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### Trait-based studies of páramo vegetation in the northern Andes

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# General Introduction

Marian Cabrera

High Andean grasslands also called páramos are key ecosystems for water regulation, carbon storage and for sustaining high levels of biodiversity (Buytaert et al. 2006, Farley and Bremer 2017). About 40 million people depend on páramos for their water resources, not only in the highlands but also downstream the Andean region. Páramo soils receive abundant inputs of aboveground and belowground organic matter (Podwojewsky and Poulenard 2005). Key factors such as a high organic matter input, low decomposition rate and a low annual temperature, promote a high carbon storage capacity in the soil (Podwojewsky and Poulenard 2005, Farley et al. 2013). The large amount of carbon in páramos constitutes a valuable terrestrial carbon store for climate change mitigation (Farley et al. 2013). Moreover, páramos maintain the highest diversity in vascular plant species among highland ecosystem in the world (Cleef 1981). The conservation of páramo ecosystem depends on the capacity to sustain its ecological functions. There is invaluable information from different perspectives (e.g., Mora-Osejo and Sturm 1994, Llambí 2013, Rangel-Ch and Sánchez 2005, Rangel-Ch 2018) and still, there will be a long path to fully understand the complexity of this ecosystem. In here, I wanted to bring new insights into the functional structure and functional composition of páramo plant communities in semi-natural and in successional stages

## 1.1 - THE PÁRAMO BIOME

The biogeographical region of páramo ecosystems encompasses the open vegetation between 2800 m to the permanent snow line at 4200 m in the northern Andes (Luteyn 1999). Páramos extend from Costa Rica at 11°N to the northern Huánaco in Perú at about 8°S (Luteyn 1999, Cuatrecasas 1968) (Figure 1-1).

This ecosystem was established approximately 4 -3 Ma (early Pliocene) (van der Hammen 1974). Its development was driven by complex ecological and evolutionary processes between abiotic (e.g., topography and elevation) and biotic factors (e.g., immigration of taxa, speciation) as a result of the Andean uplift (Rull 2014, Gregory-Wodzicki 2000, Cleef 1981). The gradual upheaval generated a change in the ecological conditions from tropical to temperate and cold, facilitated immigration of floristic elements from the Holarctic and Antarctic regions, and promoted evolutionary adaptations from the neotropical flora and the development of highland biomes (van der Hammen et al. 1973) (see Box 1). As a result of the elevational zonation, páramo has been classified in three subdivisions a) subpáramo, which is the lower limit and is characterized by shrubby vegetation mixed with grasses; b) proper páramo which is the middle belt mainly dominated by grasses and giant stem rosettes; and c) superpáramo, in the upper limit, is characterized by scarce vegetation, mainly dominated by basal rosettes, cushions and short grasses (Cleef 1978).

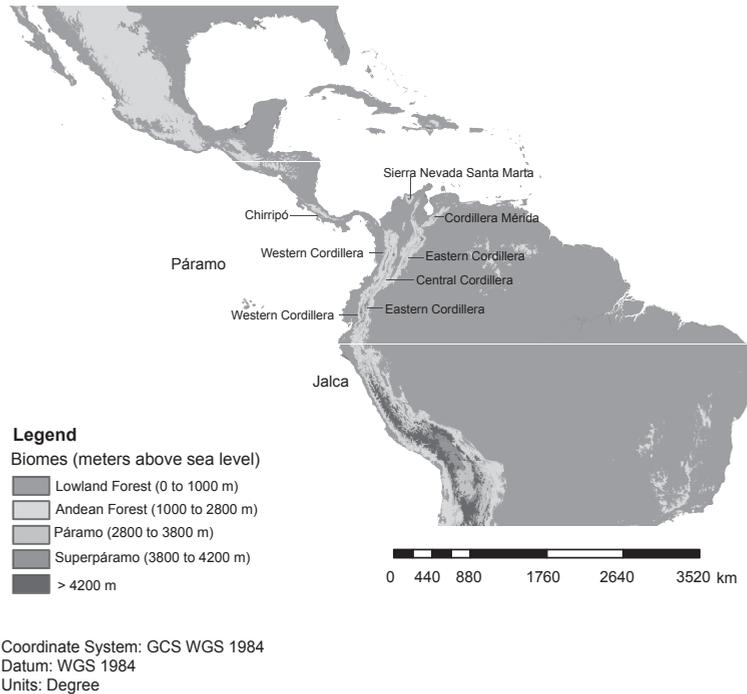


Figure 1-1: Localization of páramo biome in the northern Andes.

