

## An ecological overview of *Prosopis pallida*, one of the most adapted dryland species to extreme climate events

Pablo Salazar Zarzosa<sup>a,b,1,2,\*</sup>, Glenda Mendieta-Leiva<sup>c,d</sup>, Rafael M. Navarro-Cerrillo<sup>e,2</sup>, Gastón Cruz<sup>a,1</sup>, Nora Grados<sup>a,1</sup>, Rafael Villar<sup>b,2</sup>

<sup>a</sup> Facultad de Ingeniería, Universidad de Piura, Av. Ramón Mugica 131, Piura, Perú

<sup>b</sup> Área de Ecología, Universidad de Córdoba, Edificio Celestino Mutis, Campus de Rabanales, 14071, Córdoba, Spain

<sup>c</sup> Faculty of Geography, University of Marburg, Marburg, Germany

<sup>d</sup> Plant Ecology Division-CORBIDI, Lima, Peru

<sup>e</sup> Departamento. Ingeniería Forestal, Laboratorio de Selvicultura, Dendrocronología y Cambio Climático, DendrodatLab-ERSAF, Universidad de Córdoba, Campus de Rabanales, 14071, Córdoba, Spain

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### ABSTRACT

*Prosopis pallida* (algarrobo) is a highly adapted species to extremely dry and wet conditions. Its geographic distribution at both sides of the Pacific Ocean is associated with its plastic response to El Niño event, an extreme climate event that changes precipitation regimes. In this review, we summarized the current knowledge of this versatile species based on scientific literature. Our analysis conducted identify three main research topics: geographical distribution, ecophysiology and population plasticity, and ecosystem services provision to guide the review in a methodological and unbiased way. In the geographical distribution section, we describe the origin, history, and native distribution of algarrobo, as well as the current distribution and the degree of invasiveness in some countries. In the ecophysiology and population plasticity section, we focus on the mechanisms used by algarrobo to avoid water stress during drought and maximize plant growth during El Niño. We discuss how this is reflected in the most important leaf functional traits, such as leaf mass per area (LMA) or gas exchange-related traits. We analyse the importance of phenotypic plasticity and intraspecific variability as adaptive ways to resist extreme rainfall and prolonged droughts on *P. pallida* growth during the last 50 years. Finally, we summarized the main ecosystem services and ecological benefits provided by *P. pallida* as well as its potential industrial uses. With this review, we wish to consolidate the current scientific knowledge of this species, to point out gaps of knowledge and suggest future research directions. As the world becomes a warmer place, *P. pallida* can be a key species to understand plant resilience to extreme events in dryland ecosystems.

### 1. Introduction

The “algarrobo” (*Prosopis pallida* [Willd.] Kunth) is a facultative deciduous tree that thrives in dry ecosystems where salinity, drought and high temperature are predominant features (Felker et al., 1981). As the effects of climate change intensification across the world, dryland ecosystems face increasing temperatures and unexpected changes in precipitation regimens, which negatively affect plant production, regeneration, plant-plant interactions, and changes in species distribution. Moreover, these changes also undermine the capacity of these ecosystems to provide ecosystem services such as biomass production

and soil fertility (Berdugo et al., 2020).

Scientists have focused their research on dryland ecosystems looking for species adapted to extreme environmental conditions to understand their underlying mechanisms. Particularly, algarrobo indigenous populations are located in the North Peruvian dryland forests, which are no stranger to unexpected climate conditions. The long-prolonged drought periods (5–7 years, less than 200 mm of annual rainfall) are interrupted by extreme precipitation events (1–2 years, about 2000 mm per year) during the El Niño phenomenon, a worldwide climate event originated in the Pacific Ocean that changes precipitation regimens (Box 1). Furthermore, the increase in precipitation intensity (over 20 mm day<sup>-1</sup>)

\* Corresponding author. Facultad de Ingeniería, Universidad de Piura, Av. Ramón Mugica 131, Piura, Perú.

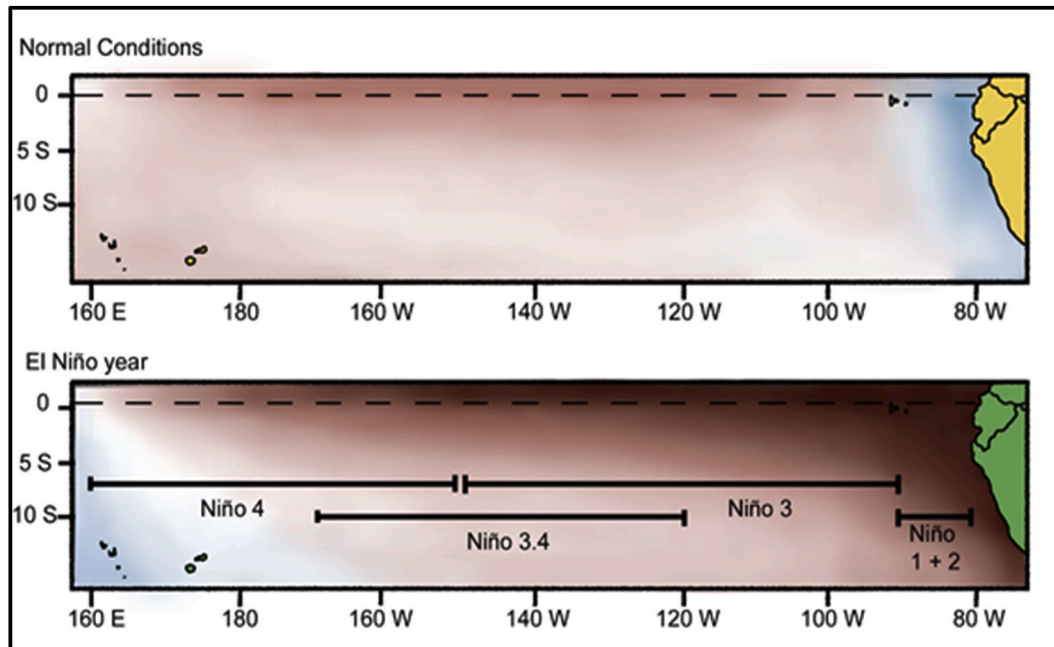
E-mail address: [pcsalazarz@gmail.com](mailto:pcsalazarz@gmail.com) (P. Salazar Zarzosa).

<sup>1</sup> <http://udep.edu.pe/>

<sup>2</sup> <http://www.uco.es/>.

**Box 1****El Niño Southern Oscillation in the Pacific Ocean****El Niño in a brief**

The El Niño event (EN) is a change in precipitation regimens with global impact effects. It is the result of abnormal changes in surface sea temperature (SST) in the Pacific Ocean and a shift in oceanic currents (from west to east). This phenomenon starts with an unexpected increase in SST in the Pacific Ocean, and the weakening of the Humboldt Current. At a global scale, this event produces short term changes (6–12 month) in precipitation regimens in America, Oceania and Asia. Locally, the increase in SST increase evapotranspiration and precipitation in the North Peruvian coast. To model the SST anomalies, the Pacific Ocean is studied in regions from the west (region 4) to the east (region 1 + 2). The North Peruvian coast is considered the “Ground Zero” area of impact of EN due to its close proximity to the region 1 + 2.



