Calculation of carbon storage of invasive species (*Opuntia* spp.) in Tenerife

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Content

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Abstract

Opuntia maxima and *Opuntia dillenii* are two of the most widespread invasive species in the Canary Islands. Their absolute integration in the Canarian culture and ecosystems, as well as the absence of a precise cartography, make their management and study difficult. In the current context of climate change, investigating the carbon capture and storage function of terrestrial ecosystems is essential. The present work attempts to estimate the distribution and area occupied by these two invasive species on Tenerife, as well as the total amount of carbon accumulated in their biomass. In addition, the basis for a future study of the capture and storage capacity of native scrub species of the island is established.

1. Global atmospheric carbon increase and its environmental consequences

During the last century, anthropogenic activities such as electricity and heat production, agriculture, forestry, and other land uses, industry, transport, and building, have promoted an increase in the release of greenhouse gases (GHG) to the atmosphere: CO_2, CH_4, N_2O, O_3 and CFCs. CO_2 is the main GHG due to its elevated concentration and long-term persistence in the atmosphere (IPCC, 2014). Before the industrial revolution, natural processes balanced the carbon cycle, compensating the liberation of carbon to the atmosphere with its sequestration within carbon sinks such as the oceans, land vegetation and soils, and the Earth´s crust. However, this balance has been disturbed by human activities, which have accelerated the pace of emissions, preventing carbon sinks to maintain relatively stable atmospheric CO_2 levels (Falkowski et al., 2000). As a result, incident radiation on Earth´s surface has caused an increase in global average temperature. The concentration of atmospheric CO_2 has seen an increase from 280 ppm during the preindustrial time to exceeding 410 ppm during 2020, the highest levels detected since, at least, the last 800,000 years, according to the Antarctica ice cores (Lüthi et al., 2008). The result is an increase in average surface global temperature, known as anthropic global warming, along with a series of physical global changes such as the increase in mean sea level, the reduction of sea ice extent, the change of annual precipitation over land, the retreat and disappearing of glaciers, the melting of terrestrial and marine permafrost, and the acidification of oceans. All these processes are consequently altering global ecosystem dynamics (IPCC, 2014).

Since the acceptance of the United Nations Framework Convention on Climate Change (UNFCCC) during the Río de Janeiro Earth Summit (1992), through the Kyoto's Protocol (1997) and the Paris Agreement (2015), which applicability started last year, the European Union (EU) has been encouraging member countries to adopt new measures to manage this environmental problem. The main goal is a reduction of the European CO_2 emissions by 30% compared to 2005 levels, by 2030. The member states will contribute to the overall EU reduction with targets ranging from 0% to 40% below 2005 levels, depending on their GDP per capita, as well as adopting new green technologies and developing their own strategies to increase carbon sequestration. These measures are intended to keep the global average temperature increase below 2°C (trying to limit this increase to 1.5°C) relative to pre-industrial levels, in the long term, among other objectives (Federación Española de Municipios y Provincias, 2011; Lal, 2011; UNFCC, 2015).

In the context of these new guidelines, last April, the Spanish Government approved the new Law of Climate Change and Energetic Transition (Law 7/2021) according to which CO_2 emissions will be reduced by 23% for 2030 compared to 1990 levels. The main goal is to achieve "climate neutrality" before 2050, which means that the country intends to reduce its CO_2 emissions to levels that would allow existent carbon sinks to sequester it.

2. Ecosystems as carbon sinks

During the UNFCCC in 1992, the term "sink" related to anthropic climate change was adopted for referring to any process, activity, or mechanism that absorbs or removes a GHG, its

precursors, or an aerosol from the atmosphere, as opposed to "source" (Federación Española de Municipios y Provincias, 2011). During the 90s, the scientific community started to study the role of terrestrial ecosystems, mainly forests, as potential carbon pools to their balancing potential in the carbon cycle (Dixon et al., 1994). Although the main carbon sink are the oceans, which store 38,000 GT of inorganic carbon (Friedlingstein et al., 2020), terrestrial ecosystems have different factions where carbon can also be stored: vegetation (including aboveground and underground biomass), necromass (fallen branches, trees, dead roots, leaf litter, and organic matter in decomposition in general), and soil organic matter, taking in to account the important activity of microorganisms in decomposition and respiration (Federación Española de Municipios y Provincias, 2011). It is estimated that vegetation and soil store 2,000-3,000 GT of carbon (Friedlingstein et al., 2020). The three storage compartments (ocean, land vegetation and soil) have the potential to maintain a dynamic balance between them and the atmosphere. If the balance of a system results positive, this is, the ecosystem fixes more carbon than it is released, it can be considered that is acting as a sink. On the other hand, if the ecosystem releases more carbon than it captures, we talk about a carbon source (Federación Española de Municipios y Provincias, 2011).

2.1 Uncertainty on the current status and future projections of the terrestrial carbon sink

There is an increasing body of literature assessing how terrestrial ecosystems act as large carbon sinks (Huang et al., 2020). Evidence supports that terrestrial carbon sink has experienced a huge increase during the last century, and model simulations point that this has been driven by the increment of CO_2 concentration of the atmosphere (CO_2 fertilization), due to anthropogenic activities (Liu et al., 2019). CO_2 fertilization may stimulate photosynthesis (CO_2 fixation) which, in turn, may enhance woody biomass growth. This process is also known as the "CO_2 effect", the effect of increasing atmospheric CO_2 on terrestrial carbon storage by increasing photosynthetic rates (Schimel et al., 2015), and it is believed to lie behind the stimulation in growth observed in old forest stands (Brienen et al., 2015; Liu et al., 2019). For the decade 2010-2019, around 11 GT of carbon were released to the atmosphere each year from the use of fossil fuels and land-use changes, while vegetation was only able to uptake around 3.4 GT (Friedlingstein et al., 2020). Although terrestrial vegetation cannot uptake most of anthropic carbon emissions, the CO_2 effect is probably acting as negative feedback in today's global carbon cycle (Schimel et al., 2015).

There is controversy over the current status of the terrestrial carbon sinks and their future trajectory under the influence of global change, due to contradictory information provided by different data sources (Keenan & Williams, 2018; Fatichi et al., 2019). Due to the increase in atmospheric CO_2, the temperature is also increasing, and this could result in climate effect and the land-use trends exceeding the CO_2 effect, by increasing respiration rates and promoting an enhanced CO_2 release rate, according to model simulations (Liu et al., 2019). In addition, although the photosynthetic response to CO_2 saturates at concentrations well above current levels, the net primary production of ecosystems may be limited by resource availability (water, nitrogen, phosphorous) at much lower CO_2 concentrations. There are also evidences that enhanced growth at high CO_2 concentration may cause trees to accelerate their lifecycle, increasing biomass turnover rates and therefore limiting any CO_2-driven enhancements in the carbon sink (Pugh et al., 2019). On the other hand, it is suggested that, beyond CO_2 fertilization, other factors such as nitrogen deposition, forest regrowth, high latitude warming, and an

increase in growing season length can all contribute to an increased terrestrial sink. The balance of all these interactions is complex and not well-known, but it determines if the different ecosystems act as a net source or sink of carbon (Huntzinger et al., 2017).

Tropical forests store large amounts of carbon, but there is no agreement about their net contribution to the terrestrial carbon balance. Recent studies state that the greatest tropical forests of America, Africa, and Asia are currently acting like net sources of carbon, opposing the general expectation of a strong and continuous sink of tropical biomass. Carbon losses, mainly from deforestation and reductions in carbon density within standing forests due to degradation or disturbance, are exceeding gains by forest growth on every continent (Baccini et al., 2017). Regional-scale and long-term studies in the Amazon detected a progressive decline in its productivity, as well as a sustained increase in tree mortality over time. Droughts that have occurred in recent decades in the Amazon are proposed to be responsible for this reduction in productivity, as well as temperature increases associated with such events (Brienen et al., 2015). The trends in the carbon sink of the African tropical forests (including 11 countries) were also assessed. Despite it has been stable since the 80s, the data of intensively monitored plots agreed with the increase in carbon losses from 2010 onward. Also, future projections considering CO_2, temperature, drought, and forest dynamics predict a long-term future decline in the African sink, as it is currently happening with the Amazonian sink (Hubau et al., 2020).

In the face of future global change scenarios, the extent of the terrestrial carbon sink's storage capacity, as well as its driving processes, are still to be investigated on a case-by-case basis (Zhu et al., 2018). But all the available evidence of the reduction in the capacity of terrestrial ecosystems to maintain the atmospheric CO_2 balance highlights the necessity to implement policies designed to reduce atmospheric CO_2 emissions and stop deforestation. Article 3 of the Kyoto Protocol allows the ratifying countries to use the CO_2 uptake by their carbon sinks to offset part of their emissions (UNFCC, 1997). But only CO_2 uptake by terrestrial areas where any "direct human-induced activity related with changes in land use" is underway, at least, since 1990, can be considered for this offset. These activities must be measurable and testable. Here lies the importance of practices such as afforestation and reforestation, the restoration of degraded ecosystems, and the sustainable management of croplands, forests, and grasslands (UNFCC, 1997).

2.2. Mature vs developing ecosystems

Theoretically, the increase in an ecosystem biomass, linked to CO_2 uptake by primary producers, is limited by its age. Young ecosystems show much higher rates of CO_2 uptake than mature ecosystems because, over time, their growth in total biomass starts to curb, and its renewal processes increase to reach an equilibrium between growth and decay. In the long term, when the ecosystem is closer to maturity, the carbon stored will remain relatively constant, as CO_2 assimilation by photosynthesis and CO_2 release by respiration will balance out. This is because grown-up individuals need more energy to maintain their structures, so they invest it in maintenance instead of biomass gain (Zhu et al., 2018). Thus, there can be great differences between carbon fixation carried out by ecosystems depending on their maturity or their successional stage, but also depending on the type of communities that comprise the mature vegetation.

It has been considered that the increased capacity of CO_2 uptake of some early-successional forests is due to their regrowth or restoration following historical disturbances, which drives

changes in forests demography. Vegetation recovery in abandoned lands and deforested areas is returning these communities to earlier stages of succession. Thus, if forest recovery is the mechanism currently driving their role as carbon sinks, the system is expected to become saturated as forests mature and reach the latest stages of succession (Pan et al., 2011; Pugh et al., 2019). For example, according to Zhu's models, under ideal conditions and without ecosystem disturbances, carbon sequestration by North American forests will be only 22% greater by 2080 than current sequestration levels. Moreover, the successional trajectory is being affected by the current environmental changes and continuous disruptions, so the uptake is likely to be lower than predicted under optimum conditions (Zhu et al., 2018). The first signs of biomass saturation in European forests have been seen; the stem volume increment rate is decreasing and thus the sink is curbing after decades of increase (Nabuurs et al., 2013).

Although further research is needed, these studies point to the fact that biomass growth and carbon fixation are decreasing on terrestrial ecosystems, not only in tropical regions but also in other of the world. This implies that a large proportion of the terrestrial carbon sink is limited and temporary (Pugh et al., 2019).

3. Invasive species

Invasive species are those that have been introduced to an area by anthropic causes, both intentional or unintentional, which have become naturalized (autonomously maintaining populations) and have accomplished a huge dispersion throughout the territory. Invasive species usually exert a significant negative impact on native biodiversity, economic values, or even human health (Pyšek et al., 2020). These allochthone organisms cause great pressure on native species due to competition, predation, herbivory, and diseases (Blackburn et al., 2019), becoming one of the main causes of extinction worldwide (IUCN, 2017). Islands are known to be hotspots of alien species introductions and their biodiversity is more vulnerable to them (Russell, 2017).

The increment of atmospheric CO_2 can improve invasive plant species growth, (and consequently their biomass on ecosystems), accelerate their reproduction, and overall enhance their competitiveness (Kao-Kniffin & Balser, 2007). Positive interactions between climate change and invasive species are also expected, leading to alterations in their introduction and transport mechanisms, the establishment of new invasive species, the impact of existing invaders, and the effectiveness of control strategies (Russell et al., 2017).

But besides being a major cause of extinction, invasive species also disturb ecosystem processes (above and below ground), including those involved in carbon sequestration. The alterations can be both long-term and short-term, and not mutually exclusive. Long-term changes in the ecosystem are due to direct causes, like the modification of primary production rates, through the invasive individual's photosynthesis and respiration, and due to indirect causes, such as altering decomposition processes and nutrient fluxes, by changing the chemical and microbiological soil properties. The short-term disturbances are associated with changes in the dominant species composition of the ecosystem (Kao-Kniffin & Balser, 2007; Potgieter, 2007; Peltzer et al., 2010).

In the event of global warming, there are models which predict that the influence of climate change in the number of expected naturalized plants for the future follows a strong latitudinal pattern. Invasive species richness already follows latitudinal patterns, decreasing with latitude,

although the highest alien richness occurs at around 40° in both hemispheres, especially on islands, where there are higher invasion levels than in continental regions (Pyšek et al., 2020). At low latitudes, islands also have more variability in invasion levels than islands at higher latitudes (Guo et al., 2021. Thus, according to the models, temperate regions of the Northern Hemisphere will suffer greater pressure from alien plants because of climate change than tropical and subtropical regions of the Southern Hemisphere (Bellard et al., 2013; Seebens et al., 2015). The underlying mechanism involves increasing temperatures in temperate regions, which will increase environmental overlapping with the more biodiverse subtropical regions, while warming in tropical and subtropical regions is expected to decrease climatic similarity with the current major source countries of alien plant species (Seebens et al., 2015).

To sum up, the combination of global change factors (CO_2 rising concentrations, higher frequency of extreme climate events, land-use changes, and others) may have synergic effects on its influence on the magnitude and direction of the ecological impact resultant of species invasions.

In this study, we focus on two cacti belonging to the genus *Opuntia*, original from Central America (Esparza, 2010) and considered invasive in the Canary Islands (Acebes et al., 2010). We try to approximate the total amount of carbon sequestered by both species. This estimation will be useful to assess the balance between CO_2 emissions and fixation, resulting from their management, including their removal in ecological restoration actions, in areas of Tenerife.