Climate is characterized by a low mean annual temperature and extreme fluctuation in daily temperature (Luteyn 1999). There is not a marked seasonality and the daily cycle is the major environmental pulsation for páramo biota (Sarmiento 1986). Temperature and precipitation depends primarily on two aspects: the latitudinal gradient and the elevation gradient (Buytaert et al. 2006). Daily temperatures can fluctuate from 25°C to temperatures below 0°C (Sarmiento 1986). At larger scale precipitation is influenced by the Pacific Ocean and by the Amazon basin (Rangel-Ch and Sánchez 2005, Buytaert et al. 2006). At local scale precipitation is determined by variation in wind direction and wind speed, which are controlled by the steep slopes, the heterogeneous topography, and the permanent fog (Cleef 1978, Buytaert et al. 2006). Among páramos, annual precipitation is highly variable, ranging from 700 mm up to 3000 mm (Luteyn 1999). The relative humidity varies from 50% to the saturation point (Rangel-Ch and Sánchez 2005). In association with a higher elevation, there is an increase of solar radiation intensity, wind speed, and carbon dioxide while there is a decrease of atmospheric pressure (Billings 1974). Radiation is controlled by frequent fog, and is mainly converted into heat by the soil surface and vegetation (Cleef

1981). Soils are in general humid with high content of organic matter, these properties and the low temperature contribute to keep low decomposition rates (Buytaert et al. 2006). Soil characteristics are also influenced by elevation, slope, and geographical location (Malagón and Pulido 2000). Most soils in páramo have a volcanic origin; soil thickness ranges from a few centimetres to several meters; the cold and wet climate and the low atmospheric pressure favour organic matter accumulation (Buytaert et al. 2006). Soils are acidic, with a high content of aluminium, in contrast to a low phosphorous content (Podwojewsky and Poulénard 2004, Rangel-Ch 2018).

## 1.2 - PLANT ADAPTATION IN PÁRAMO

High mountain plants are generally small and have a long life span (perennials), which take several years to become established (Billings 1974). Not all of the morphological peculiarities observed in the flora of an extreme environment need to have developed in response to conditions resembling the actual ones - some may just have been inherited from ancestors who acquired them under entirely different conditions (Hedberg 1964). However, some features of páramo plant species suggest that these species have certain adaptations as response to the challenges faced in this environment such as frost resistance, high light intensity, drought, and shortage of nutrients (Hedberg 1964, Cleef 1981, Beck 1994). Plants cope with low temperatures either by protecting plant organs from freezing (i.e. insulation) or by preventing the formation of ice at sub-freezing temperatures (Beck 1994). In tropical highlands, one of the most conspicuous characteristics of plant adaptation for insulation is their growth forms (Cuatrecasas 1968, Hedberg 1964). Each plant individual and patch of vegetation creates to some extent a microclimate of its own. Plant cover interferes both with the incident sunlight and the outward radiation, modifying the temperature gradient above the ground and ameliorating the climate at the soil surface. The denser a plant - or plant community- is growing, the better its possibility to create a microclimate of its own (Hedberg 1964). Thus, a compact type of growth might contribute to a species' ability to cope with environmental conditions (Hedberg 1964). I will give more detailed information of each growth form in the following section. In highlands, the open vegetation allows a high intensity in solar radiation to reach the vegetation and even the soil surface (Billings 1974). Plants protect them from this strong radiation by an indumentum that covers one or both sides of the leaves, which reflects the incident radiation (Cleef 1981, Hedberg 1964). Páramo plants are xeromorphic, an adaptation that regulates transpiration demands under precarious water supply. Xeromorphic leaves are characterized by having much sclerenchyma, a thick cuticle and numerous stomata (Hedberg 1964). Xeromorphic leaves have a long leaf life span a low values of specific leaf area (leaf area per unit leaf mass) (Diemer 1998a,1998b, Llambí et al. 2003).