Recently, these events have been classified according to the location of the peak SST anomalies. Peak anomalies in the far eastern Pacific (100–80W) are referred to as Eastern Pacific (EP) El Niño, whereas peak anomalies at 180° longitude are referred to as Central Pacific (CP) El Niño (Kao and Yu, 2009). The extended area of impact, intensity, atmospheric interaction and frequency are different for each type of EN, and the methods proposed to identify them are still under debate (Wang et al., 2017).

during the El Niño increases air humidity and temperature, drastically altering abiotic conditions for plant growth (Grimm and Tedeschi, 2009; Holmgren et al., 2001; Soden, 2000) (Fig. 1). Climatologists, oceanographers and ecologists have invested time and effort to monitor the North Peruvian Pacific coast which is the epicentre of EN studies and its effect on vegetation. The El Niño is one of the most prominent inter-annual climatic variation sources in the planet. Therefore, the North Peruvian dryland forest is one of the best ecosystems to study the responses of plant physiology, growth and ecology to erratic precipitation regimens.

Within its native distribution, the potential of algarrobo to grow in stressful conditions provides ecological, environmental, and financial benefits for humankind. The leaf litter production and large canopy area create a micro-environment suitable for high microbial activity that increases soil fertility (Salazar et al., 2019a, b, 2020). While a wide range of metabolites from the pods and leaves have been found for the pharmacological and food industry.

Despite the relatively high number of publications on algarrobo, the amount of scientific knowledge is clearly insufficient. Currently, algarrobo populations are being depleted by illegal logging, pests, and changes in land use (Zorogastúa Cruz et al., 2011). In South America, this species is considered as the tree genetic resource at the highest risk

(van Zonneveld et al., 2018). An assessment of the ecosystem services and financial opportunities of algarrobo needs to be carried out to highlight its importance and being used to support initiatives to preserve the species and the people whose livelihoods depend on it (Larrauri García and Saura Calixto, 2000; Pasiecznik et al., 2001).

Our main goal is to review the current state of the art of algarrobo ecology in the scientific literature and explore what are the main thematic axes highlighting the most studied subjects and pinpoint the current lack of knowledge in some areas to fully understand algarrobo ecology. Ultimately, we will (1) describe the current geographic distribution of algarrobo and the evolutionary theories that led to it; (2) analyse the spatial and temporal variability of algarrobo associated with its population plasticity and describe the ecophysiological adaptations related to extreme conditions; finally, (4) we explore the most recent findings in ecological, environmental, and economic benefits that Algarrobo provides as ecosystem services. To avoid any potential bias made during the literature screening and provide an objective statistical analysis, we use a text mining approach to analyse the relevant topics. Additionally, we used data from the Global Biodiversity Information Facility (GBIF) and the CABI's Invasive Species Compendium to explore the distribution of algarrobo alongside the available scientific literature. We expect this review provides a general overview of the research done



**Fig. 1.** *Prosopis pallida* dryland forest during normal (dry) climatic conditions (left), and El Niño 2017 climatic conditions (right) in the Sechura desert (Northern Peru).

in algarrobo so far, and how these topics are connected between them.

## 2. Materials and methods

### 2.1. Literature review

To carry out an impartial assessment of the main thematic axes of the state of art on *Prosopis pallida*, we carried out the literature search in the online databases Web of Science Core Collection (Philipps University of Marburg subscription, WoS), Google Scholar (GS) on January 11, 2021. On WoS, we searched for the words “Prosopis” AND “pallida” within title/keywords/abstract and on GS (free access) we used the words (*Prosopis pallida*) within parenthesis. We complemented the search of WoS with a search on GS which is known to be a super set of WoS and Scopus and consistently exhaustive across several subject categories (Gehanno et al., 2013; Martín-Martín et al., 2018). We also carried out literatures searches in both CABI – Invasive Species compendium (<https://www.cabi.org/isc/>) and the Scopus database to complete our results.

The searches resulted in a total of 103 and 8460 accessions for WoS and GS, respectively. References from WoS were manually revised in EndNote, 71 remained after excluding 32 references which were not strictly related to *Prosopis pallida*. References excluded publications containing either term of the species name (*Prosopis* or *pallida* only) which referred to different species entirely, and publications where algarrobo was not the main focus (i.e., animal behavior, chemical characteristics or ecological characteristics of forages, vegetation composition and structure, and bird ecology). Publications containing the species name in the title or abstract were automatically included, when this was not the case, the whole publication was revised to assess whether *Prosopis pallida* was an important component or whether it was analysed. The GS engine ordered the 8460 accessions based on relevance, language, speed access, and location. The GS result was browsed in this order and contrasted with the list obtained from WoS to check whether any new reference was obtained. In GS, after 250 articles, the results obtained showed only documents where the keyword “Prosopis pallida” only appeared in the reference section. After reviewing the GS results, a total of 25 references were added from GS to EndNote. The CABI results found 38 articles, the list was manually explored and only 5 new articles were found and added to our database. Finally, the Scopus

database found 128 results, among which 35 were not related to “*Prosopis pallida*” and 73 were already in our database. The remaining 20 articles had a title and abstract in English, but the main article was on a language different from English. Regardless we decided to include them to get a full overview of the research in *Prosopis pallida*. Finally, the results using the different search engines (WoS, GS, CABI, and Scopus) gave the total of 121 references.”

These references were exported (Annotated) with RTF extension and standardized in Microsoft Word, e.g., by replacing tab (special) characters for empty spaces and eight abstracts reformatted (e.g., removing subheadings or split paragraphs). Finally, six out of 96 references did not have an abstract and were removed (i.e. Bragg, 1982; Sharma et al., 1993), thus leaving a total of 90 publication abstracts for the analyses.

### 2.2. Statistical methods

To categorize the current literature into the most relevant research about *Prosopis pallida*, we combined a text mining approach with a joint cluster-ordination *sensu* (Muenchow et al., 2018). We detected clusters of the most relevant topics, for guiding the review and avoiding biases, using *k*-means clustering. Cleaning of the abstract list involved the removal of stop words (e.g., abbreviations and connectors) and special characters (e.g., punctuation, digits and symbols) as well as word stemming (e.g., removing or reducing derived words). This cleaning process resulted in a word-matrix with 2293 columns which represented the stemmed words and 95 rows which represented the publications, where the matrix cells indicated the number of times a word was found in the abstract of each publication. Text cleaning and management were carried out using the R packages striptrf (Mori, 2019), tm (Fienerer and Hornik, 2019), tidyverse (Wickham, 2009), and data.table (Dowle et al., 2019). A detrended correspondence analysis (DCA, Hill and Gauch, 1980) was carried out using the obtained word-matrix with the command decorana from the R package vegan (Oksanen et al., 2019) down-weighting the rare occurrences to reduce the influence of rarely occurring words. This ordination method is used to reduce dimensionality and to obtain a low-dimensional representation of the word-matrix (2–3 axes generally). After that, we applied *k*-means clustering to the ordination scores to find homogeneous groups within the word-matrix. We use the command fviz\_nbclust from the R package NbClust (Charrad et al., 2014) to estimate the optimal number of clusters from the



word-matrix variance. This method finds groups by minimizing within-cluster variation (James et al., 2013), by computing the total within-cluster sum of squares (wss) for each run, for a total of self-defined 10 clusters. The number of adequate clusters was chosen by visual inspection of the wss as a function of clusters (Supporting information, Fig. S1A). Complementarily, we run the same analysis using a different clustering method (Average silhouette method) and the output was similar (Supporting information, Fig. S1B). Afterwards, we assigned each abstract to a group. For that, when an abstract was constituted by a high number of words characterizing a particular group then it was assigned to it. A list of papers assigned to each group is included as supporting information (Supporting information, Reference group list file). All selected articles were read and reviewed base on the cluster they belong, the objectives they achieved, and their results to compile our manuscript.