4. *Opuntia maxima* and *Opuntia dillenii*, early invaders in the Canaries

Opuntia maxima Mill. and *Opuntia dillenii* (Ker-Gawl.) Haw. are two invasive species very extended through the Canary Islands. They belong to the genus *Opuntia*, from the Cactaceae family, which contains about 300 species (Inglese et al., 2019), with a complex phylogeny. As well as *O. maxima* and *O. dillenii*, there are some other species of the genus present in the archipelago, also considered invasive or potentially invasive: *O. robusta* H.L. Wendland, *O. tomentosa* Salm-Dyck, *O. tuna* (L) Mill, and *O. vulgaris* Mill (Acebes et al., 2009). There are other *Opuntia* species cited in the archipelago as potentially invasive, but they are probably not yet in the wild: *O. basilaris* Engelm. & J.M. Bigelow, *O. leucotricha DC.*, *O. lindheimeri* Engelm., *O. macrocentra* Engelm., *O. microdasys* (Lehm.) Pfeiff., and *O. pilifera* F.A.C. Weber (Biota, 2021).

O. maxima (commonly known as prickly-pear tree or cactus) was domesticated in Mexico. Due to anthropic selection pressure over thousands of years, clarifying its phylogenetic origin and its original native distribution remains challenging (Kiesling, 1998). *O. maxima* (better known as *O. ficus-indica* or *O. ficus-barbarica*), is an arborescent cactus, up to 5-6 m, but usually 2-3 m high. Terminal cladodes are large (30-50 cm long and 2.5-3 cm thick), oblong or elliptical; when old they become subcylindrical and get lignified, forming woody basal trunks and branches that can reach 30 cm in diameter. Growing cladodes are more greenish-yellow than the adult cladodes, which are more greyish-green. Areoles are much conspicuous in developing cladodes than in older cladodes, with numerous brownish and early deciduous glochids. Spines are white and very variable in density and size: from 2-5 mm in some forms to 10-40 mm in others, and from almost non-existent to dense and in clusters of 3-6 per areole. Leaves are tinny, conical, and early deciduous. Flowers are yellow-brilliant to deep orange, with 7-8 cm in diameter. Fruits are red-orange, sweet, and fleshy, about 5-6 × 3-4 cm, oblong, and with numerous areoles. Fruits

are also polyspermic and seeds are 4 × 3 mm (Berthet, 1997). The prickly-pear tree domestication process was oriented to obtain large and fleshy fruits and cladodes with few spines since they are very convenient for the cultivation and consumption of both cladodes and fruits (Reyes-Agüero et al., 2005).

In contrast to *O. maxima*, *O. dillenii* reaches heights from 0.5-2 cm. They grow erectly. Cladodes are dull green or bluish-green, smaller than in *O. maxima* (10-40 cm long and 1-2 cm thick), and more obovate. Areoles are 7-8 mm in diameter in young cladodes and approximately 1 cm in adults, covered with a fascicle of glochids (5-8 mm). Spines are more sizable than in *O. maxima*. There are 6-8 spines per areole and they are 1.5-5 (6) cm long and up to 2 mm in basal diameter, divergent, and usually arched. Leaves are also short and broad (3 × 2 mm), conical, and early deciduous. Flowers are yellow and 7.5-8 cm in diameter. Fruits are large and fleshy, pyriform, purplish carmine red, and often spiny. Fruits are also polyspermic and seeds are about 4 mm in diameter (Berthet, 1997; Böhm, 2008).

4.1 Native distribution

Despite the belief that the genus *Opuntia* originated in central Mexico, recent biogeographical analyses suggest a South American origin, specifically in the southwest of the continent, and its subsequent dispersal to Peru, Ecuador, and the desertic region of western North America. However, phylogenetic analyses support that the large radiation of the genus took place in North America, mainly due to polyploidization and hybridization mechanisms (Majure et al., 2012). The central and southern regions of Mexico are the current center of diversity of the genus (Arakaki et al., 2011; Inglese et al., 2017), with around 100 species, most of them endemic (Sandoval, 2010).

The natural distribution of the genus is considered to extend from Alberta (Canada) to La Patagonia (Argentina), latitudinally, and from the Caribbean to the Galápagos islands longitudinally. The individuals can be found from sea level to 3000 m above sea level (a.s.l.) (Reyes-Agüero et al., 2005). In particular, the current native distribution of *O. maxima* and *O. dillenii* is Mexico. The former, occurs in the center, and the southwest of the country; while the latter, is present in the northeast, and the south, but also in Jamaica (www.plantsoftheworldonline.org). *O. dillenii* is one of the most distributed species through Mexico, but restricted to low elevations, near the sea level, as occurs in the Canary Islands (Sandoval, 2010). *O. maxima* is mainly found on the Central Mexican Highlands, above 1500 m a.s.l. to 2200 m a.s.l. (Inglese et al., 2017). As well as in its native distribution, it is strongly linked to anthropized environments on the Canary archipelago (Reyes-Agüero et al., 2005).

Opuntia species are distributed worldwide. *O. maxima* can be found as naturalized or invader in all continents. In the Mediterranean basin it is a major invader but can be also found in the East and South of Africa, the United States, many countries of South America, East Asia, India, Hawaii, the Antilles, other Macaronesian archipelagos, Australia, and New Zealand. *O. dillenii* is not as widespread as its sister species, but it is present in many regions out of its native distribution, like the Antilles, the south of the United States, Colombia, Ecuador and Brazil, France, Italy and Portugal, the Arabian Peninsula, the south of Asia and the east of Australia (www.gbif.org; www.plantsoftheworldonline.org).

4.2 Introduction in the Canary Islands and traditional uses

The *Opuntia* species introduction in the Canary Islands probably took place after Columbus' first or second voyage to the New World, between the end of the 15th and the beginning of the 16th century. The first references to *O. maxima* date back to 1608, in the work of the Canarian poet Silvestre de Balboa, *Espejo de Paciencia*, in which he mentions the importation of the prickly-pear cactus. At the end of the 18th century, Viera y Clavijo described the species as "widely spread throughout the islands". This statement suggests the presence of the species on the islands for some time. The earliest illustrated references to the genus show *O. maxima* and *O. dillenii*, meaning they were the first species to be introduced. This evidence is supported by the widespread distribution of both species throughout the islands today, compared to other species of the genus, such as *O. tomentosa*, which may have been introduced later (Salas & Cáceres, 2003).

Although the expansion of *Opuntia* through Europe was strongly linked to ornamental purposes and botanic curiosity, and maybe its fruits were consumed on the islands, the main reason for cultivation in the Canary Islands, from the 18th century onwards, was the production of carmine cochineal (*Dactylopius coccus*) (Godoy, 2012). This mealybug is a parasite of *Opuntia*s. From the female's dried body carminic acid is extracted, a natural highly prized dye in the textile industry (Salas & Cáceres, 2003). The species was introduced first in Tenerife, in 1825, by Quintero Estévez, who brought it from Cádiz, and in 1835 it was brought to Gran Canaria and Lanzarote (Chinea et al., 2001). By the 1850s, the production of cochineal in the Canary Islands doubled the importations from Mexico (Godoy, 2012), but sales dropped in the 1860s when the synthetic dyes started to be used (González, 2019). Today, the production of cochineal for obtaining dye only continues in Lanzarote (Chinea et al., 2001).

Concerning the current uses of the species, besides the consumption of fruits and the production of forage, there are several studies about the potential of *O. maxima* as biofuels, such as biogas or bioethanol, especially in arid and semi-arid regions of the world (Godoy, 2012; Ramos-Suárez et al., 2014; Calabrò et al., 2018). This species has certain features that make it appropriate for this aim: it is rich in sugars, accumulates high quantities of water, has a high C/N ratio, and as we saw earlier, it can reach very high biomass productivities (Ramos-Suárez et al., 2014).

4.3 Carbon fixation by *Opuntia* spp.

4.3.1   Acid Metabolism of the Crassulaceae (CAM) and Water Use Efficiency (WUE)

Opuntias are CAM species, which means that they express the Crassulaceae's acid metabolism. These species open their stomata at night to capture CO_2, while temperatures are lower, so they can reduce the loss of water by transpiration. The CO_2 uptaken is stored on the vacuoles of the cells as malic acid and during daylight hours it is fixed via the Calvin cycle, turning it into organic matter (Nobel & Hartsock, 1983). With these physiological mechanisms, CAM species tend to be very efficient in water use, especially in arid and semi-arid environments (Snyman, 2013). Water-use efficiency (WUE) is defined as the amount of plant material (dry matter of the cladodes, roots, etc.) produced per unit of water used (evapotranspiration). On average, a CAM species presents a WUE three times higher than C4 species, and almost five times higher than C3 (Potgieter, 2007). The CAM metabolism takes place in mature cladodes and other organs, whereas younger parts such as flower buds and developing cladodes express C3 pathways. Very likely, *Opuntia* species adopt the CAM metabolism as they mature (Acevedo et al., 1983).

Although in its native distribution area prickly-pear trees could receive around 500 mm of annual rainfall, these physiological mechanisms allow them to resist in areas where annual rainfall is 200 mm or less (Acevedo et al., 1983), as occurs in many areas of their distribution in the Canaries (Otto et al., 2001). This special metabolism and its high WUE, make them very competitive against native species, that are dominant in arid and semi-arid environments, such as sweet tabaibas (*Euphorbia balsamifera*), which are C3 species, but also very efficient in terms of water use.

In the Canary Islands, there are some CAM species which could compete with *Opuntia* within their distribution area, especially those that are main elements of the coastal scrub of the archipelago in the lowlands. This is the case of *Euphorbia canariensis*, distributed throughout the seven islands, *E. handiensis*, endemic to Fuerteventura, and *Ceropegia* species, endemic to central and western islands (Mies, 1998; del Arco et al., 2006). Additionally, *E. aphylla*, also common in the coastal shrub of the central islands, is described as an optional CAM plant or facultative CAM, since it can express both C3 and CAM pathways, depending on environmental conditions (temperature and water availability) (Mies et al., 1996). Other optional CAM species are *Mesembryanthemun crystallinum* which expresses CAM metabolism in coastal zones, with higher hydric stress due to salinity levels, but shows the C3 pathway at offshore areas, and *Kleinia neriifolia,* an important element of the coastal scrub, that is also present in secondary scrubland at higher elevations (Mies et al., 1996).

It is worth mentioning the high proportion of water contained in prickly-pear trees biomass. Dry matter usually accounts for about 10% of its total weight (Acevedo et al., 1983; de Cortázar & Nobel, 1991; Otto et al., 2001). Water content varies along the year, with the lower percentages reached just before the rainy season. Native CAM species of the coastal scrub present similarly high values of water content, e.g., *Euphorbia canariensis*, (90.1% of the total weight), *Kleinia neriifolia* (85.2%), and *Ceropegia fusca* (87.2%) (Otto et al., 2001).

4.3.2 Annual biomass production of *Opuntia maxima*

Prickly-pear trees are very appreciated species for their commercial value in their native area but are also cultivated around the world, in tropical, subtropical, and warm zones of temperate regions, to produce fruits and forage, therefore, most of the literature available on its productivity is based on *Opuntia maxima* crops (de Cortázar et al., 1985; de Cortázar & Nobel, 1992; Pimienta-Barrios et al., 2000). Under optimal conditions, C3, C4, and CAM species can achieve similar values of productivity per unit ground area, but with arid or semiarid conditions CAM species show significantly higher values (Nobel, 1991a). An important parameter for studying the productivity of this species is the SAI (stem area index), i.e. the total stem surface area per unit ground area. Higher productivities of *O. maxima* are achieved with a SAI between 4 and 6, while SAI < 3 is more appropriate for low-density crops. With SAI above 7, the productivity generally shows stability (de Cortázar & Nobel, 1986).

Studies about productivity of *O. maxima* in Mexico and Chile showed that crops with a SAI of about 4-6, yielded 35 tons hectare^{-1} year^{-1} of dry matter (de Cortázar & Nobel, 1986). Nevertheless, productivities of almost 50 tons hectare^{-1} year^{-1} have been achieved in young plantations two and three years old, under optimal conditions and very high densities (24 individuals/m^2), including fruit production (de Cortázar & Nobel, 1991, 1992; Nobel et al., 1992). Annual fruit production can reach 30 tons per hectare in fresh weight (5.5-6 tons hectare^{-1} year^{-1} of dry matter). In addition, annual productivity per unit area tends to increase with the age of

individuals, especially for fruits (Acevedo et al., 1983). Although *O. maxima* has the potential to reach these extreme productivity values, most of the world's crops do not meet the required conditions for maximum yield. Low-density crops (0.2 individuals/m^2 and SAI of 1.4), which are more appropriate for fruit production, are more common. These can reach productivity values between 10-20 tons hectare^{-1} year^{-1} (Nobel & Hartsock, 1983). Furthermore, *O. maxima* usually produces less than 10 tons of aerial dry matter hectare^{-1} year^{-1} under non-irrigated conditions (de Cortázar & Nobel, 1986; de Cortázar & Nobel, 1992). A global-scale study using the most relevant environmental factors to assess the productivity of the species (photosynthetic photon flux, temperature, and rainfall), obtained a theoretical estimation of 2 tons hectare^{-1} year^{-1} of *O. maxima* aerial dry matter for the Canary Islands (Nobel, 1991b).

In terms of underground biomass, several studies carried out by Snyman (2005, 2006), estimate the percentage of root biomass in *O. maxima*, between 7-13% of the total weight, for young individuals with 1-2 years of development. On the other hand, Liguori et al. (2014) found that underground biomass accounted for 17.5% of the total dry weight for 10-year-old individuals in Sicily. For *O. robusta* (one of the invasive *Opuntia* species in the Canary Islands), the percentage of dry biomass corresponding to roots ranged between 11-21%, giving similar values to those of *O. maxima* (Snyman, 2005, 2006).

O. maxima is the most widely studied *Opuntia* species in terms of physiology, while there is less information about *O. dillenii*. The great effort dedicated to studying this species is mainly because of its commercial value. Regarding its potential for carbon sequestration, the few direct measurements of CO_2 absorption made on cladodes of *O. maxima* show daily values of 0.344 and 0.393 mol per unit cladode area (m^2) (Nobel & Hartsock, 1983). This last value is an average of data obtained for the different seasons of the year, while the maximum daily fixation reported was 618 mol m^{-2}. The annual carbon sequestration values according to these data would be around 144 mol m^{-2} (Pimienta-Barrios et al., 2000).