### 1.3 - GROWTH FORMS

Growth forms provide a classification for plants based on their morphological or physiological characteristics, independent of their relatedness or origin. This classification is sometimes confounded with that of life form, which represents the position of growth buds during the less favourable season (Raunkiær 1934). However, in tropical highlands this life form classification is hardly applicable because of the lack of seasonality (Hedberg 1964, Hnatiuk 1978, Cleef 1981). In tropical highlands, morphological and ecological aspects are closely related and distinct growth forms can be clearly recognized (Hedberg 1964, Cleef 1981, Ramsay and Oxley 1997). Hedberg (1964) recognized five growth forms adapted to tropical highlands: giant leaf rosettes (caulirosettes), tussocks, rosettes, cushion, and sclerophyllous shrubs. Apart from these growth forms, we distinguished herbs and sedges/grasses. Although these growth forms do not represent a special plant adaptation to the páramo environment, they are often encountered.

#### *Caulirosettes*

Caulirosettes are also called giant leaf rosettes, caulirosula or stem rosettes (Cuatrecasas 1968, Cleef 1981, Ramsay and Oxley 1997). These plants are characterized by a thick stem, which is terminated by a huge dense leaf rosette. The stem is usually covered by dead leaves or by a cork-like bark, as a mechanism for temperature insulation (Hedberg 1964). Most giant rosettes species have a water-storing pith tissue in the centre of the stem, which might be used to avoid drought stress and stomata closure (Smith and Young 1987). The centre of the rosette contains a dense core of young leaves and leaf buds, protecting the shoot apex against extreme temperatures (Hedberg 1964). Leaves are wide and in general have a dense pubescence, but among species this is highly variable. Leaf hairs might play a role in regulating the microenvironment and leaf water relation (Baruch and Smith 1979).

#### *Tussocks*

Tussocks consist of grasses of which their basal parts of the culm are intermingled with dead or decaying leaves forming a dense felt-like mass (Hedberg 1964). Innovation shoots are formed mainly in the central part where they are protected against changes in temperature and moisture. Leaves are distinctly xeromorphic, usually densely folded, and appearing in more or less filiform (Hedberg 1964). For tussocks, plant height is a function of leaf length and it varies according to micro-environmental conditions (Hnatiuk 1978).

#### *Basal rosettes*

Basal rosettes are also called acaulescent rosettes or sessile rosettes (Hedberg 1964, Cleef 1981). These plants are characterized by a very small or completely absent aboveground stem; the leaf rosette is located at the level of the soil surface (Hedberg

1964). The subterranean part of the stem is usually firm. Some species have a robust tap-root, while others show tough side roots. In most species leaves are large and moderately xeromorphic (Hedberg 1964).

#### *Cushions*

Cushions are characterized by a branched stem with very short internodes; each branch terminates in a dense leaf rosette. The spaces between the branches are filled with decaying leaf remains and soil (Hedberg 1964). Cushion plants can form soft or hard mats, and form semi-spherical or flat shapes (Ramsay and Oxley 1997). Most of the species have xeromorphic leaves.

#### *Sclerophyllous shrubs*

Sclerophyllous shrubs are small woody plants, usually with small rigid and coriaceous leaves; leaf surfaces are often covered by a pubescence. These shrubs can be unbranched (e.g., *Monnina*) or abundantly branched (e.g., *Vaccinium*) (Hedberg 1964).

#### *Herbs*

Herbs have a non-woody stem. Plants can have an erect or prostrate habit. Ramsay and Oxley (1997) subclassify these plants as erect, prostrate and trailing herbs. Some of the species might have xeromorphic leaves.

#### *Sedges and grasses (non-tussocks)*

Sedges and non-tussock grasses constitute mainly species from the family Cyperaceae or grasses that do not form tussock forms.

Growth forms exhibit morphological differences in size, woodiness and lifespan (Lavorel et al. 1997). They also represent different mechanism of carbon assimilation and carbon storage (Cáceres et al. 2015). However within growth forms, there is a high variation in the functional responses to environmental conditions (Hernández 2005). In this study, growth forms are considered in some cases (Chapter 2 and Chapter 3) as a factor to control for the variability in the analysis.