To complement the information of the resulting cluster related to geographical distribution, we retrieved information on the current occurrences of *P. pallida*. We used data from the Global Biodiversity Information Facility (GBIF) to explore algarrobo distribution alongside the available scientific literature. A total of 3536 occurrences were available in (GBIF.org, 2020) and were distributed across 16 countries (downloaded on January 19, 2021). The cleaning process involved the removal of occurrences without geographical coordinates (274), occurrences with low coordinate precision (17), and occurrences with an unknown basis of record or registered as a living specimen (2); which resulted in 3243 coordinates across 10 countries (Australia, Bolivia, Brazil, Ecuador, Papua New Guinea, Peru, Puerto Rico, Timor-Leste, United States of America, Virgin Islands (U.S.)). Additionally, we retrieved information on the current occurrences of *P. pallida* according to the CABI invasive species compendium (<https://www.cabi.org/isc/>, updated 17 Feb 2021). A list of 20 countries were obtained including Botswana, Cabo Verde, Djibouti, Kenya, Mauritania, Senegal, India, Israel, Jordan,

Hawaii (U.S.), French Polynesia, and Colombia that were not found in the GBIF database. References to the GBIF and CABI datasets providing distribution data are included (Supporting information, GBIF Distribution reference data file and CABI Distribution reference data file). Occurrence data was cleaned using the R package CoordinateCleaner (Zizka et al., 2019). All statistical analyses were carried out with the statistical software package R (R Core Team, 2017).

### 3. Results and discussion

#### 3.1. Main research topics on *Prosopis pallida*

We obtained a DCA ordination with three clusters explaining 61.7% of the total variance observed in the word-matrix in the first two axes: Ecophysiology and population plasticity (Ecophysiology & Pop plast), Geographical distribution (Geog dist) and Ecosystem services (Ecos services, Fig. 2). The first axis encompassed a trade-off between basic and applied research on *Prosopis pallida*. The second axis reflects a general ecological gradient of algarrobo related to the geographical distribution and the ecophysiology and population plasticity (Fig. 2). We reviewed the papers of each cluster to illustrate their differences. The cluster “Geog dist” covers mainly papers focused on algarrobo geographic distribution, its taxonomic identification through genetic markers, and land cover. Most of those papers deal with the genetic variability of algarrobo and its morphological characteristics. The cluster “Ecophysiology & Pop plast” covers papers related to algarrobo tolerance to aridity, its root characteristics to uptake groundwater, and nitrogen fixation. The third cluster “Ecos services” contains papers focused on the chemical compounds located in the fruits and seeds, other industrialisable products, and nutritional value. We used these main clusters to guide the review of *P. pallida*.

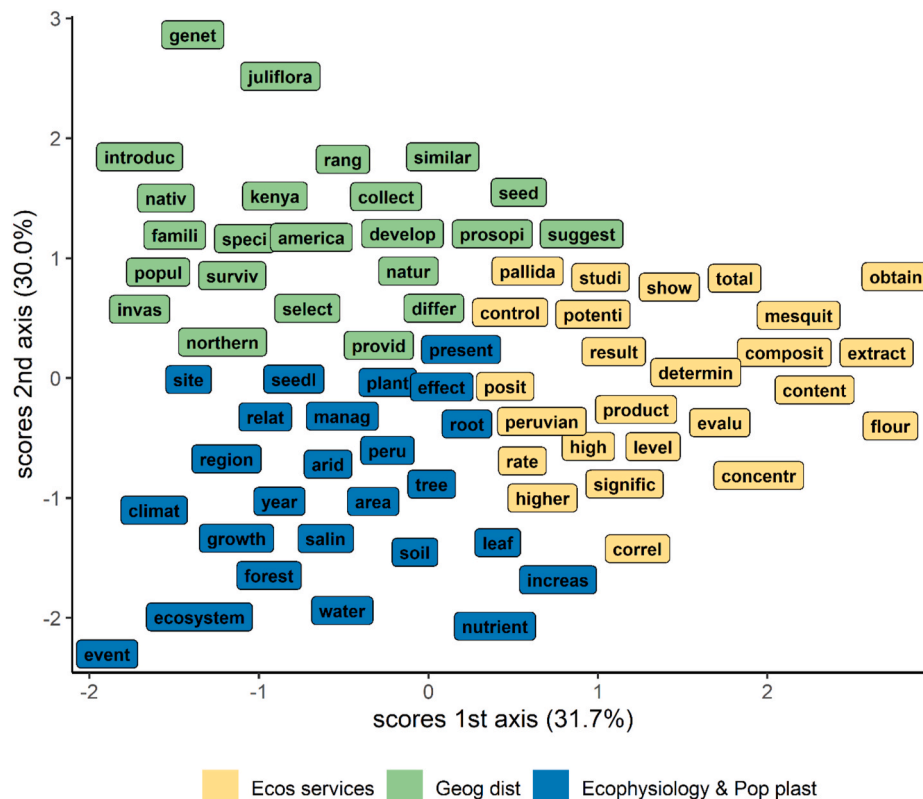


Fig. 2. Detrended component analysis (DCA) biplot displaying *k*-means clusters and showing two main axes (and their eigenvalues). The DCA portrays abbreviations for the 25 most frequent words for each cluster class (full names are included in the Supporting information, Table S1). Cluster class abbreviations represent, Ecophysiology & Pop plast: Ecophysiology and population plasticity, Ecos Services: ecosystem services, Geog dist: geographical distribution.