In this study, we will try to approximate the amount of carbon stored in the total biomass of *Opuntia* spp. present in Tenerife. For this purpose, we will use the values of total carbon content in the dry biomass of *O. maxima*, obtained by Yang et al. (2015) in their study on the biomass composition of this species.

5. Main aims of this study

This study presents a novel approach to the estimation of the carbon footprint generated by the management of invasive species on islands, by estimating the dry biomass of two *Opuntia* species on the island of Tenerife. Considering the advantageous competing traits of *Opuntia* species, i.e. CAM metabolism, high WUE, and biomass production capacity, and their invasive character and widespread distribution in the Canaries, understanding the role of these plants as carbon pools is important for future management strategies. The aim of this study is to estimate CO_2 capture in *Opuntia* spp. addressing the following specific tasks:

1. Estimate the amount of dry biomass of *O. maxima* and *O. dillenii* per unit area (m^2) on the island of Tenerife.
2. Estimate the area currently occupied by *O. maxima* and *O. dillenii* on the island of Tenerife.
3. Assess the total amount of carbon stored by *O. maxima* and *O. dillenii* at present on the island of Tenerife.

4. Setting up an allometric equation to estimate aboveground dry biomass of individuals of *Opuntia* spp. from biometric data.

6. Materials and methods

6.1 Study area

The study was carried out in Tenerife, the largest and highest island of the Canary Archipelago, with an area of 2034 km² and a maximum altitude of 3718 m a.s.l. On the island, we can recognize elevational belts with different climatic conditions and thus diverse ecosystems. On the lower lands, with an annual average temperature of 18-22 °C and annual rainfall of 50-500 mm (with aridity in the south flank from February to October), we find the coastal scrubland, dominated by the genus *Euphorbia.* The midlands have an annual average temperature of 11-18 °C and 300-800 mm of precipitation. Due to the continuous influence of the NE trade winds over the northern flank of the island, there is a significant difference between the south (leeward) and the north (windward) slopes. The trade winds bring humidity and generate cloud banks (known as "mar de nubes") at 1,500 m a.s.l. on the windward slopes, hence the north of the island can achieve maximum precipitation peaks of 1,300 mm. It is just under these conditions that the evergreen laurel forest, known as *monteverde*, can grow. Below and above the *monteverde*, in northern flanks, and at equivalent elevations in the south, the absence of *monteverde* allows the more xeric ecosystems to expand, such as the endemic pine forest, and the thermophilous woodland. Finally, at the upper zones above 2000 m a.s.l., temperatures can be much lower, from 3.5 to 11 °C, and precipitation is about 500-600 mm, where the dominant vegetation is the summit broom scrubs and the Teide Peak violet community (del Arco et al., 2010).

Concerning our study species, *O. dillenii* is commonly found in the lower areas of the island, especially in the south and the northwest, usually living within the coastal scrubland, where the species can tolerate aridity and limited salinity (Otto et al., 2001; Da Re, 2015). However, it is possible to found it growing up to 800-1000 m a.s.l. (Biota, 2021). *O. maxima* prefers an altitudinal range within 250 and 1,500 m a.s.l., and it is less adapted to arid conditions than *O. dillenii*. It is also strongly linked to anthropized and impacted areas, thus it is usually found in secondary scrublands at midlands in both island slopes (Da Re, 2015; Biota, 2021).

6.2 Sampling design

Sampling points (n = 20) were selected based on information about the presence of *Opuntia* spp., in Biota (Banco de Datos de Biodiversidad de Canarias) and the Canarian vegetation map (CVM) (del Arco et al., 2006), elevation, and exposure to winds. Using QGIS 3.14.16© (2020) and the orthophoto of Tenerife, at a resolution of 20 cm/pixel and taken in 2019 (IDECAN, 2021), we established four points in 400 m intervals, up to 800 m a.s.l. for *O. dillenii* and 1200 m a.s.l. for *O. maxima*. At each elevation interval, two points were located on each major exposure (windward and leeward). Within each exposure, one point was located on the east and the other on the west. The land registry (IDECAN, 2021) was checked to ensure that we stayed away, if possible, from private and urban areas. For those locations within natural protected areas (NPAs), we asked for permission from the Cabildo de Tenerife. Occasionally samples were taken near the border of NPAs when we could not find the conditions needed within them. The NPAs included in this study were:

- Corona Forestal Natural Park
- Montaña Amarilla Natural Monument
- Montaña de Tejina Natural Monument
- Anaga Rural Park
- Teno Rural Park
- Barranco del Infierno Especial Natural Reserve

At the selected locations (Figure 1) we finally sampled 18 individuals (n=18), due to the absence of *Opuntia* in some of the sites. Despite performing exhaustive searching in different locations of the island that could meet the necessary conditions for the study, we could not find *O. maxima* at elevations over 800 m a.s.l. on windward in the northeast, neither *O. dillenii* above 400 m a.s.l. in the east, windward or leeward (Table 1). However, we found *O. dillenii* above 800 m a.s.l. on leeward south.

Figure 1. Images of field and lab work methods. a: *Opuntia maxima*, b: *Opuntia dillenii*, c: *O. maxima* community, d: *O. dillenii* community, e-g: sampled collection and measurement in the field, h-j: sampling processing in the lab.

Figure 2. Map of sampled locations for individuals of *Opuntia maxima* (circles) and *O. dillenii* (triangles) on Tenerife, with elevations (contour lines every 400 m a.s.l.) and natural protected areas (in orange).
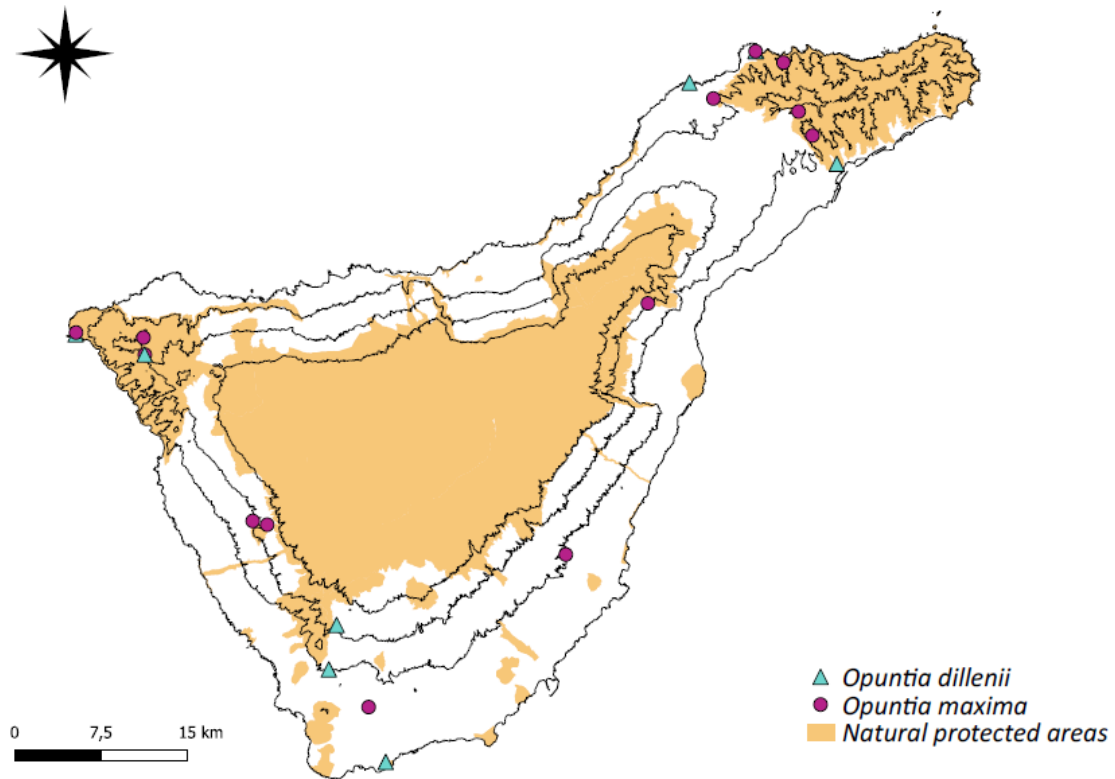

Table 1. Number of *Opuntia maxima* and *O. dillenii* samples by elevation range and wind exposure in Tenerife.

Species	*Opuntia maxima*		*Opuntia dillenii*	
Elevation/exposure to winds	Windward	Leeward	Windward	Leeward
0-400	2	2	2	2
400-800	2	2	1	1
>800	1	2		1

6.3 Field sample collection and biomass estimation

At each location, we recorded general data: samplers, date, locality, coordinates, altitude, and plant community. Then, we chose a representative individual of prickly-pear cactus (*O. dillenii* or *O. maxima*) within the selected site and measured their largest diameters, height, basal stem diameter, phenology, and vitality scored from 1, damaged plant, to 5, healthy plant. Once abiotic and biotic information was collected, we delimited an area of 1 m^2 below the plant where we cut off all the aboveground biomass of the individual, including cladodes and fruits. The collected cladodes were classified into three types and weighted in the field:

- 1: terminal cladodes
- 2: secondary cladodes from which other cladodes grew
- 3: basal and lignified cladodes, or stems

Field weight measurement gave us the fresh biomass weight (kg) of the plant per area (m^2). The first individuals collected of each species were taken to the lab and dried completely. Then, to accelerate the drying process, a representative selection of different cladode types, accounting for 5-15 kg, was taken to the laboratory, to estimate dry weight by stove drying at 60 ˚C. The cladodes that were left on the field were piled together, trying not to promote the plant dispersal. In the laboratory cladodes and stems were marked with codes for their identification and weighted regularly until they stopped losing weight, once all the water content had evaporated and only the dry biomass remained. We then assessed percentages of water content for each type of cladodes of the sample and extrapolated these values to estimate the total dry biomass weight per m^2.

In addition to biomass, we also recorded data on the plant cover using the line-intersect method, setting two perpendicular transects of 50 m (or four of 25 m, depending on the accessibility of the site), to obtain the cover percentage of each species at each location (18 sampling points). To increase the number of individuals for the biomass estimation we also measured the biovolume (main diameters and height) from additional individuals (80 *O. maxima* and 75 *O. dillenii*) at several of the sampled sites (3 windward, 3 leeward sites). We also measured the basal steam diameter from some of these additional individuals (15 *O. maxima*).

6.2 Presence and cover data and spatial analysis

Once we get the amount of biomass per m^2 for each species, we need to calculate the area occupied by both plants in Tenerife, to obtain the total amount of carbon stocked on them. To assess their total cover with precision, in addition to our field data, we used available data of presence and plant cover for both species, from different sources, which are shown in Table 2.

Table 2. Summary of the data used to infer presence and cover of *Opuntia spp*. in Tenerife, their sources, and year of publication.

Type of data	Number of samples	Source	Year
Presence and plant cover	71 transects	Silvia Fernández-Lugo et al.	2013
Presence and plant cover	37 transects	Fernández-Palacios	1987
Presence and plant cover	7 transects	de Nascimento et al.	2014
Presence and plant cover	5 transects	González-Escudero (unpublished)	
Presence	824 polygons	del Arco et al.	2006
Presence	118 grids (*O. dillenii*) 312 grids (*O. maxima*)	Biota (Gobierno de Canarias)	2021

We created a point layer with all sites where plant cover was measured, using the free software QGIS v3.14., and overlapped it with all the polygons from the CVM, to assign cover data value of the sites to each CVM polygons. We then calculated the area occupied by the two *Opuntia* species in each polygon. The CVM polygons contain information about their main plant community, thus cover averages obtained from all the points that fell within a community type

were used to approximate the percentage of the area occupied by the prickly-pear trees in all the polygons classified within the same community (Figure 3).

Figure 3. Scheme of the steps followed for obtaining the polygons from CVM where *Opuntia* spp. were present, with QGIS.
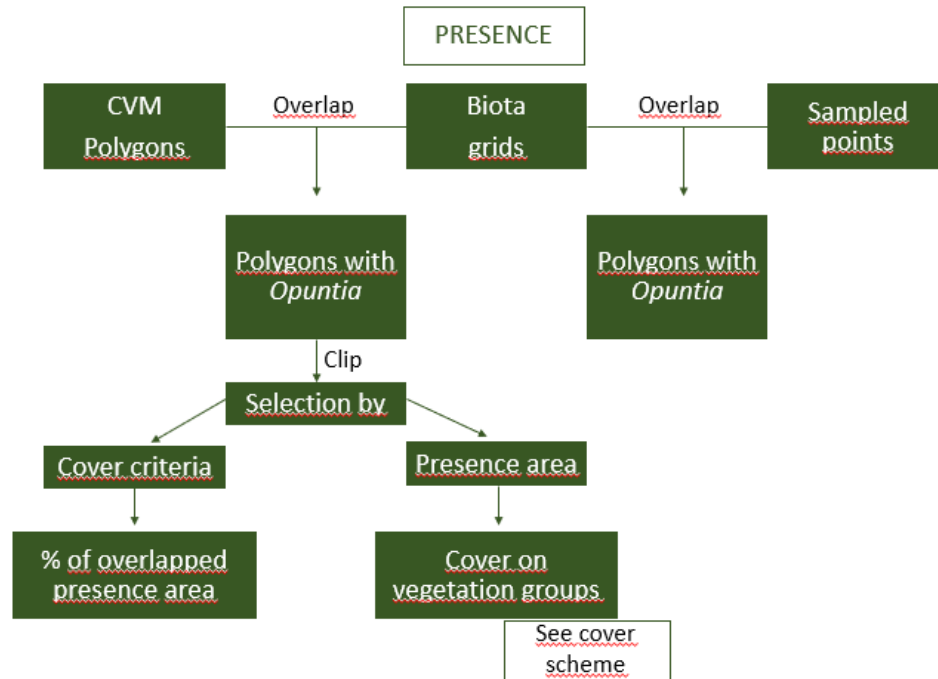
For some polygons, the occurrence of *Opuntia maxima* was confirmed according to Attributes from the CVM (fields: C2_VEGDOM, C4_VEGET2, C6_VEGET3). However, we could not assume that *Opuntia* was present in all the polygons of a particular plant community, and data on *O. dillenii* occurrence was not available from the CVM. To decide in which polygons the studied species of *Opuntia* were present so that we could assign their community corresponding cover data, we downloaded 500 x 500 m grids from the Biota database where *O. maxima* and *O. dillenii* were cited. We only used grids with the highest levels of Precision, "1", and Confidence, "Sure". A problem found was that we did not have cover data for each one of the communities where, according to CVM and Biota's information, prickly-pear trees were present. To solve this, we had to classify and cluster communities from the CVM, according to del Arco et al. (2010), to accurately assign the cover values to each community. Once the communities with no data were grouped, they were assigned coverage percentages based on the average obtained for those communities that were within the same group and did have coverage data (Figure 4). Additionally, the dimensions of Biota's grids were different from the polygons of the CVM, thus when the overlapping was not complete, we used two criteria to select polygons where *Opuntia* occurrence was highly likely (Table 3):

- The percentage of each polygon's area overlapped by Biota's grids: a polygon was selected if the area overlapped with Biota grids was higher than 50%.
- The percentage of *Opuntia* cover assigned for its community (calculated from the average coverage data for each community group): a polygon was selected if its community type had the same or above median percentage of all cover data.

