

Mémoire

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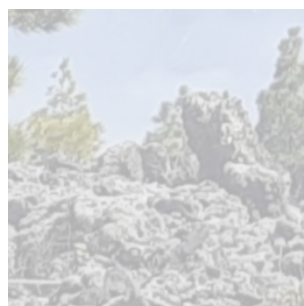
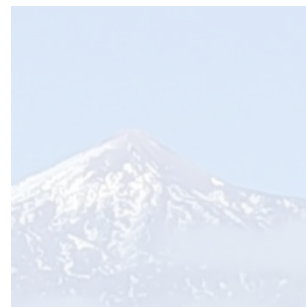
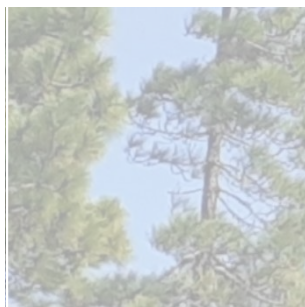
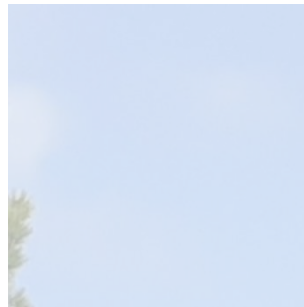
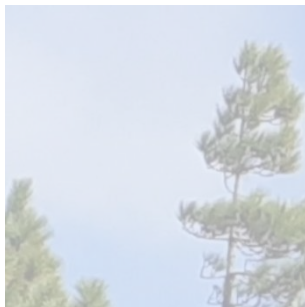
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What does render plant communities vulnerable to biological invasions? Testing Darwin's Naturalization Hypothesis in the Canarian pine forest.

Mémoire de fin d'études présenté par **Sébastien Mirolo** en vue de l'obtention du grade de Master en Biologie des Organismes et Écologie, à finalité approfondie

Sous la direction de Dr. Alain Vanderpoorten et Dr. Jairo Patiño Llorente



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Personal picture, Mount Teide and Canarian pine trees, Tenerife (Canary Islands)

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What does render plant communities vulnerable to biological invasions? Testing Darwin's Naturalization Hypothesis in the Canarian pine forest.

Supervisors: Alain Vanderpoorten, Jairo Patiño | August 2021, Biologie de l'évolution et de la conservation (aCREA) | MIROLO Sébastien

Abstract

Invasive species have been identified as one of the main threats to biodiversity. Oceanic islands are particularly vulnerable to invasions because their biota are characterized by a suite of syndromes, such as low competitive ability and loss of dispersal capacities, which have evolved in the island setting. C. Darwin (1809-1882) was among the firsts to draw hypotheses about the invasion process. He observed that alien species are more prone to establish in an ecosystem where no close native species are present. Indeed, closely related species would either share the same niche, and hence, have competitive interactions, or the pathogens and/or predators of a native species would be unlikely to shift onto a phylogenetically distant alien species (Enemy Release Hypothesis). Subsequent empirical support for this assumption has been equivocal, generating a conundrum known as Darwin's Naturalization Conundrum, which has opened a path for research on the mechanisms by which species become successful in a new environment.

This study aims at determining whether biological invasions can, in line with Darwin's hypothesis, be predicted from environmental features and/or characteristics of the native flora. We first determine whether environmental variation has an impact on the naturalization of alien, non-invasive and invasive species, i.e., whether some habitats are more prone to facilitate naturalization than others. We then determine whether the probability of invasion can be predicted from the taxonomic composition and life-history traits of native communities, i.e., whether some communities are, due to their taxonomic composition and/or life-history traits, more prone to biological invasions than others.

Community composition and life-history traits of spermatophyte species were recorded from 40 10x10m plots in the pine forest of Tenerife (Canary Islands). In total, 135 species were recorded, including 16 alien species, 8 of which are invasives. The data were analyzed using multivariate statistics and General Linear Models.