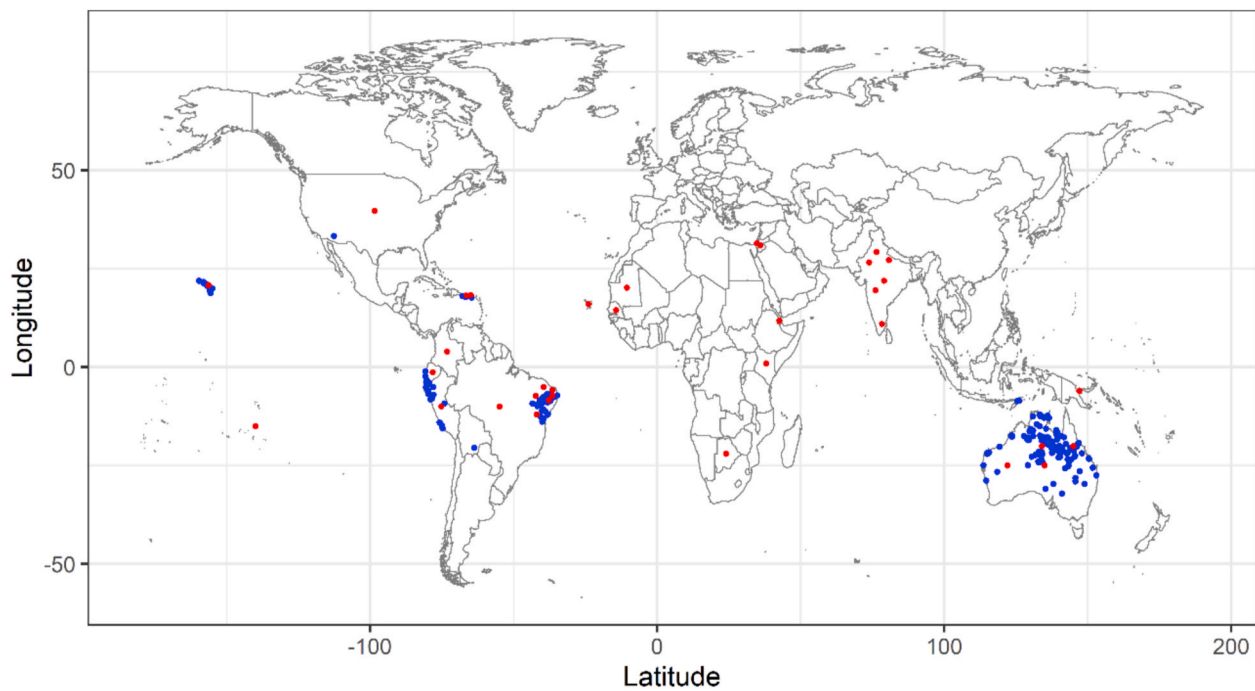


Fig. 3. Occurrences of *P. pallida* registered in the Global Biodiversity Information Facility (GBIF) website (blue dots), and the CABI Invasive Species Compendium (red dots) updated to 2020 and 2021, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### 3.2. Geographical distribution

The algarrobo belongs to the *Prosopis* L (Fabaceae) genera, it is a tropical legume species native to arid and semi-arid areas of South America, mainly along the coast of Peru, Ecuador and Colombia (Pasicznik et al., 2001). Molecular analyses have shown that the algarrobo originated evolutionarily from the mesquite clade, which includes *P. pallida*, *P. chilenses* and *P. ruscifoliae* because of their morphological similarity and overlapping geographical distribution in the South American coast (Burghardt and Espert, 2007). Genetic and morphological results indicate that the first separation between these groups may have occurred during a substantial marine incursion in the early Miocene on the Pacific coast. Thus, the high tolerance to saline content in soil and water could have led to a speciation in the Peruvian and Ecuadorian coast when part of the South American surface was partially covered by the sea (Palacios et al., 2011). Although the sea retreated during the Andean uplift, the trait which allows algarrobo to tolerate salt was preserved. Archaeological remains suggested that the process of diversification occurred in the late Miocene (Catalano et al., 2008). It is still unclear how the El Niño event played a role in the algarrobo evolution. The oldest El Niño event is dated back to 38000 years ago during the late Pleistocene (millions of years after the arrival of Algarrobo to the South American coast, Keefer et al., 2003). The survival and reproduction of drought-adapted genotypes might have been perpetuated during the El Niño events, which probably provided enough fresh water to keep populations alive, just as it does now (Holmgren et al., 2001). However, the species only became common during and after the Formative period (1000 BC) because of major human management consolidation (McRostie et al., 2017). Therefore, anthropogenic pressure was likely relevant during the early geographic distribution of algarrobo.

Currently, its geographic distribution at both sides of the South Pacific coast (Fig. 3) seems to be related to the occurrence of El Niño (Pasicznik et al., 2001). The constant change between dry and wet periods due to this climatic event create two alternative states which promote survival and growth strategies, respectively (Holmgren et al.,

2001). With such substantial and constant changes, the algarrobo developed physiological and morphological adaptations to survive under drought years and to grow after flood events. Although its distribution is native to the drylands of South America, this species is considered naturalized as well as invasive in some areas within the Americas as well as other continents. Nevertheless, the current distribution of algarrobo needs careful revision, since only relatively recent it was unambiguously recognized as a distinct taxon through functional, morphological, and molecular approaches (Palacios et al., 2011). Due to previous common confusion with *P. juliflora*, algarrobo was included in the complex *P. pallida* - *P. juliflora* (Pasicznik et al., 2001), thus creating uncertainty as to whether reports of commonly found *P. juliflora* are *P. pallida* indeed (Oliveira et al., 2018). Although these two species coexist in habitats where they are considered invasive, *P. juliflora* has a wider native distribution than algarrobo (Burkart, 1976). Several studies have shown that hybrids between these two species can be found in Peru, Ecuador, India, and Australia (Gallaher and Merlin, 2010; Landeras et al., 2006; Trenchard et al., 2008). These are more common in the non-native range of these species, and could have an ecological advantage over native species to grow and survive (Van Klinken et al., 2006). Considering all these aspects, the suggested distribution of algarrobo (Fig. 3) can be clustered in 4 geographic groups located in Peru, Brazil, Hawaii, and Australia. All of which have been documented before, even with molecular studies to distinguish it from *Prosopis juliflora* (Castillo et al., 2020; Gallaher and Merlin, 2010; Landeras et al., 2006; Palacios et al., 2011).

The high intraspecific variability of algarrobo has allowed it to expand its geographic distribution, and it is considered an invasive species in both Australia and the Caribbean islands (Gallaher and Merlin, 2010; Shackleton et al., 2014). Invasions of algarrobo are known to have taken place in areas such as the threatened semi-arid region of Brazil -the Caatinga, where seeds were introduced (Oliveira et al., 2018), in the Pacific Islands, more specifically in Hawaii (Gallaher and Merlin, 2010), and in Australia, where it is considered highly invasive (CABI, 2020). The high degree of invasiveness of this species in Australia has prompted research to find a biological control agent (Donnelly,

2002) or to understand mechanisms facilitating dispersal (Lynes and Campbell, 2000). According to our results, *P. pallida* populations have been recorded as well in Bolivia, Puerto Rico, the Virgin Islands (USA), Papua New Guinea and Timor-Leste (GBIF.org, 2020). According to the Centre for Agriculture and Bioscience International (CABI, 2020) the presence of algarrobo has been also reported, with few occurrences, in Jordan, Israel and India; it has been reported as localized in Colombia, Kenya and Papua New Guinea; and as introduced in French Polynesia, Senegal, Mauritania, Djibouti and Botswana; and not only introduced but also widespread in Cabo Verde. Whenever invasive, algarrobo is suggested to have certain detrimental effects on the local ecology (Dudley et al., 2014; Nelson-Kaula et al., 2016). For instance, it is speculated it negatively affects the availability of underground water, given its capacity to develop a very deep root system (Burnett et al., 2015; Dudley et al., 2014). Currently, Algarrobo is planted in all the places where it has been introduced. With the exception of Botswana, Djibouti, India, Puerto Rico, USA, Hawaii, Australia and Brazil where it grows naturally (CABI, 2020, Fig. 3), meaning that its value as a hardwood resource is recognized.

Although the worldwide distribution of algarrobo is becoming more and more widespread, the distribution in its native habitat (e.g. Peru) is being threatened by anthropic pressure and habitat conversion (Pasicznik et al., 2004), thus efforts for its conservation are being carried out by local organizations, particularly in Peru by the National Forestry Service (Andina Noticias, 2016; Serfor, 2015, 2020). In this context, specific knowledge of the ecology of algarrobo has become relevant, such as its reproductive biology (Alban et al., 2002; Ramesha et al., 2016), as well as its symbiotic properties with rhizobia for the enhancement of seedling survival (Räsänen et al., 2001).