Figure 4. Scheme of the steps followed for obtaining *Opuntia* spp. cover on each vegetation group, with QGIS.
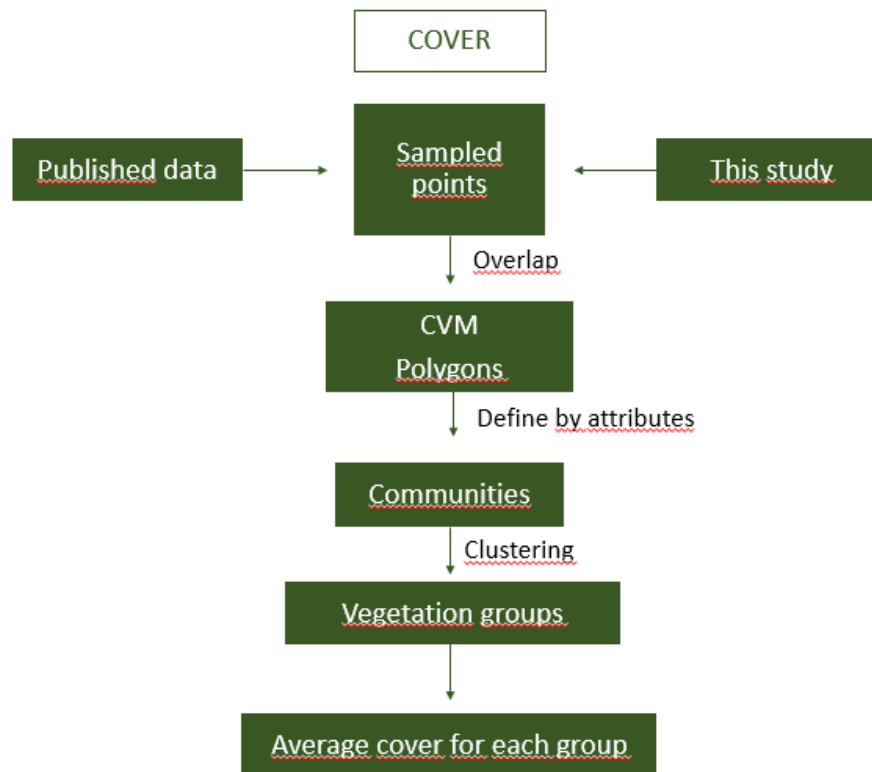

Table 4. Criteria for the selection of polygons where the occurrence of *Opuntia maxima* and *O. dillenii* was inferred from the Biota database grids that partially overlapped CVM polygons.

	Overlap < 50%	Overlap > 50%
Cover < 14.25% for *O. dillenii*	Out	In
Cover ≥ 14.25% for *O. dillenii*	In	In
Cover < 11.3% for *O. maxima*	Out	In
Cover ≥ 11.3% for *O. maxima*	In	In

Once we applied the double criteria to select the CVM polygons with *Opuntia* occurrence verified from the Attributes of the CVM and Biota database, along with those polygons with presence verified from our field data and other studies available, we applied the corresponding cover percentage for each one, according to their vegetation group (Table 4). Finally, all the areas were summed up to approximate the total area occupied by *O. maxima* and *O. dillenii* in Tenerife.

Opuntia maxima cover percentage estimated for each vegetation group (plant community grouping based on del Arco et al. 2010). Cover percentage within secondary scrubland is assigned per elevation zones (see results). For those groups with no data average cover for the species was assigned (11.3%).

Table 4. Summary of main vegetation groups and assigned plant communities, number of data points and cover percentage for *Opuntia maxima*.

Vegetation groups	Nº of communities in the group	Nº of cover data points	Cover percentage
Secondary scrubland	34	55	8± (0-400 m) 19.81± (400-800) 9.06± (800-1200)
Coastal scrubland	10	31	8.37
Secondary grassland	7	5	12.37
Halophilous belt and dune vegetation	4	0	11.3
Canary willow and palm groves	2	0	11.3
Thermo-sclerophyllous woodland	5	2	4.77
Evergreen laurel forest	3	0	11.3
Canary pine woodland	4	2	11.76
Rupicolous communities	10	0	11.3
Anthropic areas	16	20	16.24

Opuntia dillenii cover percentage estimated for each vegetation group (plant community grouping based on del Arco et al. 2010). Cover percentage within secondary scrubland is assigned per elevation zones (see results). For those groups with no data average cover for the species was assigned (14.3%).

Table 5. Summary of main vegetation groups and assigned plant communities, number of data points and cover percentage for *Opuntia dillenii.*

Vegetation groups	Nº of communities within the group	Nº of cover data points	Cover percentage
Secondary scrubland	18	5	13.21±12.6
Coastal scrubland	7	13	10.62±5.7
Secondary grassland	5	1	16.89±21.1
Halophilous belt and dune vegetation	7	2	17,1±11.7
Thermo-sclerophyllous woodland	2	0	17.1±11.7
Evergreen laurel forest	1	0	17.1±11.7
Rupicolous communities	1	0	17.1±11.7
Anthropic areas	4	3	16.28±16.1

6.2 Statistical analysis

To check for possible spatial and climatic gradient effects, we analyzed the influence of abiotic factors (elevation and wind-exposure) on the variance of the measured dependent variables, and between the different species, with PERMANOVA+ (Anderson et al., 2008). Tested variables were:

- Total biomass
- Dry biomass – Water content
- Percentage of dry biomass

- Total woody biomass
- Percentage of woody biomass
- Number of cladodes
- Number of fruits
- Total and dry fruit biomass

We also analyzed the influence of parameters related to the plant structure, i.e. the percentage of woody biomass and the number of cladodes, on the total amount of biomass and dry biomass.

Finally, we tested if the abiotic factors influenced both *Opuntia* spp. cover on the different plant communities where they are present, to determine if we could cluster them and assign the average coverage percentage to major vegetation groups.

All the statistical analyses were done with Primer 6©, a software for non-parametrical multivariate analysis (Anderson et al., 2008). PERMANOVA + is a package, within Primer6, that compares similarity between data groups based on distance measures (e.g. Euclidean distance matrix) and tests for significance by performing multiple permutation of the data. This technique is very useful in ecological studies when the sample sizes are small and data is highly variable so that often do not meet the traditional requirements for parametric analysis, such as normality and homoscedasticity (Anderson et al., 2008).

6.4 Development of allometric equations

For developing the most explanatory allometric equation from our data, we used the free software RStudio©. We considered the data from both species together to obtain an equation for *Opuntia* spp. biomass estimation, because we found no significant differences in the measured biomass between them. All data were analyzed and organized with tidyverse packages (v1.3.0; Wickham et al., 2019). As dependent variables we used total and dry biomass of the individuals sampled, and as possible explicative variables, we tested the biometric parameters measured from each sample: basal stem diameter, largest diameters, height, biovolume (a combination of height and area projection), area projection, and the number of cladodes. The Grubbs test, from package "outliers" (Komsta, 2011), was first run with total and dry biomass values. We detected one outlier (*O. maxima* weighting 180 kg/m^2) and removed it from the data set used to obtain the allometric equation.

We then tested the possible correlations between variables with the package "psych" (Revelle, 2015). The first factor dismissed due to correlation was the number of cladodes, however this parameter is not very useful for the equation since it is hard to record in *O. dillenii* without cutting the entire individual. We set up three types of equations with each one of the variables and their possible combinations:

- Simple linear regression equations
- Polynomial quadratic equations
- Multiple linear regression equations

The "lm" function of R was used to adjust the linear regression equations, and the "poly" function of the ISLR package for the polynomial equations (James et al., 2017). The package "rcompanion" (Mangiafico, 2017) was used to compare the different models. To choose the best equations, we compared their R^2 (and the adjusted R^2 in the case of multiple linear regression equation), their p-value, and the Akaike information criteria (AIC). In this cause, we use the

corrected AIC (AICc) due to the small sample size. When these selection parameters did not differ too much, we selected the simplest model able to explain the variance of the sample. This process was repeated for each species independently. The Pearson's test in package "hmisc" (Harrell, 2019) was also run to check for collinearity between independent variables, when the best model selected was a multiple linear regression. Finally, to ensure that chosen models met the requirements of residuals' normality and homoscedasticity we perform the Shapiro Wilks test and ran the "plot" function of R. Graphics were built with "ggplot2" function from tidyverse.

7. RESULTS

## 7.1 Distribution and cover of *Opuntia* spp. on Tenerife

The total surface occupied in Tenerife by *Opuntia maxima* and *O. dillenii* was calculated. *O. maxima* covers a surface of 5474.04 ha, 2.69% of the total area of the island (Figure 2), while *O. dillenii* covers 819.78 ha, 0.4% of the island (Figure 3). However, the area occupied by both species is probably underestimated, especially for *O. dillenii*, due to the absence of occurrence data in the CVM on Tenerife, and the lack of accurate presence data in Biota. Considering the entire area of the polygons with *Opuntia* spp. presence, *O. maxima* and *O. dillenii* have a total distribution area of 37,495 ha and 5,687 ha, respectively.

Figura 5. Map of *Opuntia maxima* within main vegetation groups on Tenerife.
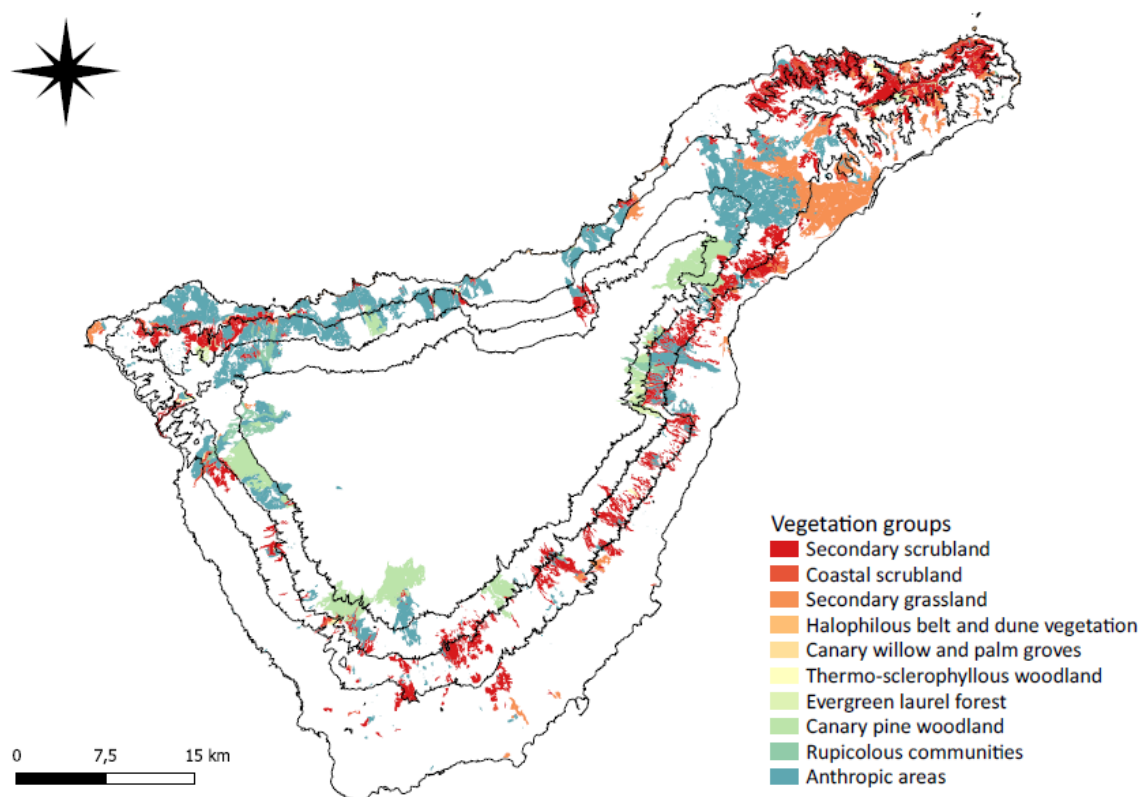
Regardless of occurrence information provided by Biota, we could not find *O. dillenii* in Anaga Rural Park (neither windward nor leeward) at elevations over 400 m a.s.l., however, it was present at higher elevations than expected, over 1000 m a.s.l. at leeward south. Additionally, we could not sample *O. maxima* on the north, windward, and over 800 m a.s.l. because it can only be found inside private properties or closely linked to urban/rural areas. While *O. maxima* is absolutely bounded to anthropic and degraded areas, *O. dillenii* is completely integrated into mature and preserved stands of coastal scrubland. Sometimes, both species overlap their distribution, but often *O. maxima* prevails over *O. dillenii*.