## 1.4 - FUNCTIONAL COMMUNITY ECOLOGY

Plant communities represent a group of species co-occurring at given time and place. Páramo plant communities have being widely described from a phytosociological perspective (Cleef 1978, 1981, Monasterio 1980, Rangel-Ch 2000, Rangel-Ch and Sánchez 2005, Cleef et al. 2005, Arellano-P and Rangel-Ch et al. 2008, Moscol-Olivera and Cleef 2009, Rangel-Ch 2018). These studies describe plant associations by selecting the most dominant or the most characteristic species in association with certain properties of the habitat (Rangel-Ch 2018). For example, plant associations that involve the presence of *Chusquea tessellata* are used as an indicator of high humidity (Cleef 1981) or associations characterized by the dominance of the species *Acaena*

*cylindrostachia* or *Paspallum* spp. denote human disturbances (Moscol-Oliviera and Cleef 2009, Rangel-Ch 2018). A complementary perspective to gain more insight into drivers of community structure can be obtained by studying plant traits (see Box 2). A plant trait is any morphological, physiological, reproductive or life-history attribute measurable at the individual level and which is linked to species' performance (McGill et al. 2006, Violle et al. 2007). Species can be seen as a complex expression of multiple traits. Having a certain set of traits, will determine the interaction of a species with its physical, biotic and abiotic environment (Cavender-Bares et al. 2009). In a plant community, the composition and variability of traits are seen as the result of ecological and evolutionary processes driven by environmental forces that act as a sorting device and filters (Keddy 1992, Weiher et al. 1998). Environmental forces are abiotic or biotic factors that may act at different spatial scales and at different levels of organization (e.g., organs, individuals, taxa) (Keddy 1992). This framework is based on niche theory which postulates that either the physiological tolerance (abiotic factors) or the competitive capacity of the species (biotic factors) determine their coexistence (Tilman 1986). In species-rich communities, disentangling what are the main processes determining trait composition and trait variability is challenging. However, the increasing evidence of consistent trait-environment relationships among species and plant communities (Berry and Calvo 1989, Díaz et al. 1998, Choler 2005, Azocar et al. 2007, Monteiro et al. 2011, Asner et al. 2014, Blonder et al. 2018) suggests that the underlying mechanisms determining trait patterns relate to both, the strategies of species to deal with limiting resources and to respond to changes in the environment (Castellanos 2013).

In páramo, established plant species grow under low mean annual temperatures, high fluctuations in daily temperatures, highly acidic soil, and a shortage of soil nutrient availability (Luteyn 1999, Podwojewsky and Poulenard 2005). As mentioned before, plants have certain adaptations to these conditions such as growth forms, sclerophyllous leaves and small height. In these habitats, the lack of seasonality produces a constant growth. However, due to environmental constraints, plant growth rate is low. Besides, plants are perennials and are adapted to strategies of resource conservation, which means a higher investment in carbon storage and higher longevity (Díaz et al. 1998, Körner 2003). A key trait that has been associated with this strategy is specific leaf area (SLA) (Díaz et al. 1998, Poorter et al. 2009). SLA is the ratio between leaf area and leaf mass, and is a manifestation of a trade-off between leaf longevity and photosynthetic capacity (Wilson et al. 1999, Westoby et al. 2002). Another trait related to carbon gain and longevity is plant height (Moles et al. 2009). Plant height represents the outcome of balancing light capture and the structural investments needed for support (Westoby 1998). Moreover, both traits are proxies for relative and total growth-rate related biomass and plant productivity (Cornelissen et

al. 2003). Intraspecific variation in ecological and life-history traits is a feature that potentially influences the abundance and distribution of species in heterogeneous environments (Murray et al. 2002, Geng et al. 2012, Umaña et al. 2015). Intraspecific trait variability expresses the range of possible trait values as well as the variability of what is functionally experienced by individuals of a given species living at certain environmental conditions (Albert et al. 2010a;b). It results from genetic and environmental mechanisms and their interactions (Albert et al. 2011). When measuring traits, it is possible to account for different sources of variation, for example within individuals, within species (intraspecific variability), and among species (interspecific). Nowadays, researchers have emphasised the relevance of the contribution of both intra and interspecific trait variability to community processes (Cianciaruso et al. 2009, Albert et al. 2010ab, Violle et al. 2012, Siefert et al. 2015). As realized niche space is essentially determined by selective mechanisms that act as a filter to species, both mean trait value and intraspecific trait variability contribute to a species' ability to pass filters imposed by the abiotic or biotic environment (Jung et al. 2010, Kichenin et al. 2013, Maracahipes et al. 2018). The mean trait values represent the position of the species ("optima") under specific environmental conditions. While intraspecific trait variability can be seen as measure to quantify how a species diversifies its potential niche space through trait variation in response to particular environmental conditions (Bolnick et al. 2011, Albert et al. 2011).

