanwhile in site 4 an increase in flora α-Diversity increased *Carabidae* density. The *Carabidae* density was also be affected by an increase in stream chlorophyll A in site 4. Finally, an increase in stream chlorophyll A also impacted benthic macroinvertebrate density with a decrease in site 2, a slight increase in site 3 and a much more significant increase in site 4.

IV.   Discussion

1) Succession patterns along the deglaciation gradient

Results showed an increasing gradient of α-Diversity and abundance with increasing deglaciation age among sites for both flora and aquatic invertebrates as found in Milner et al. (2000) for aquatic invertebrates. Increase of α-Diversity was more pronounced on late colonization stages for the flora and aquatic invertebrates. The increase in both flora cover and α-Diversity was accompanied by an increase of existing litter particularly in the latest stage of primary succession that may be due to the establishment of new vascular plants along the deglaciation gradient. The litter increase could be the responsible of the observed increase of *Enchytraeidae* at the same stage of succession. Surprisingly, α-Diversity of *Carabidae* didn't change with along the deglaciation gradient, which is opposed to the findings of Greben-Krenn et al. (2011) in the Alps where sites of later age since deglaciation presented higher values of both α-Diversity and abundance. In the Carihuairazo only *Carabidae* abundance increased along deglaciation gradient for studied sites. The first colonizers for flora and aquatic invertebrates were well-adapted taxa to cold temperature and freezing such as *Chironomidae* (Irons, Miller & Oswood, 1993) or well adapted taxa to desiccation such as Bryophyta (Proctor, Ligrone & Duckett, 2007), which have more facility to establish. Such was the case of our stream where *Chironomidae* were the dominant taxa in all sites that decreased with the establishment of new taxonomic groups. This dominance decreased along the stream as new taxa colonized it. This increase in taxa could be translated as an increase in present functional groups along the stream. Most abundant *Chironomidae* was *Orthocladiinae* followed by *Podonominae*. There was an absence of *Diamesinae* along the stream, which is opposed to the findings of Fureder *et al.* (2001) where *Diamesinae* were the dominant taxon

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in the Alps. The finding of high content of chlorophyll A (2.937 µg.cm^{-2}) among studied zones in earliest colonization stage gives us also an idea on the earliest colonization in streams by primary producers assembled in biofilms that could be one of the consumed resources by *Chironomidae*. The most homogeneous evenness values were found in a mid-late stage of primary succession (site 3), which could mean a stabilization of community structure before the colonization of a second wave of arriving taxa. Studied sites presented overall differences of community composition for all systems, of which studied sites 3 and 4 were more similar for aquatic invertebrates and sites 2 and 3 were more similar for flora. Thus, the community composition along deglaciation gradient varies with the establishment of new taxa or individuals with increasing deglaciation age as well as the species or individual turnover. Primary succession after glacial retreat along deglaciation gradient appeared to follow the following patterns for both flora and taxa: An earliest colonization (site 1) of high-tolerant taxa as pioneers of colonization; an early colonization (site 2) characterized by the arrival of new taxa and an increase in both functional and taxonomic diversity that could imply the establishment of more complex interactions within studied communities. A rather stable mid-late colonization (site 3) with arrival of a few more taxa, high values of evenness and the presence of high vascular plant DNA of taxa that possibly could not yet establish in this site because of time-lag between glacial retreat and upward migration in the tropical Andes (Zimmer *et al.* 2018). Finally a late colonization (site 4) characterized by a sharp increase in present taxa and abundance where possibly a second wave of colonizers arrived due to more favorable conditions and interactions that allowed them to establish. Studied *Carabidae* didn't follow these patterns as all species were found in all sites and only abundance increased along deglaciation gradient. This could mean that there are differences in primary succession that could depend on taxonomic systems even though we lack on information of other terrestrial invertebrates such as spiders to see if terrestrial invertebrates have a similar pattern as the one observed for studied *Carabidae*.