The relative abundance of alien species in Canarian pine forests was significantly related to environmental variables, supporting mounting evidence that environmental filtering is one of the strongest constraints determining variation in the vulnerability to introduced species of some communities as compared to others. Life-history traits, but not taxonomic composition of native species, were significant predictors of the presence of invasive species. This supports the idea that, while the taxonomic composition of the native community may not necessarily determine the opportunity of alien species to establish, the life-history traits of native species may be more important in the context of the niche pre-emption hypothesis as species sharing the same traits, regardless of their taxonomic identity, may be prone to competitive interactions. Despite retaining fairly high AUC values (>0.70) following cross-validation, the model predicting the presence of invasive species was characterized by high rates of false positives. This means that plots displaying the features that are characteristic for invaded plots, are not invaded yet, suggesting that the alien invasion of the Tenerife pine forest is an ongoing process.

Pourquoi les communautés végétales sont-elles vulnérables aux invasions biologiques ?

Test de l'hypothèse de naturalisation de Darwin dans la pinède canarienne.

Promoteurs : Alain Vanderpoorten, Jairo Patiño | Août 2021, Biologie de l'évolution et de la conservation (aCREA) | MIROLO Sébastien

Résumé

Les espèces invasives sont un des problèmes majeurs menaçant la biodiversité. Les îles océaniques, de par leur nature, sont particulièrement sensibles aux invasions, leurs écosystèmes étant caractérisés par toute une suite de syndromes ayant évolué dans ce contexte insulaire, tels qu'une faible compétitivité et une perte des capacités de dispersion. C. Darwin (1809-1882) fut l'un des premiers à émettre des hypothèses concernant le processus d'invasion. Il observa que les espèces aliens s'installaient plutôt dans des écosystèmes dépourvus d'espèces natives proches, car celles-ci pourraient partager la même niche écologique et donc entraîner une compétition entre elles, ou car les pathogènes et/ou prédateurs des espèces natives auraient moins de chances de s'attaquer à une espèce alien phylogénétiquement éloignée (Enemy Release Hypothesis). Ultérieurement, des preuves empiriques contradictoires de cette hypothèse furent à l'origine d'un débat connu sous le nom de Darwin's Naturalization Conundrum, qui ouvrit la voie à de nombreuses recherches sur les mécanismes de naturalisation des espèces dans un nouvel environnement.

La présente étude tend à déterminer si, conformément à l'hypothèse de Darwin, une invasion biologique peut être prédite à partir de données environnementales et/ou de caractéristiques de la flore native. Premièrement en déterminant si les variations environnementales peuvent expliquer la naturalisation des espèces aliens, qu'elles soient invasives ou non ; c-à-d si certains habitats sont plus susceptibles de faciliter la naturalisation. Deuxièmement en déterminant si la probabilité d'invasion peut être prédite à partir de la composition taxonomique et des traits d'histoire de vie de la communauté native ; c-à-d déterminer si certaines communautés sont plus susceptibles d'être envahies que d'autres de par leur composition taxonomique et/ou leurs traits d'histoire de vie.

La composition des communautés et les traits d'histoire de vie des espèces spermatophytes de 40 parcelles de 10x10m ont été recueillis dans la pinède de Ténérife (îles Canaries). Au total, 135 espèces furent répertoriées, comprenant 16 espèces aliens dont 8 invasives. Toutes les données furent analysées par statistiques multivariées et Modèles Linéaires Généralisés.