## 1.5 - OUTLINE AND AIMS OF THIS DISSERTATION

The general aim of this study was to gain more insight in how trait variability of páramo plant species explains patterns in páramo plant community structure. In particular, I asked myself how patterns in biomass, abundance and distribution of páramo plants found in series of small plots would be influenced by mean values and the interspecific variability of SLA and plant height. Because the biomass of páramo vegetation is the driver of two essential environmental services of páramo vegetation, i.e., carbon retention and water supply, and because understanding these services requires continuous monitoring of páramo vegetation in permanent plots, I started by looking for reliable methods to estimate páramo plant community biomass in a non-destructive fashion. In Chapter 2, I report about the development of series of multi-species allometric equation models to estimate aboveground, belowground and total biomass of páramo plants arranged according to their growth forms. Further, these models were used to estimate the biomass of páramo vegetation in 61 small plots located in South Colombia. In Chapter 3, I studied how information of two plant traits, i.e., SLA and maximum plant height, may explain the aboveground biomass observed in these 61 plots, in relation to other potential drivers of plant biomass, such

as species composition, soil and elevation. The causality of these explanations was tested using so-called d-separation tests applied to series of path models. In Chapter 4, I addressed how intraspecific trait variability of vascular plant species in semi-natural páramos is linked to patterns in local and regional abundance and to patterns in the latitudinal distribution of the species. Thus, in this chapter I asked whether the abundance and distribution of vascular plant species in the páramo of Colombia is related to intraspecific variability of specific leaf area (SLA) and plant height. In Chapter 5, the role of intraspecific trait variability in páramo community processes was further studied, in particular, regarding the variability of SLA during succession of páramo after long-fallow agricultural disturbance. Earlier studies (Sarmiento et al. 2003) suggest that páramo succession is mostly a matter of changing relative abundances of species present from the start of the succession, instead of the successive appearance and disappearance of species. Assuming that páramo succession is primarily driven by inversely correlated traits directed to resource acquisition or conservation (Huston and Smith 1987, Llambí et al. 2003; Sarmiento et al. 2003), I argued that species abundance at the extreme ends of páramo succession would be in principle determined by one single selective mechanism (related to optimizing resource acquisition in early succession and resource conservation in late -succession). As a consequence, at mid-successional stages, species would be subjected to both mechanisms to which they should be optimally adapted in order to gain dominance. This led us to hypothesize that mid-successional communities would be predominantly built up by species showing a larger intraspecific variability than early- or late-successional communities regarding traits through which species respond to maximize their fitness along the acquisition-conservation axis. Thus, in this chapter I asked how the mean SLA values and the intraspecific SLA variability in páramo plant communities would change with succession. Finally, in Chapter 6, I evaluated and synthesized the information obtained in the preceding chapters, and attempted to identify and formulate needs for new trait-based research of páramo vegetation.