2) Environmental and spatial filtering primary succession

Environmental conditions along the gradient will become more benign explaining the increase in both taxa diversity and abundance for their range establishment limits (Louthan, Doak & Angert, 2015). The differences of colonization patterns found between studies carried in the Alps and the Carihuairazo could possibly be explained by both altitudinal difference existing between studied sites in the Alps (2400-2600 m a.s.l) and the Carihuairazo (4630-4770 m a.s.l) and the latitude where the studies were carried (Castella et al. 2001).

Temperature appeared to be a strong filter for early succession where only well adapted taxa could establish (Irons, Miller & Oswood, 1993), (Proctor, Ligrone & Duckett, 2007) as well as altitude, which is highly correlated to temperature. For the stream community we can see that the late deglaciation stage (site 4) is rather structured by water temperature as found in Castella *et al.* (2001). The establishment of vascular plants and the increase in both their diversity and abundance could be explained by the strong existing soil-plant relationship (Van der Putten et al., 2013) with vascular plants playing possibly a major role in soil ecosystem properties, especially in later stages of primary succession (Mori *et al.*, 2017). Particularly in late colonization the presence of *Enchytraeidae* could possibly enhance strongly the process of podogenesis thanks to the high litter content. The importance of organisms in podogenesis is strong as they are the main source of soil organic matter, which micro spatial coverage and connectivity is higher on sites of an older deglaciation period (Schweizer *et al.*, 2018), thus explaining the fact that sites of older deglaciation period are more favorable for the establishment of some of the studied flora. Environmental and spatial conditions didn't appear to affect *Carabidae* diversity but rather their abundance. Distance to glacier is also a major filter to colonization due to the dispersion capacities of our present organisms. Particularly, *Carabidae* might have a higher dispersion capacity than our present flora and aquatic invertebrates, which would explain the fact that all described species, were found in all studied sites. Further studies could be lead using functional diversity of found taxa such as dispersion capacity to assess the importance of dispersion on primary succession.

3) Biotic interactions

In high altitudes the stress gradient hypothesis states that on harsh conditions facilitation interactions rather than competition exist among species (Callaway et al. 2002). Facilitation processes can for example be seen in plants where nurse plants, might provide suitable habitats to other plants (Choler, Michalet & Callaway, 2001; le Roux, Virtanen, Heikkinen, & Luoto, 2012). This may be the case of facilitation interactions between vascular plants and present Bryophyta and Fungi that might help out to the establishment of said vascular plants with increasing deglaciation age. Nevertheless, in late colonization stages the competition between species because of more benign conditions could be the cause of the community structures (Alexander, Diez, & Levine, 2015). CPOM's different effect among sites on taxa diversity could be actually explained by the functional groups present in the stream that would normally be higher in late colonization stage as well as the different effects of chlorophyll A among sites, which could feed on these. It has been proven that in alpine

foodplains *Carabidae* mostly feed on freshwater taxa where taxa such as *Bembidion* genera have a preference towards *Chironomidae* (Hering et al. 1997). Thus, the fact that *B. andinum* were found to be one of the dominant species in early colonization stage as the only present taxa present in the stream were *Chironomidae*. This could also explain the fact that even with apparent low resource availability in earlier deglaciation sites, all species found in *Carabidae* community were found along the deglaciation gradient. The fact that *Carabidae* are predators could have a positive impact on flora diversity by preying on potential predators as well as on the other hand, an increase of flora could enhance presence of potential *Carabidae* prey. Finally, the increase of cover and diversity of flora effect on CPOM increase could be explained by falling vegetation debris to the stream.

V. Conclusion

Primary succession after glacial retreat in tropical alpine ecosystems appears to vary depending on pioneer taxa. We could remark that for both flora and benthic invertebrates the succession followed a similar pattern with the first pioneer taxa establishing and continued by a steady increase in the new arriving taxa afterwards and in late colonization stage a sharp increase with an apparent second wave of colonizers. This wasn't the case for *Carabidae* nor for soil DNA that had completely different patterns. *Carabidae* only presented a density increase of pioneer taxa while soil DNA showed us no pattern at all. The differences of primary succession between studied systems might be explained by dispersion capacity of pioneer taxa. Environmental, spatial filters had a significant impact on primary succession for all studied systems across the deglaciation gradient. For flora and aquatic invertebrates, low temperature determined the first pioneer taxa characterized by high stress tolerance. Establishment of the following pioneers was determined by different type of strategies in terms of biotic interactions where *Carabidae* apparently fed on freshwater invertebrates along the deglaciation gradient and where facilitation played a role in flora establishment. Finally, podogenesis with increasing glacial age probably played a major role in the establishment of present flora as well as soil taxa. Complementary studies could be assessed in the Andean páramo in order to identify all these processes, particularly the dispersion capacity to have further explanations for the patterns of primary succession found in this study.