In this context, population ecology studies in its native range are urgently needed. Research needs to answer questions aiding the undertaking of corrective actions by the stakeholders. What are the current main threats for the algarrobo? What is the effect of illegal logging on the population structure of algarrobo? How does indiscriminate extraction affect the maintenance of healthy populations of the species? What is the minimum viable population size of this species? Furthermore, interdisciplinary research connecting social and ecological research should assess the social and economic value of this resource and its appreciation by the human population, to understand ways to educate it and highlight their role in the protection of this iconic species.

### 3.3. Ecophysiology and population plasticity

#### 3.3.1. Temporal variability and population plasticity to extreme events

The algarrobo is able to change its physiology and morphology to persist under drastic and opposite climate changes (Fig. 1, Reed et al., 2011). As such, the phenotypic plasticity of the species is reflected by the wide range of phenotypes formed from a single genotype as a function of the stochastic climatic conditions (Nicotra et al., 2010). Dendrochronological analyses indicate that algarrobo growth can change drastically during El Niño events, when basal area growth increases fourfold that of average years in the South American Coast (Salazar et al., 2018a).

At the population scale, the effect of extreme dry and wet seasons on algarrobo growth produces massive changes in total plant biomass (Holmgren and Scheffer, 2001; Pablo C. Salazar et al., 2019a, b). Differences between these seasons create “alternative stable states of biomass”, that is sudden transitions from one state (low plant growth) to the other (high plant growth) instead of a gradual response to changes in water availability. As a perennial tree, algarrobo adaptation for survival and growth requires either highly variable physiological traits (with high phenotypic plasticity) or exceptional traits that are adequate at both seasons.

Early dendrochronological data showed distinct growth rings in tropical species, despite the lack of a high intra-annual climate variability (Boninsegna and Villalba, 1989). Results on *Prosopis* species also showed this trend (Villagra et al., 2005), and dendrochronological

records in *Prosopis pallida* followed the global pattern of EN-induced precipitations (Rodríguez et al., 2005). That is, a high vascular cambium activity leading to thick tree-rings formation (López et al., 2005). Many scientists have tried to record previous El Niño events to understand the ecological response of algarrobo to water availability at the population level in both coast of the Pacific Ocean (Dai and Wigley, 2000). They concluded that water pulses increase plant growth and tree recruitment (López et al., 2006); however, rainfall seasonality and its interaction with temperature plays an important factor. As such, water pulses outside the growing season could reduce seedling survival and growth (Squeo et al., 2007).

Marine sediments, mollusc shells and ice cores have been used to date El Niño events during the last 20 000 years (Henderson et al., 1999; Rein et al., 2005). In modern times, sea surface temperature, photosynthetic pigments, and dendrochronology records have been used to record the occurrence and intensity of El Niño in the South American Coast (Cook et al., 2013; Garcia-Herrera et al., 2008; Rustic et al., 2015). Overall, dendrochronological studies generally support that El Niño represents the most important climatic event in South America, alongside the Pacific decadal oscillation and the Antarctic oscillation (Boninsegna et al., 2009). However, a significant correlation between annual (or seasonal) precipitation and tree-ring width has been rarely found (Pereyra Espinoza et al., 2014; Salazar et al., 2018a). Differences between populations suggest different degrees of adaptation to water availability and propose that high population plasticity is associated with highly variable environments. Algarrobo populations in the Northern Peruvian dryland forest, the core terrestrial area of EN, have provided insight on the matter. Yet, most studies fail to find a quantitative meaningful relationship between water availability and plant growth. A few methodological, statistical and ecological reasons are explained in the following.

**3.3.1.1. Tree-ring data and El Niño events do not have the same time resolution impact.** In general, tree-rings provide two-dimensional data in annual resolution. The tree-ring width is mostly related to the amount of water available, then the whole tree-ring series can be cross dated with historical records or large climate series to calculate the yearly growth for each tree-ring. During no-EN years, water availability should be related to the total annual precipitation and plant growth. However, El Niño events have stochastic effects at lower resolution. Certainly, the total monthly precipitation during El Niño can be many folds higher than the total annual precipitation of no-EN years in the South American coast. But in addition, floods associated with the El Niño elevate soil water above field capacity and may create prolonged root hypoxia. Therefore, rain intensity at a monthly resolution during an El Niño event is key to understanding its beneficial or detrimental effect on plant growth. However, changes in precipitation at this resolution are not detectable in tree-ring data.

**3.3.1.2. Different types of El Niño events.** Climatologists often say “no two El Niño events are quite alike” (Wyrski, 1975), and as such, precipitation distribution, and plant growth, cannot be easily correlated without time-space analyses. Anomalies in the Sea Surface Temperature (SST) of the Pacific Ocean are responsible for the duration and precipitation rate of EN. The Pacific Ocean is split into the 4, 3.4, 3 and 1 + 2 geographic regions (box 1) to monitor changes in the Humboldt Current and the Walker circulation. Currently, two types of El Niño events have been considered based on the region of origin of the SST anomalies (Wang et al., 2017). Variations in the region 3.4 are considered the cause of the Central EN, whereas variations in the region 1 + 2 are considered the cause of the Easter El Niño (Box 1). A time reconstruction of the anomalies at each region alongside both types of events clearly supports this claim (Fig. 4A–D). Algarrobo tree-ring index reconstructions (Fig. 4E–G) from the coast (E) to the inland territory (G) in the South American coast, show that each type of event has different effects on