Figure 6. Map of *Opuntia dillenii* within main vegetation groups on Tenerife.
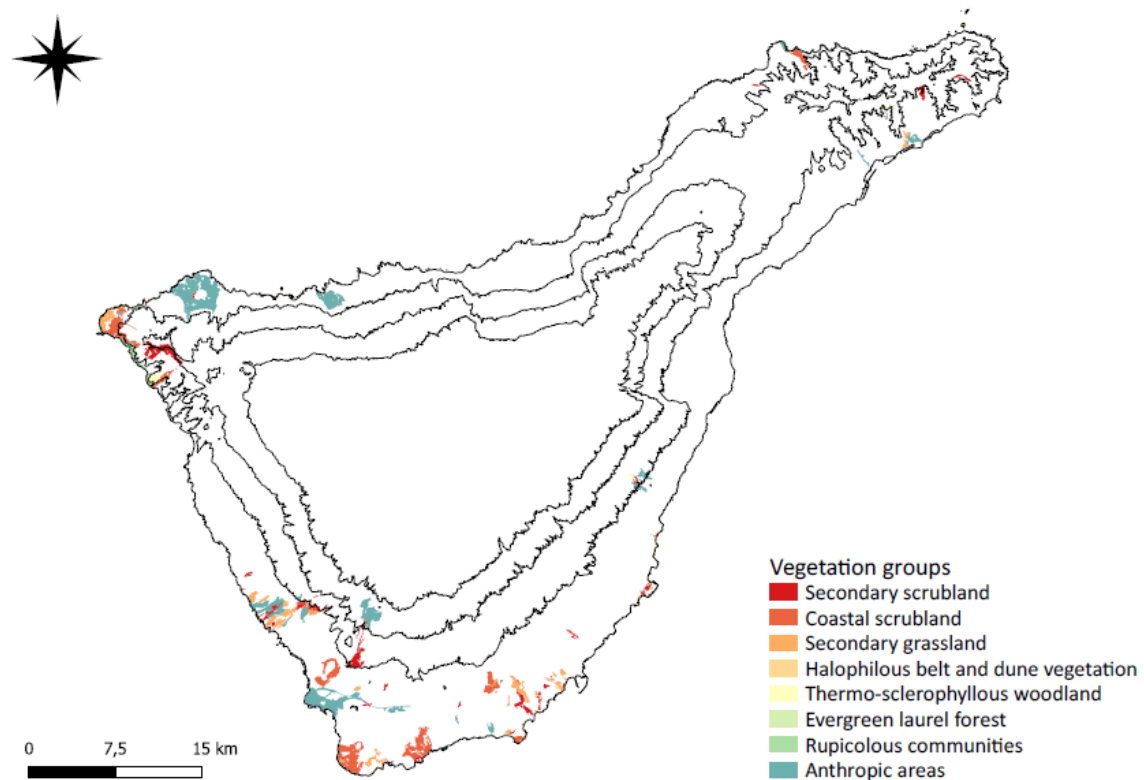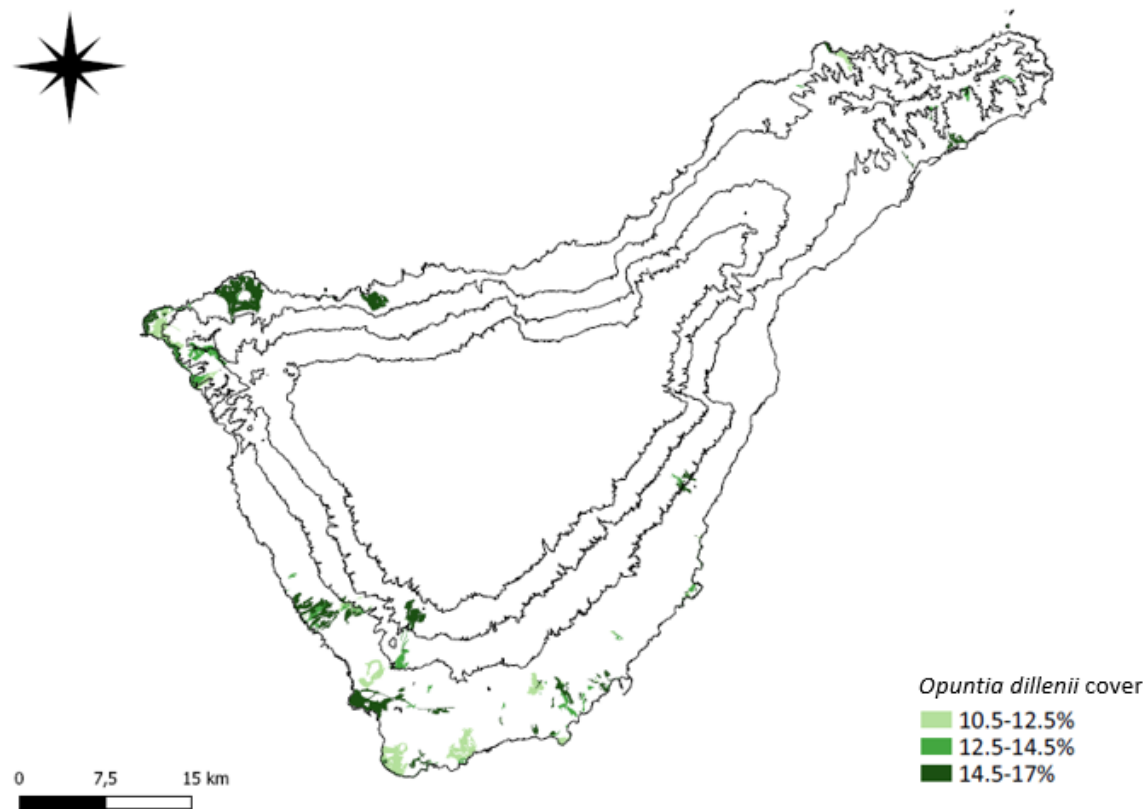

There were no significant differences (p-value > 0.05) between both species average cover percentage on the communities in which they are present, 13.8% (+/- SD) for *O. maxima* and 13% (+/- SD) for *O. dillenii* (Figure 4).

Figure 4. Plant cover percentage of *Opuntia maxima* (orange) and *O. dillenii* (green) on the island of Tenerife.
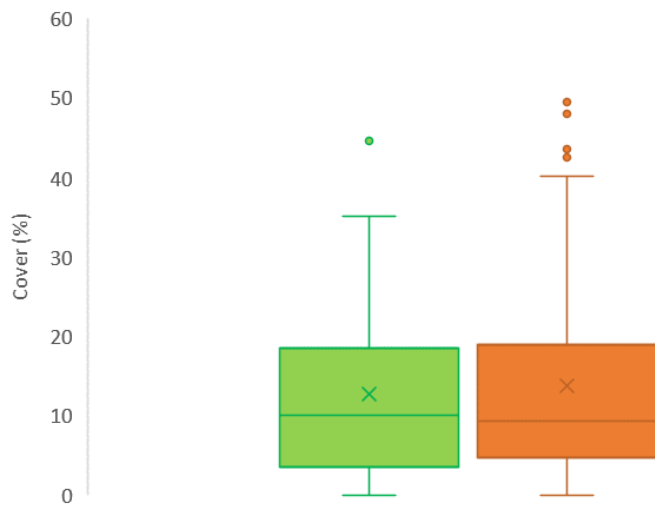

No influence of abiotic factors (elevation and wind exposure) was detected on *O. dillenii* cover on the different vegetation communities where it is present (p-value > 00.5), neither between major vegetation groups. Thus, we decided to use the average of all sampled cover data points to assign a cover percentage to the vegetation groups including communities for which we did not have information. Based on this data we elaborated the distribution and cover map of *O. dillenii* on Tenerife (Figure 7).

Figure 7. Map of *Opuntia dillenii* cover on Tenerife.

For *O. maxima*, significant differences were found between cover values at different elevational ranges within the secondary scrubland group (p-value < 0.05). No differences were found because of wind exposure or communities within the group (p-value > 0.05). In this case, we calculated the average cover for each elevational range (0-400, 400-800, 800-1200 m a.s.l.) and used these data to elaborate the species distribution and cover map (Figure 8). Average covers were 8%, 19.8%, and 9.1% in order of elevation. For the rest of the major vegetation groups, no influence of abiotic factors or vegetation communities were found on cover percentages (p-value > 0.05).

Figure 8. Map of *Opuntia maxima* cover on Tenerife.
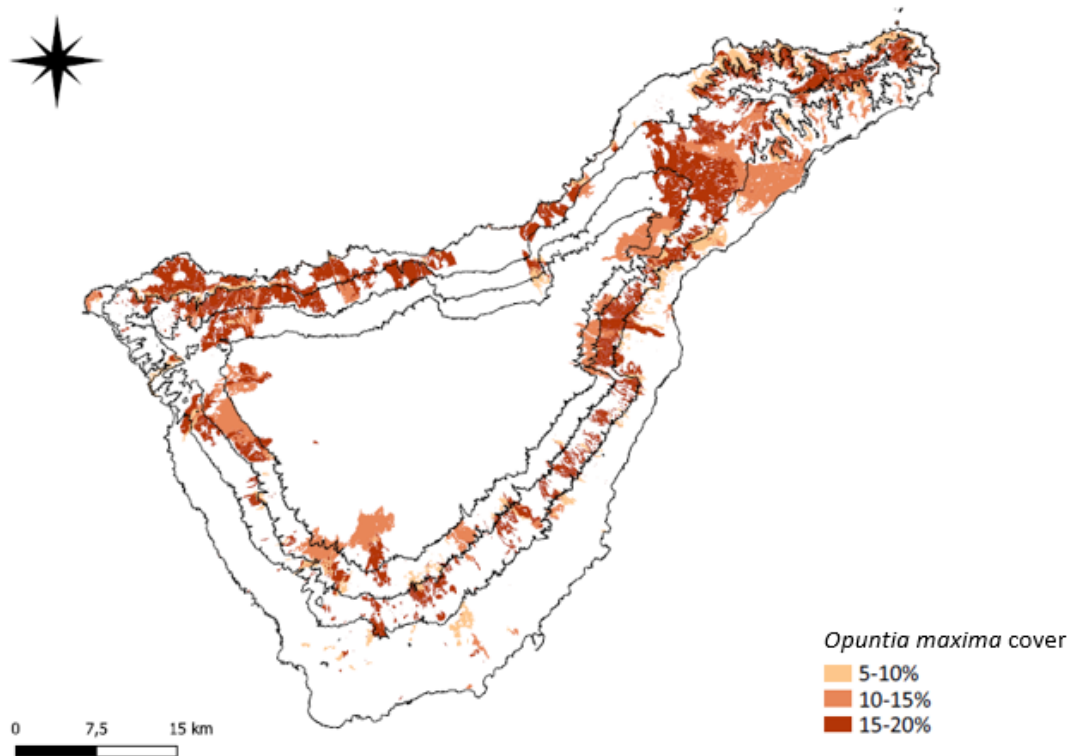
7.2 Biomass of *Opuntia* spp. stocked in Tenerife

The average of total aerial biomass contained in 1 m^2 occupied exclusively by *O. maxima* is 74.17±22.19 kg, and the corresponding amount of dry biomass decreases to 7.29±2.38 kg. For *O. dillenii*, the total aerial biomass is 44.24±16 kg/m^2, and the dry biomass 6.05±1.18 kg/m^2 (Figure 9). Considering the area exclusively occupied by both species in Tenerife, the island hosts a total amount of 4,060,274.6 tons of *O. maxima* biomass (399,311.8 tons of dry biomass) and 489,450.8 tons of *O. dillenii* biomass (66,933.66 tons of dry biomass), above ground. No significant differences were found in total biomass from individuals between different wind exposure (Figure 10), elevations (Figure 11), nor between species or the interaction of these factors (p-value > 0.05).

Figure 9. Total biomass (left) and dry biomass (right) (kg/m^2) of *O. dillenii* (green) and *O. maxima* (orange) on the island of Tenerife.
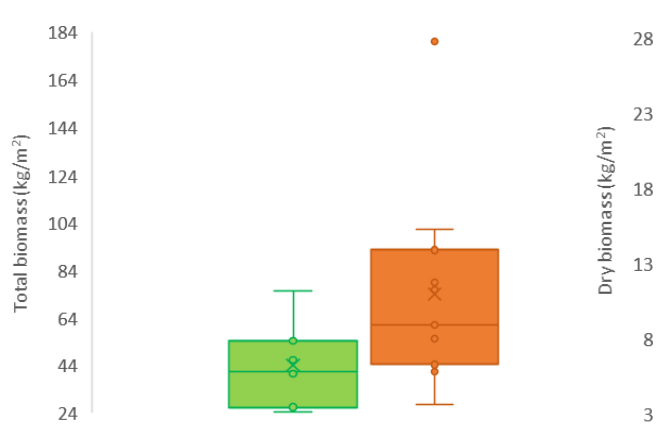

Figure 10. Total biomass (left) and dry biomass (right) (kg/m^2) of individuals sampled windward (yellow) and leeward (grey) on the island of Tenerife.
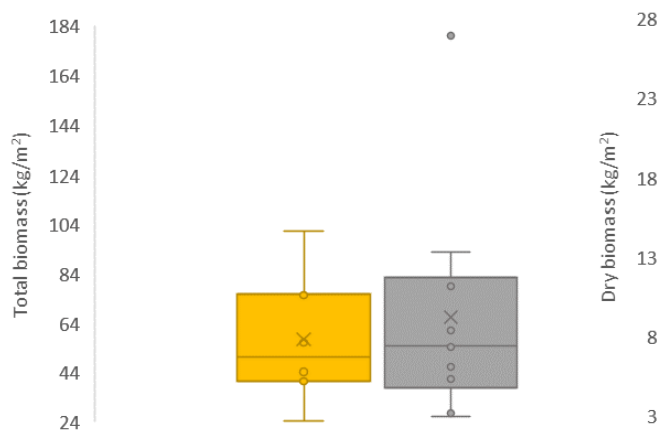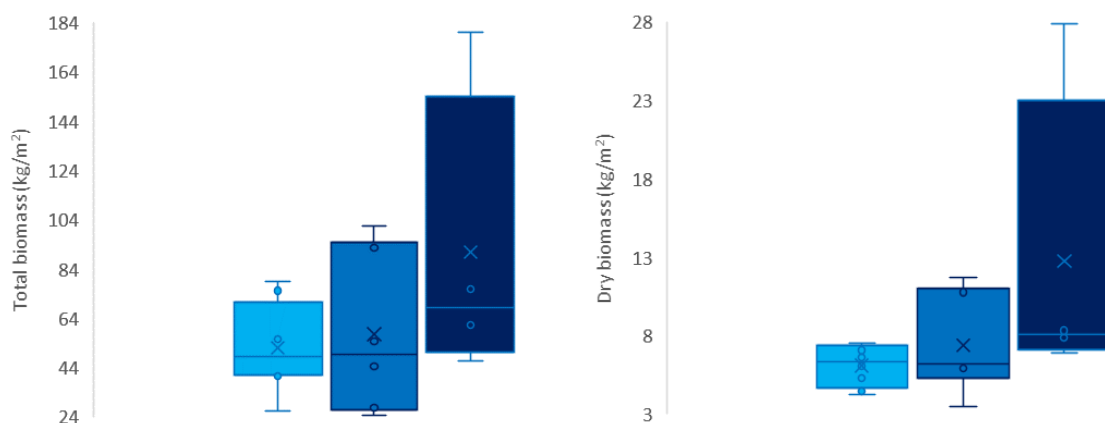

Figure 11. Total biomass (left) and dry biomass (right) (kg/m^2) of individuals sampled in each elevational range, 0-400 m a.s.l. (fair blue), 400-800 m a.s.l. (blue), and 800-1200 m a.s.l. (dark blue) on the island of Tenerife.