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Annex

Test	Aqua			
	Diversity	Density	Shannon	Evenness
Kruskal-Wallis	0,0809043	0,2182474	0,35505181	0,49240844
	Carab			
	Diversity	Density	Shannon	Evenness
Kruskal-Wallis	0,1605364	4,34E-02	3,19E-01	1,68E-01
	Density			
Dunn Post-hoc		Site 1	Site 2	Site 3
	Site 2	0,01741713	NA	NA
	Site 3	0,21294628	0,25751798	NA
	Site 4	0,01273807	0,90985003	0,2129463
	Flora			
	Diversity	Cover	Shannon	Evenness
Kruskal-Wallis	3,30E-06	1,85E-07	3,01E-06	3,46E-04
	Diversity			
Dunn Post-hoc		Site 1	Site 2	Site 3
	Site 2	3,46E-02	NA	NA
	Site 3	9,82E-04	0,42828226	NA
	Site 4	2,02E-06	0,03981974	0,4282823
	Cover			
Dunn Post-hoc		Site 1	Site 2	Site 3
	Site 2	1,26E-01	NA	NA
	Site 3	3,64E-04	0,1260369	NA
	Site 4	2,74E-07	0,00199717	0,1754526
	Shannon			
Dunn Post-hoc		Site 1	Site 2	Site 3
	Site 2	3,37E-02	NA	NA
	Site 3	9,36E-04	0,42526974	NA
	Site 4	1,85E-06	0,03891853	0,4252697
	Evenness			
Dunn Post-hoc		Site 1	Site 2	Site 3
	Site 2	0,01367196	NA	NA
	Site 3	0,73168915	0,03550589	NA
	Site 4	0,73168915	0,00061217	0,7316892
	Soil			
	Diversity	Relative Abundance	Shannon	Evenness
Kruskal-Wallis	0,0893251	1,18E-01	2,77E-01	1,18E-01

Annex 1 : Table of p-values of Kruskal-Wallis tests for calculated indices on all four systems comparing the different sites. When kruskal-wallis tests showed significant values, Post-hoc Dunn tests were done (tables under the kruskal test) to assess the differences between sites. Significant values are highlighted for p-value<0.05 (yellow highlight) and p-value<0.01 (orange highlight).
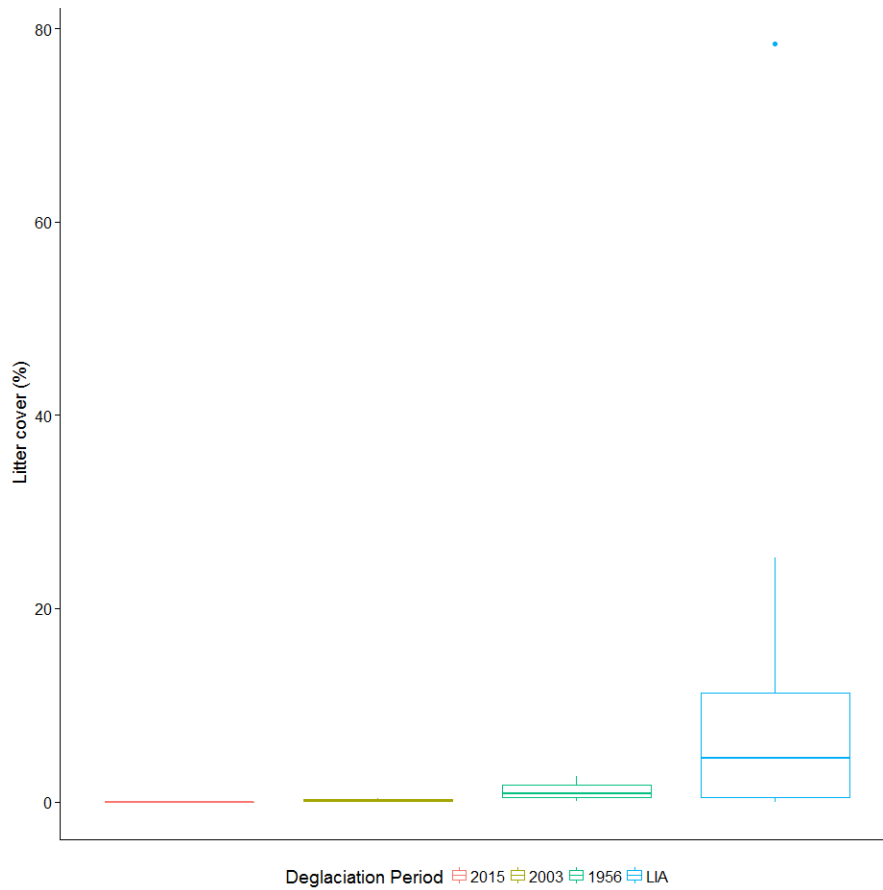
Annex 2 : Boxplot of litter cover per deglaciation period site