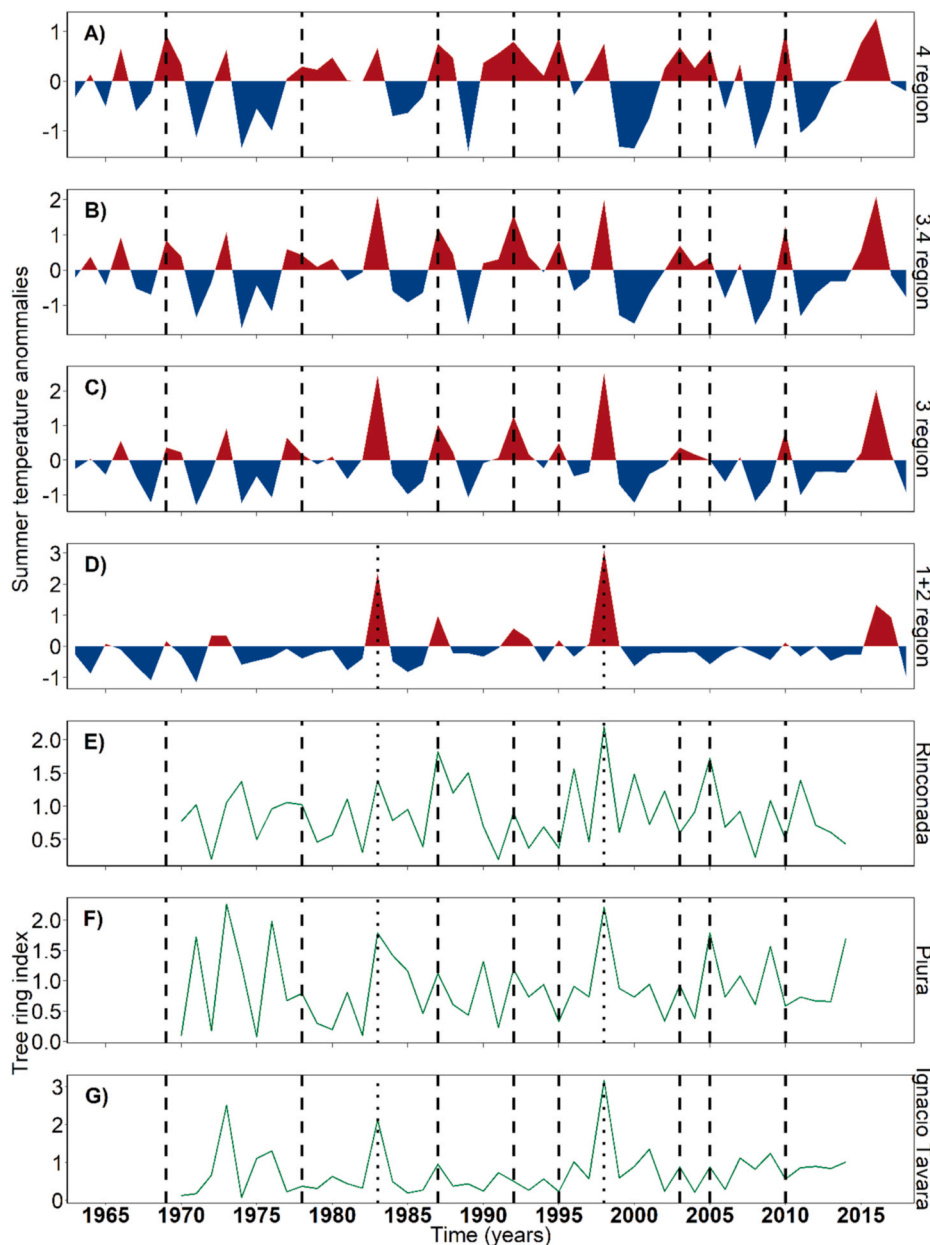


Fig. 4. Sea surface temperature anomalies during summer (January, February, and March) for the region “4”, “3.4”, “3”, and “1 + 2” of the Pacific Ocean (A), B), C), and D), respectively). Red and Blue colours indicate positive and negative anomalies, respectively, in reference to the mean temperature between 1981 and 2010. Dotted lines indicate recorded Eastern Pacific El Niño (1982-83 and 1997-98), and dashed lines indicate recorded Central Pacific El Niño (1968-69, 1977-78, 1986-87, 1991-92, 1994-95, 2002-03, 2004-05, and 2009-10) across all figures. Tree ring index of three *P. pallida* populations from the coast (E) to the inland (F and G) in the North Peruvian dryland forest showed how coastal populations growth responded to temperature anomalies, while inland populations only showed high growth during Eastern Pacific El Niño events. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

plant growth. Easter El Niño events have a higher positive effect on inland forests plant growth in comparison to Central El Niño events, while both Eastern and Central El Niño events have a positive effect on coastal populations. Therefore, the addition of multiple types of El Niño events, and different plant responses based on the proximity to the SST anomalies, increases the complexity of the relationship between algarrobo growth and the climatic conditions.

3.3.1.3. *Not enough data to include enough El Niño events.* Finding a relationship between algarrobo growth and El Niño requires climate data with enough temporal timestamps to contain several El Niño events on it. The National Oceanic and Atmospheric Administration (NOAA) keeps a public record of the main Pacific Oceanic indexes since 1900. However, this period does not provide more than 20 El Niño events at best, which eventually should be split between different types of El Niño events based on the anomaly origin. The algarrobo lifespan is also limited for dendrochronological studies. Natural individuals can live 100 years on average (Rodríguez et al., 2005); however, tree samples from the XIV and XVIII centuries showed a 50-year lifespan (Salazar

et al., 2018a). Crossdating (the statistical process that confirms the time overlap between two samples) requires a long-time tree-ring series to show meaningful results. Therefore, an enormous amount of field work is required to make reliable dendrochronological reconstructions. Alongside, other climatic proxies like isotope concentration from ice core samples or stalactites are necessary to reconstruct the El Niño event back in time (Rustic et al., 2015).

We should reconsider whether tropical dendrochronology is able to quantify El Niño events. Additional analysis, like wood densitometry and dendrochemistry may provide complementary information with seasonal resolution. For instance, high wood density in early May indicates higher precipitation rate in spring, while high Ca accumulation in late wood may suggest dry conditions in summer. Algarrobo dendrochronology is expected to produce long climate data reconstructions from archaeological samples (Ghezzi and Ruggles, 2007). However, before going any further, additionally analyses are required before using dendrochronological data from Algarrobo as a probe of El Niño frequency and intensity.



### 3.3.2. Ecophysiology (physiological response to extreme conditions)

The *Prosopis* genera is commonly known for its resistance to water stress. Its phreatophyte root system provides continuous access to water from the water table, while shallow lateral roots absorb water from precipitation events (Scott et al., 2000). In theory, root development determines the main source of water accessible for the plant, and subsequently, affects the relationship between Algarrobo growth and precipitation (Dudley et al., 2014). As such, root biomass allocation to absorb underground water is one of the main features to secure plant growth during dry years (Villagra and Cavagnaro, 2006) and during early stages of plant growth (Khazada et al., 1998; Salazar et al., 2019a, b). High plasticity in water consumption traits and root biomass partitioning seem to be associated with growth under low and high-water availability (Salazar et al., 2019a, b).

To avoid water stress during drought and maximize plant growth during El Niño, algarrobo exhibits anisohydric stomatal control (Miyazawa et al., 2016). That means that it can keep its stomata open and sustain high photosynthetic rates at the risk of reducing leaf water potential (Sade et al., 2012). To balance leaf gas exchange traits against hydraulic limitations, leaf transpiration is restricted by maintaining a high intrinsic water use efficiency (net photosynthetic rate per stomatal conductance, Miyazawa et al., 2016). This strategy reduces photosynthetic rate limitations and increases carbon gain during dry conditions (Salazar et al., 2018b); however, it comes with high risk of cavitation. As a consequence, structural adaptations in the xylem anatomy have been associated with drought resistance to reduce hydraulic failure (López Lauenstein et al., 2012). A significant reduction of vessel size in the xylem anatomy of algarrobo has been found to avoid cavitation in the hydraulic system (Sperry et al., 2008). Furthermore, a high vessel density (number of vessels per millimetre) have been found associated with higher hydraulic conductivity and lower risk of vulnerability to embolism (Martínez-Vilalta et al., 2012; Palacios, 2017).