For dry matter percentage (and hence water content) the same results were obtained as for abiotic factors, but in this case, significant differences ($p < 0.05$) were detected between the two species, with *O. dillenii* having the highest dry matter percentage, 14.64% vs 11.43%. Therefore, the water content of *O. maxima* was the highest, 88.57%. vs 85.36% (Figures 12, 13, 14).

Figure 12. Dry biomass (left) and water content (right) (%) of *O. dillenii* (green) and *O. maxima* (orange) on the island of Tenerife.
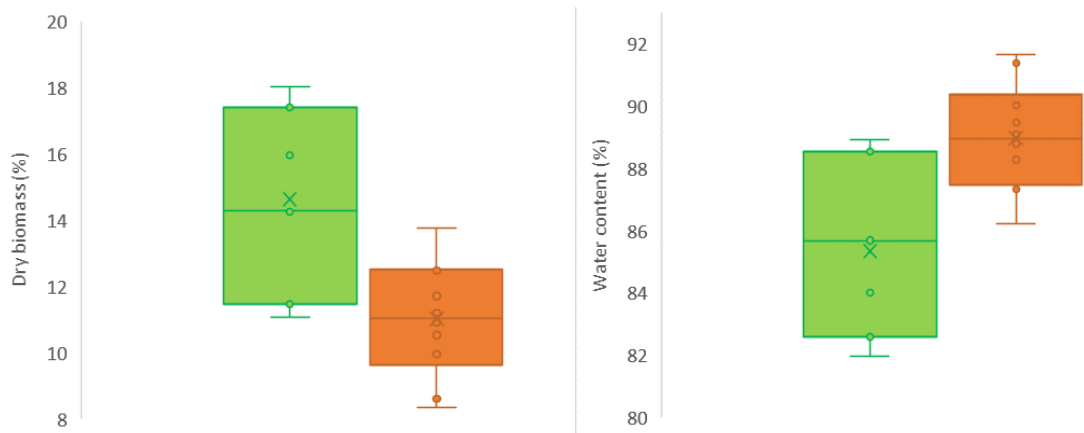

Figure 13. Dry biomass (%) of individuals sampled windward (yellow) and leeward (grey) on the island of Tenerife.
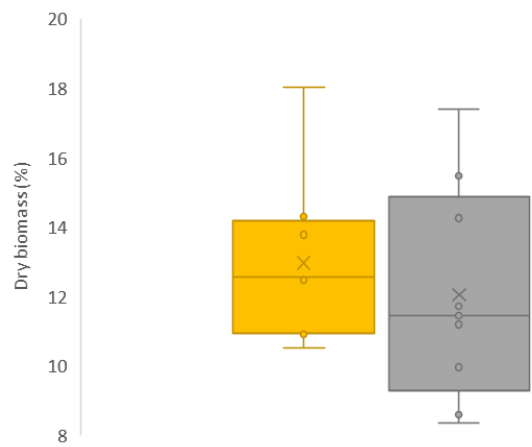
Figure 14. Dry biomass (%) of individuals sampled in each elevational range, 0-400 m a.s.l. (fair blue), 400-800 m a.s.l. (blue), and 800-1200 m a.s.l. (dark blue) on the island of Tenerife.
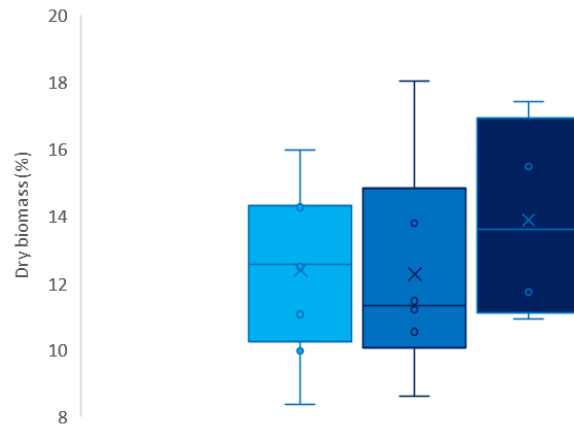
For each individual sampled, we obtained data of dry biomass from terminal or intermediate cladodes, and trunks or lignified steams. For woody biomass (trunks or lignified stems), there was no influence of abiotic factors, but significant differences ($p < 0.05$) were observed between species, having *O. maxima* higher values 3.73±1.62 kg/m^2 than *O. dillenii*, 2.17±0.66 kg/m^2 (Figure 15).

Figure 15. Dry woody biomass (kg/m^2) of *O. dillenii* (green) and *O. maxima* (orange) on the island of Tenerife.
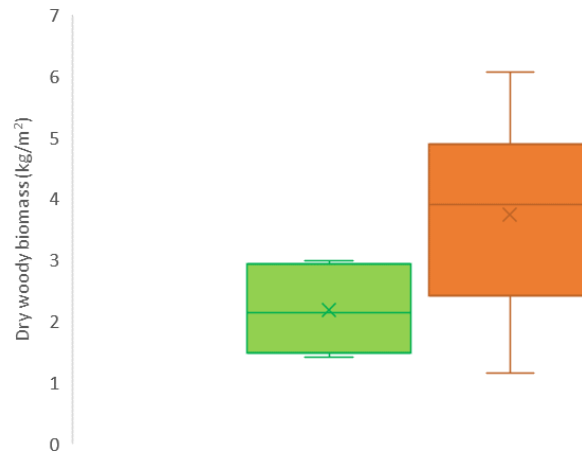
Significative differences were found between the number of cladodes per m^2 and their weight average (p-value < 0.05). *O. dillenii* showed a higher number of cladodes per individual (162±64) than *O. maxima* (49±29), but the average weight per cladode for the first (0.2 kg) is much lower than the latter (1.1 kg) (Figure 16).

Figure 16. Number of cladodes (left) and average weight of cladodes (kg/m^2) of *O. dillenii* (green) and *O. maxima* (orange) on the island of Tenerife.
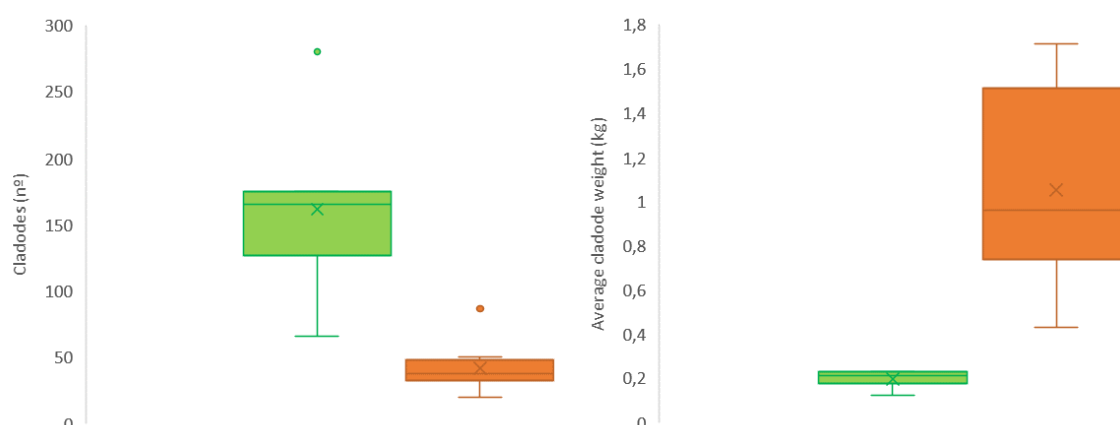
Due to differences in phenology between species, we only have data on fruit biomass for *O. dillenii*. Total fruit biomass was 0.7±1.1 kg/m^2, while dry fruit biomass was 0.26±0.2 kg/m^2, and the average percentage over fruit dry biomass was 22.61%. Again, no influence of abiotic factors was found for total and dry biomass, neither for the dry biomass percentage of fruits ($p < 0.05$).

Based on published data on the proportion of total dry biomass from *Opuntia* that accounts for belowground biomass (17.5%) (Liguori et al., 2014), we estimated the total and dry biomass of the root system of our sampled plants. The estimated average of the total biomass for the root system was 14.04±7.6 kg/m^2 in *O. maxima* and 7.5±2.8 kg/m^2 in *O. dillenii*, while average root dry biomass was 1.6±1.2 kg/m^2 for *O. maxima* and 1.1±0.2 kg/m^2 for *O. dillenii*.

Finally, we compared the percentage of water content for *Opuntia* spp. with values obtained from other native species with which they share distribution on the island (Otto et al., 2001). As seen in table 6, water content is higher for *Opuntia* spp., which means that they store less dry biomass per unit of total biomass than several native species of the island. To be able to compare data on the amount of dry biomass of native species with that of *Opuntia* spp., we converted our data from kg/m^2 to kg/m^3.

Table 6. Water content (%) and dry biomass (kg/m^3) of some Tenerife native species (adapted from Otto et al., 2001). Data of *Opuntia maxima* and *O. dillenii* are from this study.

	Water content (%)	Dry biomass (kg/m^3)
Opuntia dillenii	88.6	6.55
Opuntia maxima	85.4	4.55
Euphorbia canariensis	90.1	4.8
Euphorbia balsamifera	78.8	1.4
Euphorbia lamarckii	73.8	0.8
Plocama pendula	57.8	0.7
Launaea arborescens	44.5	1.3
Lycium intricatum	34.5	1.2
Kleinia neriifolia	85.2	0.7
Periploca laevigata	57.7	0.9
Schizogyne sericea	61.7	1.9
Campylanthus salsoloides	47.7	1
Rumex lunaria	61.3	1.9

Neochamaelea pulverulenta	43.3	1.1
Rubia fruticosa	57.1	1.3
Rhamnus crenulata	40.1	0.6
Artemisia thuscula	39.3	0.9
Salsola divaricata	35.4	2.8
Lavandula sp.	61.9	0.8
Atalanthus microcarpus	64.2	2
Ceropegia fusca	87.2	1.7
Drimia maritima	88.1	0.1
Asphodelus ramosus	83.5	0.7

Our estimations of dry biomass per volume (4.5-6.5 kg/m^3) are only similar to that of *Euphorbia canariensis* (4.8 kg/m^3), while the other species showed considerably lower values (0.1-2.8 kg/m3). However, dry biomass content of *Opuntia* spp. estimated by Otto et al. (2001) is half the value (2.8 kg/m^3) of our estimations.

7.3 Allometric equations for biomass of *Opuntia* spp.

We developed two allometric equations based on our data, for the estimation of total biomass and dry biomass for *Opuntia* spp. (Equation 1 and Equation 2). From all the biometric parameters tested, only the basal stem diameter could explain the variance of both total and dry biomass. After comparing all the possible models, the most explicative and simple model for predicting dry biomass was a simple linear regression with the basal steam diameter as independent variable (Figure 17). The number of cladodes, largest diameters, height, biovolume, and area projection of the measured individuals were not able to explain by themselves the values of dry biomass in any of the tested models. For total biomass, height seemed to be a good predictor too, but not better than the basal stem diameter. Although eight multiple regression equations and two polynomial quadratic equations had significant p-value for explaining total biomass, comparing with function "rcompanion", the most simple and accurate equation for this dependent variable was the same as for dry biomass, a simple linear equation with the basal stem diameter as independent variable (Figure 18). The proposed allometric equations for the estimation of *Opuntia* spp. biomass are:

$$(1) \; Dry \; biomass = 1.5403 + Basal \; stem \; diameter \times 0.3231$$

$$(2) \; Total \; biomass = -10.0842 + Basal \; stem \; diameter \times 4.1121$$

Table 7. Different models tested for the development of allometric equations to estimate dry biomass of *Opuntia* spp. The independent variables and values of the corrected Akaike information criteria (AICc), squared R (R^2), p-value and Shapiro Wilks test are shown for each model.

Simple lineal regression models				
Independent variable	AICc	R^2	p-value	Shapiro test p-value
Basal stem diameter	60.83	0.4147	0.0175	0.2232
Biovolume	80.08	0.0514	0.3815	0.1266
Area projection	80.92	0.0028	0.8382	0.1332
Diameter 1	80.88	0.0052	0.7816	0.1284
Diameter 2	80.76	0.0123	0.6714	0.0811
Height	80.91	0.0035	0.8214	0.1638
Polynomial quadratic models				
Basal stem diameter	64.53	0.4423	0.0539	0.0555
Biovolume	79.88	0.2363	0.1516	0.8450
Area projection	84.09	0.0215	0.8587	0.1262
Diameter 1	84.03	0.0247	0.8390	0.1733
Diameter 2	83.89	0.0328	0.7914	0.0976
Height	79.80	0.2397	0.1469	0.9134
Multiple lineal regression models				
Independent variables and interaction	AICc	R^2 adjusted	p-value	Shapiro test p-value
Basal stem diameter * Height	69.79	0.2745	0.1243	0.2989
Basal stem diameter + Height	65.16	0.4149	0.2979	0.2096
Basal stem diameter * Biovolume	70.00	0.2624	0.1329	0.3991
Basal stem diameter + Biovolume	64.66	0.3244	0.0565	0.5728
Basal stem diameter * Diameter 1	70.24	0.2490	0.1431	0.1603
Basal stem diameter * Diameter 1	64.93	0.3103	0.0627	0.2598

Table 8. Different models tested for the development of allometric equations to calculate total biomass of *Opuntia* spp. The independent variables and values of the corrected Akaike information criteria (AICc), squared R (R^2), p-value and Shapiro Wilks test are shown for each model.