L'abondance d'espèces aliens dans la pinède canarienne fut significativement liée aux variables environnementales, étayant les preuves croissantes que le filtre environnemental est l'une des plus importantes contraintes à l'introduction d'espèces, expliquant la vulnérabilité de certaines communautés. Les traits d'histoire de vie, contrairement à la composition taxonomique des espèces natives, furent des indicateurs significatifs de la présence d'espèces invasives. Ce résultat soutient l'idée que la composition taxonomique des communautés natives ne détermine pas nécessairement la possibilité d'établissement des espèces aliens, tandis que les traits d'histoire de vie des espèces natives seraient plus importants dans le contexte de l'hypothèse de la préemption de niche : les espèces partageant les mêmes traits ont plus tendance à entrer en compétition, indépendamment de leur position taxonomique. Malgré des valeurs élevées d'AUC (>0.70) après validation croisée, le modèle prédisant la présence d'espèces invasives fut caractérisé par un haut taux de faux positifs. Cela signifie que certaines parcelles non-envahies ont les mêmes caractéristiques que celles envahies, suggérant que le processus d'invasion des pinèdes de Ténérife n'est pas terminé.

Table of content

1. Introduction	1
2. Material and method	8
2.1 Field sampling and environmental plot characterization.....	8
2.2 Characterization of the life-history traits of native species	8
2.2.1 Trait measurements	9
2.2.2 Literature survey	10
2.3 Statistical analyses.....	11
3. Results	14
3.1 Fieldwork results	14
3.2 Statistical analyses.....	15
3.3 Cluster analysis.....	18
4. Discussion	19
5. Conclusion	23
6. Appendices	24
Appendix 1 – CHELSA variables	24
Appendix 2 – Species encountered	25
Appendix 3 – PCA results.....	28
Topographic data PCA	28
Climatic data PCA	30
Coverage data PCA	33
Dispersal mode data PCA	35
DBH data PCA	37
Plant volume data PCA.....	39
Shape factor data PCA.....	41
SLA data PCA	43
LDMC data PCA.....	45
7. Bibliography	47

1. Introduction

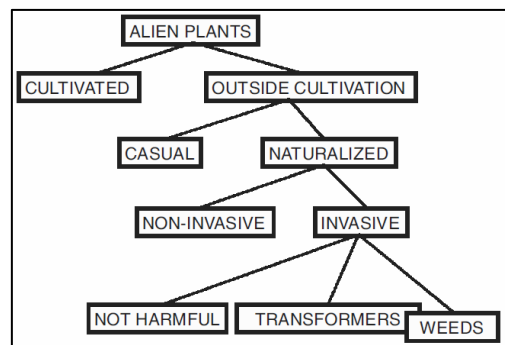
Invasive species all across the world are among the most important issues facing humankind nowadays (Reid, 2005) because of their impact on natural ecological processes and dynamics (Ehrenfeld, 2010; Vilà et al., 2011) and due to their socioeconomical consequences (Pimentel et al., 2005; Pyšek & Richardson, 2010). Alien species can drive local species to extinction by means of biotic interactions like interspecific competition and were reported as one of the most important threats for biodiversity (Bellard, Cassey, et al., 2016). The most important ways of introduction of alien species are mainly linked to trade: the concentration of alien species is high near airports and seaports and decreasing around them (Bellard, Leroy, et al., 2016; Hulme, 2009). Alien species especially spread through certain activities, such as horticulture (Bradley et al., 2012), terrestrial and aquatic exotic pet trade (Lockwood et al., 2019; Padilla & Williams, 2004), and transportation in ships ballast water (Bailey, 2015), among others (Hulme, 2009; Reaser et al., 2007).

The history of species invasion can be summarized into three different phases corresponding to periods when species were transported between regions of the world (Hulme, 2009). The first period is informally known as the Age of Discovery, at the end of the Middle Age (15th and 16th century), when Europeans rediscovered the American continent and started colonization and global trade (Preston et al., 2004). The Industrial Revolution is the second period, when the world trade rate increased sharply due to improvements in transport, with the construction of infrastructures like railways, canals and highways, but also with the invention of the steam engine that allowed faster shipment and the emigration of thousands of Europeans to other continents (Findlay & O'Rourke, 2007; McNeely, 2006). We entered the third period around 1950, the Era of Globalization, during which the goods could be exported and transported very quickly. The traceability is almost inexistant and, thus, no pest checks can be efficiently deployed (Hulme, 2009; Seebens et al., 2015). Even though the problem has been known for centuries, it was demonstrated that the number of alien species in every region of the world is increasing and will continue to do so in the near future (Seebens et al., 2017). Indeed, it has been predicted that the development of the world trade network with emerging economies will increase the communications between the currently mostly preserved territories with the rest of the world and lead to the introduction of alien species (Seebens et al., 2015). On the other hand, these newly connected territories have endemic species that could become invasive in other regions of the world, increasing the number of potential alien species as the network expands. At present time, it is not possible to predict which species may become invasive as a non-negligible fraction of the newly recorded alien species worldwide had never been reported before (Seebens et al., 2018).