Test	Litter		
	Cover		
Kruskal-Wallis	9,71E-06		
Dunn Post-hoc		Site 1	Site 2	Site 3
	Site 2	0,538	-	-
	Site 3	0,00083	0,18456	-
	Site 4	2,90E-05	0,02446	1

Annex 3 : Kruskal-Wallis p-value for litter cover across studied sites and table containing the Dunn Post-hoc test p-values between sites on litter cover. Significant values are highlighted for p-value<0.05 (yellow highlight) and p-value<0.01 (orange highlight).
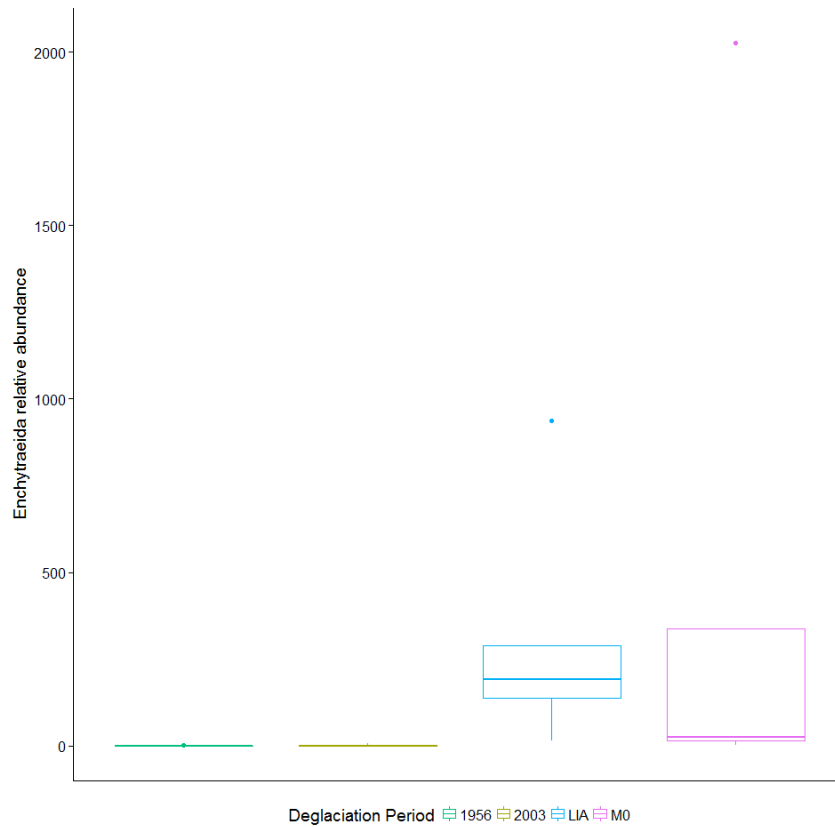
Annex 4 : *Enchytraeidae* **boxplot per deglaciation period site**

Test	Enchytraeidae			
	Relative Abundance			
Kruskal-Wallis	2,77E-03			
Dunn Post-hoc		Site 2	Site 3	Site 4
	Site 3	0,6229	-	-
	Site 4	0,0111	0,0024	-
	Site 5	0,0269	0,0068	0,7431

Annex 5 : Kruskal-Wallis p-value for *Enchytraeidae* relative abundance across studied sites and table containing the Dunn Post-hoc test p-values between sites on *Enchytraeidae* relative abundance. Significant values are highlighted for p-value<0.05 (yellow highlight) and p-value<0.01 (orange highlight).