Simple lineal regression models				
Independent variable	AICc	R^2	p-value	Shapiro test p-value
Basal stem diameter	115.2	0.6366	0.0010	0.9669
Biovolume	158.6	0.1449	0.1317	0.0809
Area projection	161.1	0.0079	0.7330	0.2115
Diameter 1	161.0	0.0150	0.6387	0.1561
Diameter 2	160.7	0.0326	0.4877	0.2114

Height	161.2	0.0004	0.9380	0.3433
Polynomial quadratic models				
Independent variable	AICc	R^2	p-value	Shapiro test p-value
Basal stem diameter	118.0	0.6114	0.0035	0.8786
Biovolume	159.3	0.1691	0.1074	0.3853
Area projection	163.8	-0.0852	0.6961	0.4468
Diameter 1	163.4	-0.0581	0.5832	0.6193
Diameter 2	161.2	0.07113	0.2343	0.4341
Height	154.0	0.3927	0.0119	0.8091
Multiple lineal regression models				
Independent variables and interaction	AICc	R^2 adjusted	p-value	Shapiro test p-value
Basal stem diameter * Height	120.9	0.6486	0.0056	0.2386
Basal stem diameter + Height	119.5	0.5658	0.0062	0.9490
Basal stem diameter * Biovolume	119.7	0.6796	0.0037	0.4439
Basal stem diameter + Biovolume	115.1	0.6898	0.0011	0.3088
Basal stem diameter * Diameter 1	122.4	0.6077	0.0091	0.7229
Basal stem diameter * Diameter 1	118.1	0.6106	0.0035	0.6465

The AICc values for total biomass and dry biomass equations were 115.2 and 60.83, respectively. R^2 obtained for the total biomass equation is 0.64, considerably higher than that of the dry biomass equation, 0.42. The p-values from the Shapiro Wilks test were 0.2232 for the residuals of the dry biomass model and 0.9669 for the residuals of the total biomass model, indicating their normality in both models (Tables 7, 8).

It must be mentioned that the measurement of the stem basal diameter in *O. dillenii* is impossible without cutting off a fraction of the individual to reach its basal stem, due to its cushion shape and higher number of lower cladodes. Considering data of both species independently, no equation could be developed for *O. dilleni* that accomplished the necessary requirements (p-value < 0.05 and acceptable R^2). In contrast, *O. maxima* showed eight possible explanatory equations for the estimation of its total biomass. Despite this, none of them explained the sample variance as well as the equation with values from both species. Thus, those equations were dismissed.

Figure 17. Graphic representation of the developed allometric equation for estimating total biomass per m^2 with the basal stem diameter (cm) for *Opuntia* spp. on the island of Tenerife.
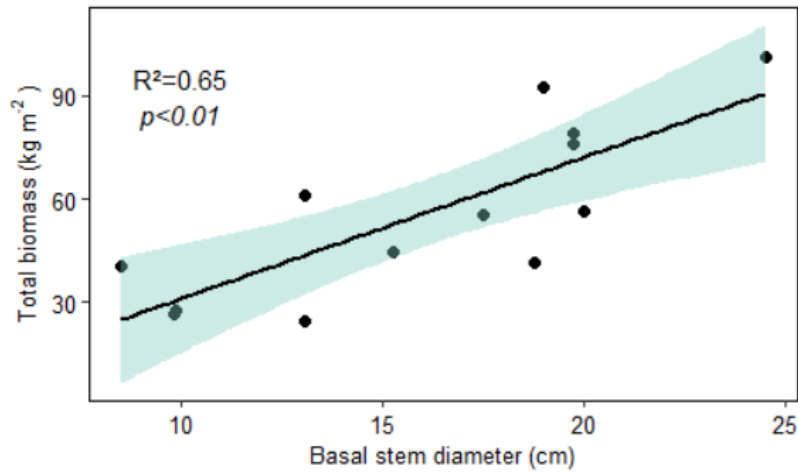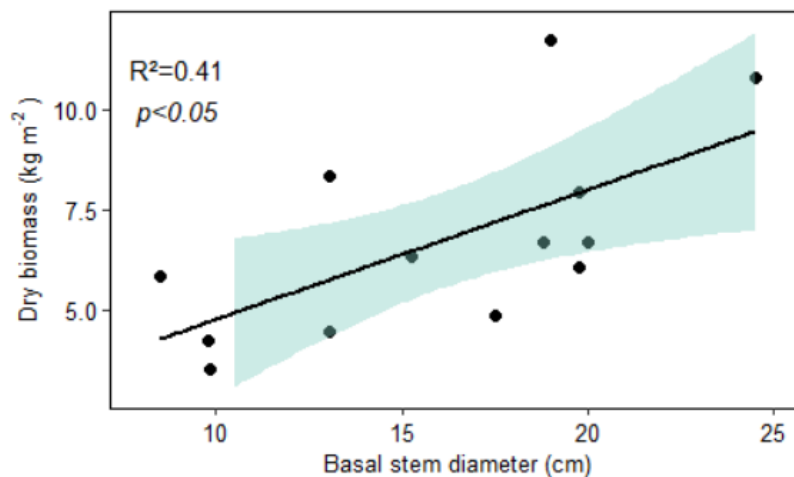

Figure 18. Graphic representation of the developed allometric equation for estimating total biomass per m^2 with the basal stem diameter (cm) for *Opuntia* spp. on the island of Tenerife.

7.4 Carbon stored by *Opuntia* spp. in Tenerife

The carbon stored by *O. maxima* in Tenerife is 25.6 tons/ha and 21.24 tons/ha for *O. dillenii*. Considering our estimations of the total area occupied by both species, *O. maxima* stores an amount of 137,093.37 tons of carbon on the island, while *O. dillenii* stores 29,493.71 tons. These values are equivalent to 502,675.68 and 86,221.93 tons of CO_2, respectively.

Both allometric equations were applied to the basal stem diameter data of the 15 additional individuals sampled, to calculate their total and dry biomass. We compared these values with the mean of our samples and test the accuracy of our equations. Average of the 15 individuals was 6±1 kg/m^2 for dry biomass and 46.5±12.3 kg/m^2 for total biomass, showing no differences with field measurements.

8. Discussion

8.1 Distribution and cover of *Opuntia* spp. on Tenerife

The total area occupied by *Opuntia maxima* is five times larger than that of *O. dillenii*. Although the earliest references on the occurrence of the genus already mentioned both species on the island (Salas & Cáceres, 2003), differences in their current distribution area may be due to their different historical uses. While *O. maxima* was cultivated in some islands for the carmine cochineal production, this was not the case for *O. dillenii* (Chinea et al., 2001; Godoy, 2012). *O. maxima* is also mostly related to anthropic areas, thus the historical rural and urban development during the last centuries may have enhanced its dispersal too. Degraded areas resulting from grazing, abandoned fields, fragmentation, or roads, became perfect niches for the species (Otto et al., 2001; Arévalo et al., 2010; Bacaro et al., 2015), where cover reaches the highest values according to our data. Their Its use as hedges or fences to delimit properties (Lloret, 2016) may also have boosted their spread. The elevational range within we can find *O. maxima* is also greater than for *O. dillenii*, which points to a better adaptation of the first to variable environmental conditions. In the context of climate change, higher islands providing more surface and different habitats, could favor the dispersal of invasive species as competitive as *O. maxima* (Baret et al., 2006; Arteaga et al., 2009; Irl et al., 2020).

Opuntia spp. have a set of characteristics that give them competitive advantage over native species, such as their CAM metabolism, which allows them to fix CO_2 at night, reducing water loss through the stomata by transpiration (Acevedo et al., 1983). In addition, their relatively thick cuticle, their lower density of stomata, and a serous layer on their surface prevents water loss (Lozano, 2011; Lloret, 2016). They can reproduce both sexually, by seeds, and asexually, by dispersing cladodes that root quickly and easily (Reyes-Agüero et al., 2005). Moreover, they have become so well established in Canary Island ecosystems that are now an essential part of food webs being their dispersal favored by the native fauna that consumes their fruits, such as lizards (*Gallotia* spp.,) and birds (*Cianistes teneriffae*, *Phylloscopus colibita*) (Padrón et al., 2011).

Estimations of *Opuntia* spp. distribution done in this work has been conservative, thus the area occupied by both species could be underestimated, especially for *O. dillenii*. Our assessment was limited by the lack of information on the distribution of invasive species available for the Canary Islands, which has not received much attention in terms of mapping. This is especially the case for *Opuntia* species, which seem to be perfectly integrated in the Canarian culture and are not a main target for invasive species management. The sources from which we obtained occurrence information, such as Biota, have sometimes proved to be inaccurate. Presence data are often based on old literature, with species geolocation data of low precision, and can accumulate errors related to species misidentification and database curation. In addition, the CVM does not include information on plant communities with *O. dillenii* on Tenerife, and neither represents all populations of *O. maxima* due to scale limitation (1:20000) (del Arco et al., 2010).

There is data available on the current distribution of *O. maxima* for all islands, estimated with Maxent. In Tenerife, a total distribution area of 81,819 ha was estimated (Brouwer, 2019). According to our data, the area occupied by *O. maxima* estimated for Tenerife was 4,680.33 ha, based on its cover. However, when considering the whole area of those CVM polygons where the presence of *O. maxima* was determined, its area of distribution amounted to 37,495 ha. Still, this value is lower than the distribution area estimated with Maxent. There is no such information about *O. dillenii*, probably due to the little attention dedicated to the study of this invader. Another reason as to why *O. dillenii* occurrence recording and mapping has been

neglected could be that this species was less common in the past and is now spreading favored by climate warming (Fernández de Castro et al., 2018).

Another study sampled 47 populations of *O. maxima* and used Maxent to estimate the area climatically suitable in the Anaga Rural Park, 120 ha (Betancourt, 2020) while our estimation is that *O. maxima* distribution area in Anaga is approximately 600 ha. It should be noted that Maxent elaborates environmental niche models by using mainly climatic data and presence/pseudo-absence data. These estimations do not take into account important variables such as which plant communities occur in those predicted areas and the presence of species that could be potential competitors for the invaders, the level of conservation/degradation, the influence of the proximity to anthropized areas, or the density and cover of the exotic species themselves. For such reasons, these models could be over or underestimating the distribution of *O. maxima* in these studies.

Analyzing both species occurrence on the different plant communities we observed that *O. dillenii* is mainly restricted to the coastal scrubland on the island. This could be explained by its CAM metabolism, that makes it very competitive on arid zones (Nobel, 1991a; Snyman, 2013). Also, in its native distribution *O. dillenii* is a species restricted to lowlands (Esparza, 2010). In contrast, *O. maxima* with a long history of traditional uses, is dominant on degraded and anthropized areas, where natural recovery is more unlikely. For this reason, its management is more complex than for *O. dillenii*, since it is usually growing in private properties, or nearby. Based on their observed distribution, we consider that *O. dillenii* is ecologically more threatening and problematic than *O. maxima*, as it is well represented in mature communities and natural protected areas, whereas *O. maxima* is abundant on secondary scrublands, but it is not usually established on mature communities and well-preserved areas. Therefore, *O. dillenii* management, at least in natural protected areas, should be seriously considered. Its eradication could be achieved by focusing actions on small areas (Russell et al., 2017), but extremely sensitive to invasive species because of their high biodiversity (Pyšek et al., 2020). As an example, a control experiment of *O. dillenii* was developed at Teno Rural Park. There, individuals were mechanically removed, releasing the space and the niche for native shrub species characteristic of the coastal scrub, such as *Ceballosia fruticosa, Euphorbia lamarckii* and *Plocama pendula*, that were rapidly favored, although other invasive species also benefited from the new space and resources released (Arévalo et al., 2011). The density of *O. dillenii* in the Teno Rural Park has been estimated as 1,200 individuals/ha (Padrón et al., 2011), while the total area of the CVM polygons where we determined the presence of the species account for 570 ha approximately in the Park. These data allow us to estimate that around 684,000 individuals of *O. dillenii* are present in this protected natural area, a figure that is worth considering and indicates that its management is advisable.

Another reason in favor of the control of this species is its associated risks. *O. dillenii* is commonly found in coastal areas, heavily frequented by people accessing to the coast, beaches, and footpaths. The plant is armed with spines larger than 5 cm that can be very harmful. Its areoles become detached, and the spines fall to the ground, where they accumulate forming minefields where it is impossible to walk through without being harmed. Roads and paths require maintenance to avoid this type of incidents that could be prevented by removing the species from those areas. A potential site for the control of *O. dillenii* could be the Site of Scientific Interest of La Caleta (Adeje), where the plant is very abundant and widely spread. This natural protected area is small (78.3 ha), accessible, and thus manageable, comprising 53 taxa of vascular flora, of which 25 species are endemic, and where human traffic is intense due to its

popular beaches (Gobierno de Canarias, 2006). While surveying the site to search for sample individuals, we realized that it is completely invaded by *O. dillenii*, especially the areas that are closest closer to the golf course.

8.2 Biomass of *Opuntia* spp. on Tenerife

The collection of biomass data from whole plant individuals can be laborious and time-consuming. Obtaining dry weight from all the aerial biomass per m^2 of both species took three months using three fully packed stoves. To save some time, only a representative portion (5-15 kg) of the biomass collected in 1 m^2 was dried for the following samples. Consistency in the results obtained proved that this subsampling procedure for the estimation of dry biomass is reliable.

Despite the morphological differences between the two species (*O. maxima* has a more arboreal shape and *O. dillenii* a cushion form), there are no differences between the total biomass per m^2 of the two species. *O. maxima* showed higher variability in total biomass values overlapping the narrower range of *O. dillenii* weights, which could explain the lack of difference found between both species.