Changes in leaf structure are a fundamental response to dry conditions. For instance, a significant reduction of leaf size to reduce transpiration water loss and leaf temperature at expenses of productivity has been described in algarrobo (Dudley et al., 2014; Salazar et al., 2018b). The leaf mass per area (LMA) is a morphological trait that describes the carbon biomass invested in the photosynthetic activity, and it is highly sensitive to environmental changes. A low LMA is related to a low construction cost and a high photosynthetic rate but low leaf longevity (Villar and Merino, 2001), whereas a high LMA implies the contrary (Wright et al., 2004). The relationship between LMA and the net photosynthetic rate represents the basis of the leaf economic spectrum theory, which describes the trade-off between resource consumption and acquisition strategies in the leaf (Wright et al., 2004). Under dry

conditions, leaf cells are generally smaller and compacted, which increase leaf density and LMA (Poorter et al., 2009). In algarrobo, there is a negative relationship between LMA and photosynthetic rate which indicates that leaf functioning follows the leaf economic spectrum theory (Salazar et al. 2018a, b). A tendency to increase resource consumption by maximizing photosynthetic rate and reducing LMA can be seen by overlaying algarrobo data with leaf physiology data collected worldwide for many species (Fig. 5). This overlap indicates that algarrobo leaf morphology should be highly sensitive to environmental factors. However, other studies suggest that LMA in algarrobo is not affected by drought (Dudley et al., 2014; Salazar et al., 2019a, b; Vilela et al., 2003). This odd finding contradicts a large body of literature built on functional traits (de la Riva et al., 2016; Moore et al., 2020; Niinemets, 2001). Tentatively, it is possible that the algarrobo anisohydric stomatal control is associated with its functional traits because stomatal regulation has implications for balancing carbon acquisition, as we already mentioned. Functional traits associated with the anisohydric response require a predisposed leaf morphology with high stomatal density, high leaf turgor, and high LMA (Meinzer et al., 2017). As such, algarrobo water balance could be controlling leaf morphology to respond to fluctuating climatic conditions. Alternatively, it is possible that LMA (and the leaf carbon balance) does not play a significant role in the plant water status, and it is unresponsive to drought. Even though there is evidence to suggest this, it is unclear how LMA can have a high variability without being sensitive to water availability (Salazar et al., 2018b).

The likely ecophysiological oddities of algarrobo response need further addressing. In this regard, continuous monitoring of ecophysiological changes of permanent traits pre and post El Niño is key to provide in depth understanding of the actual changes and adaptations this species undergoes during El Niño events.

### 3.4. Ecosystem services provision

As the dominant tree species within its geographic distribution, algarrobo forests provide a physical barrier that protects the bare soil against environmental deterioration (Okin and Gillette, 2001). Under its canopy, soil humidity and air temperature is lower than normal, which creates a microenvironment more suitable for life (Berry et al., 2013). Accumulation of organic matter from leaf litter production promotes microbial activity and nutrient recycling (Salazar et al., 2019a, b; Salazar et al., 2020), while symbiotic relationships in the soil allow for N fixation and increase nutrient availability. In combination, these characteristics create a “fertility island” effect under the canopy, and it is a common environmental effect of most *Prosopis* species (Abril et al., 2009; Reyes-Reyes et al., 2007).

The intensity of the fertility island effect is tightly associated with the microbial activity and soil humidity, and it is dependent on the El Niño frequency and intensity (Salazar et al., 2020). During drought years, leaf litter decomposition is limited by temperature and humidity, even though it may partially happen by photodegradation (Austin and Vivanco, 2006), and as such, soil biomass accumulation under the canopy leads to little to non-significant increase in soil nutrients (Salazar et al., 2019a, b). Sporadic rainfall pulses of at least 30 mm can shift these conditions and activate microbial activity, germination, and decomposition temporally (López et al., 2008; Squeo et al., 2007). However, most of the ecological processes and environmental benefits associated with algarrobo are tangled with El Niño frequency (Holmgren et al., 2001). Soil respiration can be up to ten folds higher during El Niño, and double that amount under the Algarrobo canopy (Salazar et al., 2020). As such, these events bolster the algarrobo ecosystem services by improving soil quality, biodiversity and aiding ecosystem functioning.

The ecological benefits of algarrobo forests have been used as heavy arguments in reforestation and conservation programs in dryland ecosystems. Alternatively, other properties associated with its biology can be used to improve environmental conditions. High accumulation of

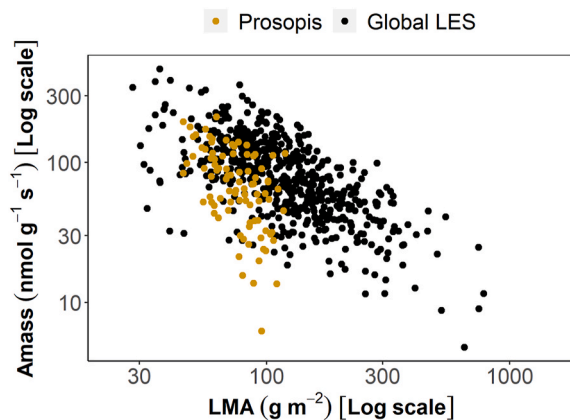
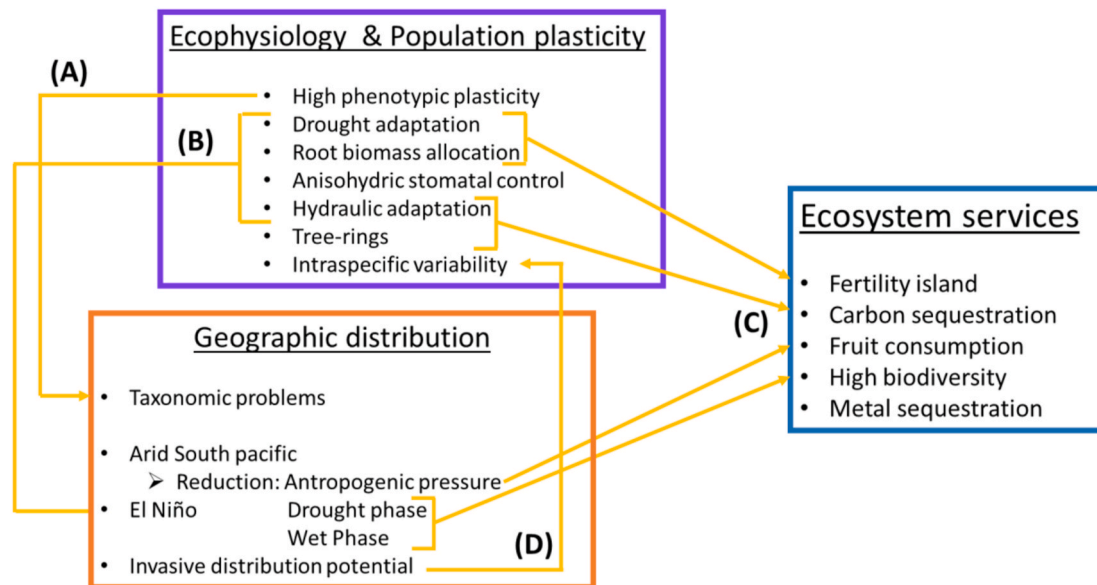


Fig. 5. Bivariate relationship between net photosynthetic rate ( $A_{mass}$ ) and leaf mass per area (LMA) for the global leaf economic spectrum (LES), and 8 *Prosopis pallida* populations in North Peru. Adapted from Wright et al., (2004). More details related to these populations can be found in Salazar et al. (2018b).