Migration is part of the natural process in island ecosystems, new species arrive and colonize the region and the different available ecological niches, with often great diversification and the apparition of numerous endemic species through genetic drift (MacArthur & Wilson, 1967;

Whittaker et al., 2008). However, the introduction of alien species is a particularly big issue on islands, which are among the most invaded environments of the world and where many extinctions are due to these introduced species (Blackburn et al., 2016; Donlan & Wilcox, 2008; Whittaker & Fernández-Palacios, 2007). It has been shown that insular ecosystems are more susceptible to the effects of invaders than any other region of the world, and that invasive species are the main driver of population decline and species extinction in these regions, maybe also the most significant factor of environmental degradation (Reaser et al., 2007). All the ecosystem can be deeply modified by those invaders, not only by competition with local species but also by replacing keystone species and, therefore, by eliminating a series of ecological niches and creating new ones facilitating the naturalization of other aliens (Asner et al., 2008; Reaser et al., 2007). The underlying mechanisms of invasion are different between islands and mainland because of the insular ecosystem dynamics itself. For example, the number of taxa is limited to those that can naturally reach the island. Island species subsequently evolve a series of life-history traits known as the island syndrome, such as the loss of competitive ability and decrease of dispersal capacities, making them very vulnerable to fast-spreading alien species (Reaser et al., 2007; Richardson & Pyšek, 2006).

The first study to focus on biological invasions and to provide hypotheses on the mechanisms underlying naturalization of alien species was published in 1958 by Charles Elton, whose predictions extended to higher risks of damage for island ecosystems (Cadotte & Colautti, 2005; Elton, 1958; Richardson, 2011). Since this first attempt, numerous studies were conducted independently about the subject, sometimes using confusing terminology (Blackburn et al., 2011). The classification of alien plants and the definition of their different categories now widely accepted in the field of invasion biology (Occhipinti-Ambrogi & Galil, 2004; Pyšek et al., 2004; Richardson, 2011; Richardson et al., 2000) are illustrated in Figure 1 and Table 1, respectively.



1 - Hierarchical scheme proposed by Pyšek et al. (2004) for the classification of alien plants. See Box 1 from the original paper for definitions of terms not included in Table 1.

Table 1 – Definition of species status and origin in invasion biology

	Definition
Native species	“Species that have evolved in a given area or that arrived there by natural means (through range expansion), without the intentional or accidental intervention of humans from an area where they are native (see Pyšek et al. (2004)).” (Richardson, 2011)
Alien species	“Those whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers (i.e., human-mediated extra-range dispersal).” (Richardson, 2011)
Naturalized species	“Those alien species that sustain self-replacing populations for several life cycles or a given period of time (10 years is advocated for plants) without direct intervention by people, or despite human intervention (Pyšek et al., 2004; Richardson et al., 2000).” (Richardson, 2011)
Invasive species	“Alien species that sustain self-replacing populations over several life cycles, produce reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and have the potential to spread over long distances (Occhipinti-Ambrogi & Galil, 2004; Pyšek et al., 2004; Richardson et al., 2000)” (Richardson, 2011) “if this species [alien species] becomes problematic, it is termed an invasive alien species (IAS).” (<i>IUCN: Invasive Species</i> , 2016)
Non-invasive species	Alien plants that are not invasive (see Fig. 1, from Pyšek et al. (2004)).