The lack of differences between total biomass at different altitudinal ranges and orientations demonstrates that environmental conditions do not excessively influence the biomass production of both species, probably due to their plasticity to adapt to different environments. On high islands as Tenerife, the altitudinal range create humidity and temperature gradients. At lower elevations, water stress is tolerated by *Opuntia* spp. through its CAM metabolism, which makes them very efficient in the use of water (Snyman, 2013). On the other hand, although the optimal temperatures for these species are 25/15 ˚C day/night, they can stand temperatures below 0 ˚C for short periods of time, as well as temperatures over 50 ˚C (Godoy, 2012). Such extreme conditions do not occur in their distribution area on Tenerife (AEMET, 2012).

There were no significant differences between the dry biomass per m^2 of both species at different altitudes and orientations. This simplified the mapping work and biomass estimations per total area, as the mean weight per area could be used to calculate the dry biomass of *O. maxima* and *O. dillenii* considering their total distribution on the island. Additionally, the results obtained on water content agree with previous studies (Godoy, 2012). More than 80% of the total weight of *Opuntia* spp. is water. This imply that, the amount of dry biomass and thus carbon stored by both species is much lower than would be expected per unit area at first impression.

In terms of dry matter there were no differences between species either. However, the percentage of dry biomass over total biomass was higher for *O. dillenii*, as this species might be storing less water. *O. dillenii* is found on sites with higher water stress than *O. maxima* thus the reduced availability of the resource probably restricts the species' storage capacity. *O. maxima* is distributed in less dry environments, and the more water available the more the plant accumulates. When assessing the total amount of dry biomass for each species within the island, *O. maxima* has a higher contribution because its distribution area is greater.

In contrast, *O. maxima* has a higher percentage of dry biomass on its lignified parts, such as trunks or basal stems. A possible explanation is their different shape arrangements. *O. maxima* is more arboreal, slenderer and may sustain more weight per basal stem. Thus, it is likely that this species needs to invest more in resistant supporting tissues, such as the trunks and basal cladodes. The lower and cushion-shape growth habit of *O. dillenii* may allow the plant to

distribute its dry biomass more evenly among the three cladode types (according to our classification). The significant differences seen in the number of cladodes per m^2 of each species and their average weight between species showed that *O. dillenii* had more cladodes with less dry weight per cladode, while *O. maxima* showed the opposite pattern. The differences in morphology could be related to the different life strategies adopted by each species. The cushion shape is common in plants growing on arid and exposed windy and rocky areas, under the influence of sea spray where *O. dillenii* is more abundant, while the arboreal habit of *O. maxima* might be indicative of its wider distribution with less stressing environmental conditions.

Due to the sampling season (winter and early spring) we could only measure fruit production for *O. dillenii*. Fruit dry biomass percentage did not show significant differences compared to that of the cladodes and basal stems. Although fruits are not water storage organs, their main function is reproduction and attraction of seed dispersers by being fleshy and supplying water. The data obtained for fruit dry biomass agrees with other works with values between 20 and 25% of the total fruit weight.

Belowground biomass was estimated, according to measurements of the percentage of dry biomass in the root system of *O. maxima*, as 17.5% (Snyman, 2005, 2006; Liguori, 2014). We applied this percentage to both species. Similar data on the percentage of root biomass of native species on Tenerife has not been estimated. However, it is known that *Euphorbia canariensis* can extend its roots up to 35 m away from the individual at surface level (Lüpnitz & Ladwig, 1992) ref). This proves the importance of roots for the species occurring in the coastal scrub. Plants tend to invest more biomass and energy in those organs that capture their limiting resource(s). Therefore, in environments with high levels of water-stress as the lowlands of the island, species should invest in developing radicular systems capable of capturing as much water as possible. Considering this, the relatively small percentage of *Opuntia* dry biomass allocated in the roots reported by Snyman (2013) could be due to measurements taken under favorable conditions, with no water limitation, so that developing large roots is not necessary. Another explanation is that *Opuntia* spp. present a high efficiency storing water on their tissues so that they do not require to developed deep root systems. Their strategy could be to accumulate water when it is available, and do not invest in searching when there is not. In addition, places where *O. maxima* is more abundant on the island, do not usually present extremely hydric stress. In the case of *O. dillenii*, the percentage of dry biomass allocated in the roots could be different, but again, there is no data available for comparison.

If, in fact, the belowground biomass of *Opuntia* spp. was much lower than that of native species, added to the lower amount of carbon contained in their dry biomass, this would imply that native shrub species might be better carbon stores over *Opuntia* spp. Still, much work remains to be done to understand the allocation of dry biomass and carbon belowground in native Canarian species.

In a previous work studying vegetation structure on the Tenerife coastal scrub, Otto et al. (2001) calculated dry biomass per volume for several species. Using the height of each individual we transformed our dry biomass values from m^2 to m^3 for comparison. A first analysis of the biomass per m^3 showed that there were no differences between both species in our study. The cushion shape and shorter habit of *O. dillenii* makes it more compact and denser in terms of number of cladodes per volume, while *O. maxima* is usually higher than 1 m, with more spread branches and a lower density of cladodes per volume, however this did not translate in differences in the dry biomass per volume.

Comparing with other native species of the coastal scrub (Otto et al., 2001) our estimations of dry biomass per volume (4.5-6.5 kg/m^3) are only similar to that of *E. canariensis* (4.8 kg/m^3), while the other species showed considerably lower values (0.1-2.8 kg/m^3). However, dry biomass content of *Opuntia* spp. estimated by Otto et al. (2001) is half the value (2.8 kg/m^3) of our estimations. Again, the similarity in structure between *Opuntia* spp. and *E. canariensis*, with succulent cladodes and stems branching from the base of the plant could be explaining the higher values of biomass estimated by the volumetric method. In fact, *E. canariensis* within Euphorbiaceae family has adopted a cactus like shape, with succulent stems and reduced leaves, due to convergent adaptation to stand hydric stress at lowlands. The other native species included in the comparison do not show such anatomy of basal branching, and although many are succulent plants, they show present a common shrubby habit with a main trunk, branches and leaves. This type of shape would include less dry biomass when fitted in a cylinder for volumetric estimation, thus dry biomass might be underestimated. Unfortunately, we do not have the data to transform dry biomass per volume, from Otto et al. (2001), into area (m^2), but perhaps, comparison of biomass per area would be more accurate when different plant habits are present in the same communities. An approach using this methodology is needed for coastal scrub species biomass estimation in the future.

When comparing water content between species from both studies, dry biomass percentage over total biomass is very similar between *Opuntia* spp. and *E. canariensis* (10%), and lower than that of the other native species (10-65%), while our dry biomass percentage shows intermediate values (8-18%). Such values could be attributed due to the higher number of *O. dillenii* samples included in our study, since the species contributes more on dry biomass per total weight. But in general, the amount of dry biomass is similar between *Opuntia* spp. and *E. canariensis* and the three species are showing the highest level of succulency.

At community level the contribution of *Opuntia* spp. to total dry biomass is higher compared to other native shrubs but in proportion to total weight is lower. For instance, considering similar total weights, native plants would accumulate more dry biomass than *Opuntia* spp. Thus *Opuntia* spp. will require more space to produce the same amount of dry biomass than native shrub species. Comparing these data is complex because of the methodology used to measure biomass by volume that might be biasing the dry biomass estimation data. Additionally, because *Opuntia* spp. are so widely distributed on the island, they are is contributing with higher dry biomass content over other native species, despite the fact that most of its their weight is water.

8.3 Allometric equations

There are no published allometric equations to calculate total or dry biomass per area exclusively for *Opuntia* spp. and for the purpose of calculating their carbon storage. Thus, we aimed to develop a single allometric equation to estimate dry biomass for *Opuntia* spp. growing wild on Tenerife. From the biometric data collected we were able to develop one equation for total biomass and a second equation for dry biomass, both applicable for to *Opuntia* spp. These equations allow us to calculate the total and dry biomass weight from biometric data, without cutting a complete individual of *O. maxima*. In the case of *O. dillenii* a small portion of the individual needs to be cut until we are able to reach and measure the basal diameter of the stem. Still, this method is less time-consuming than cutting off the whole individual and drying it over a month to obtain dry weight.

Otto et al. (2001) developed an allometric equation for dry biomass of *Opuntia* spp., however it was obtained with just four samples of 1 m³. As we have previously discussed, the relatively low number of samples and measures by volume unit might be biasing the estimated weights. Our equation may introduce some improvement in the estimation of dry biomass for both species, since we increased the number of samples and measured biomass per area. The basal stem diameter seems to be a very good indicator of the biomass of both species, as an equivalent to the diameter at breast height of tree species. It should be mentioned that an allometric equation already exists for *O. maxima*, but this only estimates the dry weight of single cladodes from their biovolume, and it is more focused on crop yield estimation (Curt et al., 2011; Reis et al., 2018). The number of cladodes was not a good predictor. This is understandable, as the cladodes varied greatly in weight and morphology, and between species the differences in cladode number and average weight were significant, while there were no differences in biomass.

When developing the equation, we intended to calculate the carbon content stored in *Opuntia* spp. from the dry biomass. The total biomass equation provides another way to estimate this value. By estimating the total biomass per area and calculating its average percentage of dry biomass (14.64 and 11.43% for *O. dillenii* and *O. maxima* respectively), we can obtain the dry weight, and from there obtain the carbon content. According to Yang et al. (2015) the total percentage of carbon contained per dry biomass of *O. maxima* is 35.1%. This way we can obtain the carbon content per area for *Opuntia* spp. from a simple measurement.

8.4 Carbon stored by *Opuntia* spp. in Tenerife

Both *Opuntia maxima* and *O. dillenii* seem to be substantial carbon pools in Tenerife. But, as we have already discussed, the contribution to carbon storage lies in their wide distribution and abundance, since they contain a relatively small amount of carbon per unit of total biomass (35.1%), according to Yang et al. (2015). It would be of interest to compare this value of carbon content with those of native species co-occurring with *Opuntia*, but to our knowledge this data has not been measured specifically for Canarian shrub species. It is generally accepted that the percentage of carbon stored in the dry matter is around 50%. In studies carried out by Montero et al. (2005) on the CO_2 fixation of Mediterranean shrublands (mainly sclerophyllous) in the Iberian Peninsula, such values were used. For some genera present in the Canaries and shared with the Iberian Peninsula, such as *Asphodelus, Cistus, Erica, Jasminum, Juniperus, Lavandula, Pistacia, Rhamnus, Rubus* and *Tamarix,* carbon content values between 48-53 % were used. Still, there are many other genera in the Canary Islands for which these data are unknown, and the values between species may differ, as seen for *O. maxima* with a percentage of carbon content far from the generally assumed 50%. We would like to highlight here the importance of studying the coastal scrubland, as well as other native shrubland ecosystems, in terms of their carbon storage and sequestration capacity, in the current context of global change.

The Canary Islands are a hotspot that host unique biodiversity while being threatened by anthropogenic, land-use and climate changes. In this context, the need of recovery of Canarian environments in order to preserve or restore their natural heritage is more than agreed. There are many environments in need of ecological restoration in the islands. As an example, thermophilous woodland has been undergoing continuous exploitation since pre-historical times and their communities cannot recover from the few small remnants available. Likewise, the coastal scrublands are highly fragmented with well-preserved patches isolated in small areas surrounded by urban areas, abandoned fields or secondary scrubs. The recovery of these ecosystems requires specific management tasks such as the removal of exotic and invasive

species that are competing with native species for resources. Among restoration actions, the removal of plants or and plantations, involve the management of plant biomass with related modifications of the carbon cycle by the release and sequestration of carbon. Considering the carbon footprint of such actions is a novel approach that requires attention. Theis biomass calculation using *Opuntia* spp. as models in this study has been a first attempt to address it, but further research is needed. The potential carbon sequestration of native species in the different Canarian ecosystems, not only for tree species, but also for shrubs is almost unknown. Knowing the capacity to store carbon in their tissues and to capture the main greenhouse gas would be an additional strong argument in favor of the management for their recovery, in this particular case, through the control of invasive species such as *Opuntia* spp.

9. Conclusions

1. Distribution areas based on presence and covers of *Opuntia maxima* (5474.04 ha) and *Opuntia dillenii* (819.78 ha) were estimated for the island of Tenerife.

2. Estimations of *Opuntia* spp. distribution in this work are conservative and could be underestimated, due to lack of information on the distribution of invasive species available for the Canary Islands, that has not received much attention in terms of mapping. This is particularly the case for *O. dillenii*.

3. Distribution of *O. maxima* is dominant on degraded and anthropized areas, challenging its management on private properties. *O. dillenii* is more restricted to the coastal scrubland and often occurring in well-preserved and protected natural areas, where its management should be prioritized.

4. There are no differences between biomass per area of both species, and no significant effects of different elevations or expositions, suggesting that both species are well adapted to environmental conditions on the island. This simplified biomass estimations of both species per total distribution area on the island.

5. There are other biometric differences between both species: *O. dillenii* has a higher proportion of dry matter, more cladodes with less average weight per cladode, and less dry biomass allocated in lignified stems. Such differences respond to differentiated growth habits and environmental adaptations.

6. Comparison of dry biomass content between native and invasive species in the Canaries would improve by using a method estimating biomass per area, especially when different plant habits are compared.

7. If *Opuntia* spp. contribute with higher dry biomass content over other native species, even though most of its weight is water, is because it is widely distributed on the island. *Opuntia* spp. require more space to produce the same amount of dry biomass than native shrub species.

8. Two allometric equations were developed for estimating total and dry biomass of *Opuntia* spp. per unit area by measuring their basal stem diameter, reducing field work and sampling processing efforts.

9. Both *O. maxima* and *O. dillenii* contribute substantially to carbon storage in Tenerife, mainly due to their wide distribution and abundance, because they contain a relatively small amount of carbon per unit of total biomass.

10. The estimation of the carbon footprint of restoration through eradication of invasive species is a novel approach that has been addressed in this study using as a model *Opuntia* spp. In the context of global change further research to know the capacity of carbon storage of native and invasive shrub species in the Canary Islands is necessary.

11.   References

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