**Fig. 6.** Conceptual map of the key points from each cluster class in *Prosopis pallida*. (A) The high phenotypic plasticity and hybridization potential have created taxonomic problems to correctly identify its distribution. (B) El Niño event, and the ecophysiological adaptation towards it, have played an important role *P. pallida* evolution. (C) These traits are related with *P. pallida* survival and growth under these extreme climatic conditions, favouring several important ecosystem services for humanity in dryland ecosystems. (D) However, its invasive potential, related to its high intraspecific variability, has become a problem in some ecosystems.

Arsenic, Cadmium, and Chromium have been found in root and shoot tissues (Mokgalaka-Matlala et al., 2009; Santos-Jallath et al., 2012). Highly contaminated soils can be found across the South American coast, in countries such as Peru and Chile whose economies are largely sustained by the mining industry. The application of reforestation programs with this species in mining areas could add value to the environmental compensation activities carried out with rural towns. All in all, the biggest contribution of algarrobo to the environment is its capacity for carbon sequestration. The long dry periods that delay organic matter decomposition make the dryland ecosystems a relevant terrestrial carbon sink (Schlesinger and Andrews, 2000). Reducing Emissions from Deforestation and Forest Degradation (REDD+) projects to conserve and expand algarrobo forests are currently developed across the South American coast.

The algarrobo is the primary source of food, wood and well-being for rural communities within its natural distribution (Choge et al., 2007). One of the most sustainably exploitable features of the algarrobo is its fruit (algarroba), which is composed of 90% pod and 10% seeds (Marangoni and Alli, 1988). These fruits are very versatile and are used for human consumption and animal fodder (Gallaher and Merlin, 2010; Macias-Rodriguez and Usca-Mendez, 2017), given their high fibre and nutrient content (Choge et al., 2007). The seeds of algarrobo pods contain non-toxic thickening agents which have a potential application in the pharmaceutical and alimentary industries, further research needs to focus on how to efficiently obtain these compounds in an industrial setup and to assess their superiority to already established commercially agents (Bouttier-Figueroa et al., 2017; Chaires-Martinez et al., 2008). The fruit is also converted to flour, which is used as fodder for animals, for instance the cost-effectiveness of including it in the diet of rabbits has been demonstrated as it increased the weight of rabbits and reduced costs (Macias-Rodriguez and Usca-Mendez, 2017). In the case of human consumption, the flour has a high-protein content, thus it has been proposed to be used as an input to produce sweet bread (Bigne et al., 2018), it also has the potential to complement flour-based products to enhance flavour and aroma and it may also be appealing for the gluten-free market, with the appropriate marketing strategy (Bigne et al., 2018; Felker et al., 2003). In that framework, research has explored how cloning can be used to improve the production of highly palatable sweet pods (Alban et al., 2002). The pods have high fibre

concentration which provide them with the potential to be used as food ingredients (Bravo et al., 1998). Algarroba is a multipurpose fruit also used to create a dark-coloured bitter-sweet syrup called “algarrobina” (Choge et al., 2007), which can be purified without losing properties, for aesthetic and marketing purposes, to possibly broaden its usage in the food industry (Larrauri Garcia and Saura Calixto, 2000).

Several other research directed to the industrial exploitation of this resource have taken place, for instance, the trade-off between bacterial decontamination of the pods and the formation of a plausible carcinogenic (Fan et al., 2015), potential use of non-woody resources, such as exudates, as plasticizers (Gonzaga et al., 2019), and the exploration of the fruits antioxidant potential (Pinto et al., 2009). Given the ecological importance of algarrobo and its industrial potential, it is increasingly relevant to count with allometric equations to calculate above-ground biomass (Padron and Navarro, 2004) in the most accurate possible way; so that assessing native or introduced populations through remote sensing is facilitated (Padrón and Navarro-Cerrillo, 2007). The availability of such a tool would allow monitoring of this species currently and in the future to understand forest resources in native forests but also to control spreading of possible invasions.

All things considered, our results showed algarrobo studies are focused on (1) its geographic distribution (population identification through DNA analysis and invasive expansion); (2) its ecophysiological adaptation and plasticity associate to its long droughts resistance high temperature, and water pulses; and (3) the ecosystem services (fruit consumption, carbon sequestration, and nutrient recycling) that provides to humankind (Fig. 6). These three cluster are interrelated in many ways. Algarrobo geographic distribution depends on its ecophysiological adaptations and its population plasticity. The services it provides depends on its distribution. For instance, it can be considered as a symbol of soil fertility in the South American Pacific coast and source for commercial wood in the Caatinga, whereas it is considered an invasive pest in Hawaii and Australia (Gallaher and Merlin, 2010; Landeras et al., 2006). Our results also showed how these topics are related and how they have evolved. A basic-applied axis in scientific research in the first axis of our DCA suggest scientific questions can be driven by either the search of scientific knowledge or to achieve a practical benefit. A common dichotomy embedded in the way society perceive science and can be related to the core of the scientific funding programs. Future projects

should look for a common link between these two sides of science research to avoid the constant bidimensional division humankind seems to face in every aspect of modern life. Despite our best efforts to set a singular label for all the articles belonging to each cluster, some papers included within needs their own discussion as research gaps. Early studies around algarrobo were focused on seed germination through scarification to launch large scale reforestation programs in desert areas (Pasicznic et al., 2001). Mechanical, thermal, and chemical scarification treatments were applied to speed up and synchronize seed germination. Results showed that the sulphuric acid treatment was the best method and provides a 66% germination success in less than 10 days (Ramesha et al., 2016). The resistance to salinity has also been forgotten after been documented 4 decades ago (Felker et al., 1981; Velarde et al., 2003); however algarrobo susceptibility to Na toxicity seems higher when high nitrate is available which suggest high forest productivity will always be limited (Jarrell and Virginia, 1990). New research could still study germination treatments and irrigation programs to carry large scale reforestation programs, yet decision makers and national governments need to determine if these actions are possible, and whether they are willing to do it or not.

#### 4. Conclusions

In summary, algarrobo is a well-adapted species to extreme floods and long droughts. It is originally distributed in the Pacific South American coast, where years of evolution have shaped the plasticity of functional traits to deal with the dry phase of El Niño event. Its anisohydric stomatal control, and its morphological adaptations in vessel size and distribution secure water transport from the soil to the leaf in dry conditions without going through carbon starvation. This opportunistic behavior has allowed it to colonize new territories in America, Africa, Oceania, and the Caribbean islands. Its plasticity to extreme events is recorded in the tree-ring width and can be used as a proxy for climatic records. However, more work needs to be done to determine how it take advantage of the water pulse and tolerate hypoxia during El Niño events. Its ecological, economic and environmental benefits outweigh those of any other species in its native environment by increasing soil fertility and carbon sequestration. Algarrobo is key for the forestry development and life quality of rural life. Production of fruits, wood, and honey provide enough ecosystem services for the rural economy, which are strong arguments to encourage local decision makers to fund new sustainable opportunities to preserve and use this resource.

#### CRedit authorship contribution statement

**Pablo Salazar Zarzosa:** Formal analysis, Software, Writing – original draft. **Glenda Mendieta-Leiva:** Writing – review & editing, Software, Data curation, Investigation. **Rafael M. Navarro-Cerrillo:** Conceptualization, Investigation. **Gastón Cruz:** Conceptualization, Investigation. **Nora Grados:** Conceptualization, Supervision. **Rafael Villar:** Methodology, Supervision.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

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