	Aquatic	P-value	Flora	P-value	Carabidae	P-value	Soil DNA	P-value
β-Bray	ΔDG	0,046	ΔDG	0,001	ΔDG	0,007	ΔDG	0,001
					ΔMT	0,019	ΔT	<0,05
β-Bray$_{turn}$	ΔT	0,045					ΔDG	0,001
	ΔChloA	0,026					ΔT	<0,05
β-Bray$_{nest}$			ΔDG	0,001	ΔDG	0,01	ΔDG	0,001
					ΔMT	0,027		
β-Sør	ΔDG	0,009	ΔDG	0,001			ΔDG	0,001
	ΔT	0,024					ΔT	<0,05
	ΔpH	0,001						
β-Sør$_{turn}$	ΔChloA	0,048					ΔDG	0,001
							ΔT	<0,05
β-Sør$_{nest}$	ΔpH	0,009	ΔDG	0,001			ΔDG	0,009
			ΔDS	0,036				

Annex 6 : P-values table of MRM tests between spatial or environmental variables differences and Beta-Diversity calculated indices.

Résumé – Abstract

Le réchauffement climatique a un fort impact dans le retrait des glaciers, particulièrement dans des écosystèmes alpins tropicaux, qui sont peut-être les plus affectés avec un des plus rapides rétrécissements glaciaires dans le monde. Du au retrait des glaciers, de nouvelles zones deviennent disponibles pour que des taxons le colonisent que ce soit dans des systèmes aquatiques ou terrestres. Notre étude visait caractériser les mécanismes terrestres et aquatiques de succession primaire dans quatre systèmes différents (invertébrés aquatiques, flore, *Carabidae* et ADN du sol) dans le but de comprendre ces mécanismes et particulièrement pour pouvoir comparer les patrons de succession primaire entre systèmes. On a évalué la composition des communautés de ces quatre systèmes dans quatre sites différents suivant un gradient de déglaciation. On a trouvé de tendances de succession similaires entre invertébrés aquatiques et la flore avec une augmentation d'abondance et diversité tout au long du gradient de déglaciation. Les filtres biotiques, spatiaux et environnementaux ont eu un fort impact dans la succession primaire avec le dernier jouant un rôle majeur dans de stades initiaux de colonisation. Pour les *Carabidae* une tendance différente dans laquelle les filtres affectaient uniquement l'abondance tout au long du gradient de déglaciation. Aucune tendance n'a été trouvée pour l'ADN du sol.

Global warming has a strong effect on glacier retreat, particularly in alpine tropical ecosystems, which are perhaps the most affected worldwide with one of the fastest glacial shrinkage around the world. With glacier retreat new zones become available for taxa to colonize it in both terrestrial and aquatic systems. Few are the studies that have tried to compare primary succession after glacial retreat of different taxonomic systems in an alpine tropical ecosystem. Our study aimed to characterize both aquatic and terrestrial primary succession mechanisms on four different systems (aquatic invertebrates, flora, *Carabidae* and soil DNA) in order to understand these mechanisms and particularly in order to compare primary succession patterns among systems. We assessed community composition of these four systems along a deglaciation gradient in four different zones. Similar patterns of succession between aquatic invertebrates and flora were found with an increase in both abundance and diversity along the deglaciation gradient meanwhile. Biotic, spatial and environmental filtering had a strong impact on primary succession along the deglaciation gradient where the latter had a major impact on early stages of colonisation. For *Carabidae* a different pattern was found where the filters only affected abundance along deglaciation gradient. We found no specific pattern of soil DNA.