### Box 1: Origin of páramo

The geological events of the Andean rising occurred at different timescales in which diverse plate tectonic readjustments took place (Simpson 1983, Hoorn et al. 2010). In the northern Andes, these processes marked the development of three mountain chains: the Western, Central and Eastern cordilleras. These mountain formations started rising approximately 23 Ma (late Oligocene to early Miocene), with more intense peaks between 12 Ma (late middle Miocene) and 4-3 Ma (early Pliocene) (Hoorn et al. 2010). Upeavals during the Andean uplift have been correlated with a progressive development of latitudinal and elevation climatic zones (Simpson 1983), promoting changes in climate, hydrological patterns, and biophysical conditions (Flórez 2002, Mulligan et al. 2010). Global climatic events accompanied the evolution of Andean biomes, in which highly dynamic process of expansion and contraction of vegetation belts occurred during glacial and interglacial periods (van der Hammen and Hooghiemstra 2000). Records of fossil pollen showed us evidence of a long (in time) and dynamic process of continuous reorganization of floristic elements in response to global climate change (Torres et al. 2013). There are two mechanisms acting together in migrating biomes, a transitional phase of individual taxon migrations, as some species are indicative of pioneers and responded first to climate change, and a concerted association-based migration (González-Carranza et al. 2012). High Andean environments have been available for plant colonization only since the Pliocene and on an extensive scale only in the Quaternary (van der Hammen 1974, Simpson 1975, Smith and Cleef 1988). The evidence of a possible precursor of páramo (proto-páramo) is also revealed in pollen fossil records. Some pollen records such as Gramineae, Compositae, and *Hypericum* indicate the first plant arrangement of mountain vegetation, when the Andes might have had lower elevation than present-day ranges (van der Hammen et al. 1973, Torres et al. 2013). Between 3 and 2.3 Ma (Pliocene), the mountain vegetation must have been open and pollen records of Gramineae, *Ranunculaceae*, and genera as *Valeriana*, *Plantago*, *Aragoa*, and *Polylepis-Acaea* type, indicate for the first time the presence of an open páramo-like vegetation, although this ecosystem still had a lower number of species than present-day páramos (van der Hammen et al. 1973, Torres et al. 2013). Extensive areas of high-mountain environments might have appeared about 2 Ma (Quaternary), and apart from a number of Gramineae and Cyperaceae, the earliest elements of this vegetation included Compositae, Ericaceae, *Polylepis-Acaena* type, *Aragoa*, *Hypericum*, *Miconia*, Umbelliferaceae, *Borreria*, *Jussiaea*, *Polygonum*, *Valeria*, *Plantago*, *Ranunculaceae*, *Myriophyllum*, and *Jamesonia* (van der Hammen et al. 1973). A gradual enrichment of páramo flora is observed during the Quaternary, and pollen records of Caryophyllaceae, *Geranium*, *Lycopodium*, *Gunnera*, and *Gentiana* are observed in the pollen records (van der Hammen et al. 1973). Resources of páramo development flora are tropical and subtropical forest, Antarctic and Holartic elements that successively migrated from different directions (van der Hammen et al. 1973, Smith and Cleef 1988).

### **Box 2: From functional types to functional traits**

Variation among plant species has been studied using discrete or categorical classifications denominated as functional types (Reich et al. 2003). This ordering is based on the adaptive syndromes, or according to their physiological strategies of the plants (Díaz et al. 2002). Functional types represent a group of organisms (or species) that respond in a similar way to the environment or produce similar effects on the ecosystem (Gitay and Noble 1997). For example, plants can be classified according to their life cycle in annuals and perennials, or according to their photosynthetic pathway as C<sub>3</sub> and C<sub>4</sub> (Lavorel and Garnier 2002), or according to their growth form as mentioned before. Plants have been also classified according to the successional stage in which they occur (Noble and Slatyer 1980), or in functional types according to the set of characteristics related to the ability to support or not disturbances (e.g., shade tolerant, light seeds, hemi-saprophyte) (Vargas 1997, Gondard and Deconchat 2003). However, in the last decades, there has been a shift in ecology to go beyond taxonomical information towards a more quantitative and predictive approach. Thus, functional ecology has emerged as a response for searching more general laws in ecology considering as well the high complexity of biological systems (Lawton 1999, McGill et al. 2006). Functional ecology is based on measuring plant traits defined as species' characteristics that strongly influences organismal performance (McGill et al. 2006). Plant traits are continuous variables measured at individual level. Traits are used as a proxy to measure species' performance in relation to environmental factors (abiotic and biotic). It is based on the rationale that traits determine where species can establish and how they interact with individuals from other species (Reich et al. 2003, McGill et al. 2006, Cadotte et al. 2011). Variation among plant species in functional traits will tell us about the plant strategies or spectra of species' performance (Reich et al. 2003). This quantitative approach gives the possibility to scale up and predict changes from population, community, to ecosystem level (Lavorel and Garnier 2002). A functional approach was adopted as part of the framework for the Millennium Ecosystem Assessment (MEA 2002) as well as for the Intergovernmental Platform of Biodiversity and Ecosystem Services complementing a more holistic approach (Díaz et al. 2015). A central point of functional diversity is to provide information that enhances conservation, restoration and policy-makers practices (Cadotte et al. 2011, Díaz et al. 2015).