The famous biologist, naturalist and geologist Charles R. Darwin (1809-1882) was one of the first modern scientists to address the issue of invasive species and to suggest a theory explaining the invasive process in his book *“On the Origin of Species”* (Darwin, 1859). He hypothesized that the naturalization success of an alien species does not depend that much on its preadaptation ability to the new locality, but is proportional to the phylogenetic distance separating it from native species. He explained this assumption with the fact that close species should be more similar in terms of their life-history traits, promoting competition and hence potentially decreasing the chances of an alien species to spread upon colonization. He made this statement based on the observations of Alphonse de Candolle (1806-1893) in his book *“Géographie botanique raisonnée”* that aims to explain the origin of cultivated plant species (de Candolle, 1855). This theory was first synthesized and statistically tested by Marcel Rejmánek in 1996 for European and Californian Poaceae and Asteraceae under the name *“Darwin’s Naturalization Hypothesis”* (DNH) (Rejmánek, 1996). A greater focus on plant invasiveness occurred during the 21st century and several studies showed results supporting the DNH (Bezeng et al., 2015; Schaefer et al., 2011; Strauss et al., 2006), while others found the exact opposite pattern (Diez et al., 2009; Duncan & Williams, 2002; Maitner et al., 2012). This paradox was called the *“Darwin’s Naturalization Conundrum”* (DNC) by Jeffrey Diez in

2008 in his study on the invasive plants of the Auckland region in New Zealand (Diez et al., 2008).

The controversy about the application of the DNH can be explained in several ways (Fig. 2). On one hand, Darwin's Naturalization Hypothesis was based on the idea that closely related species tend to share the same niche, and hence, compete for the same resources, decreasing the chances of alien colonization upon arrival (Daehler, 2001; Darwin, 1859). This theory is consistent with the concept of niche conservatism, stating that sister species share similar ecological niche requirements because they have a recent common ancestor from which ecological characteristics were retained. Therefore, sister or closely related sympatric species are expected to display competitive interactions (Anacker & Strauss, 2014; Wiens & Graham, 2005). This theory is reminiscent of the stochastic niche theory as conceptualized by David Tilman in 2004; that is, a propagule from a species not present in an ecosystem has more chances of being successfully established if it is sufficiently different from local species, so that the native and newly introduced species do not compete for the same resources (Tilman, 2004). On the other hand, the "Preadaptation Hypothesis" developed by Anthony Ricciardi and Miriam Mottiar in 2006 from invasive fish samples around the world conversely predicts that an alien species that is closely related to a native species has better chances to spread as it is likely to exhibit the same adaptations as the native species, and hence, that its ecological niche is compatible with its new environment, following what Darwin mentioned as an intuitive explanation (Darwin, 1859; Ricciardi & Mottiar, 2006). The DNC can be summarized as which driving force is the more important in community assembly: niche partitioning (DNH) or environmental filtering (Preadaptation Hypothesis) (Lemoine et al., 2015).

The application of Darwin's Naturalization Hypothesis depends on several factors, including the scale at which the study is conducted and the invasion stage of the alien species in its nonnative environment (Cadotte et al., 2018; Diez et al., 2008; Ma et al., 2016). The environment being more homogenous at a local scale, one could expect that competition is a more important issue than at large scales, and that closely related species may not coexist (Cadotte et al., 2018). Further investigations showed, however, that during early invasion stages, preadaptation capacity plays a key role for explaining invasion potential, whereas, during late invasion stages, competition among sibling species matters, so that both hypotheses are not mutually exclusive (Li, Guo, et al., 2015). Furthermore, a long-term study revealed that alien species may naturalize more easily in ecosystems with closely related native species but that the latter were driven to extinction by the highly competitive newcomer (Li, Cadotte, et al., 2015). This last assessment increases the complexity of the DNC by introducing a third hypothesis (Fig. 2): alien species naturalize in environment where phylogenetically close native species already exist due to environmental preadaptation, but native species are driven to extinction over time (Cadotte et al., 2018).

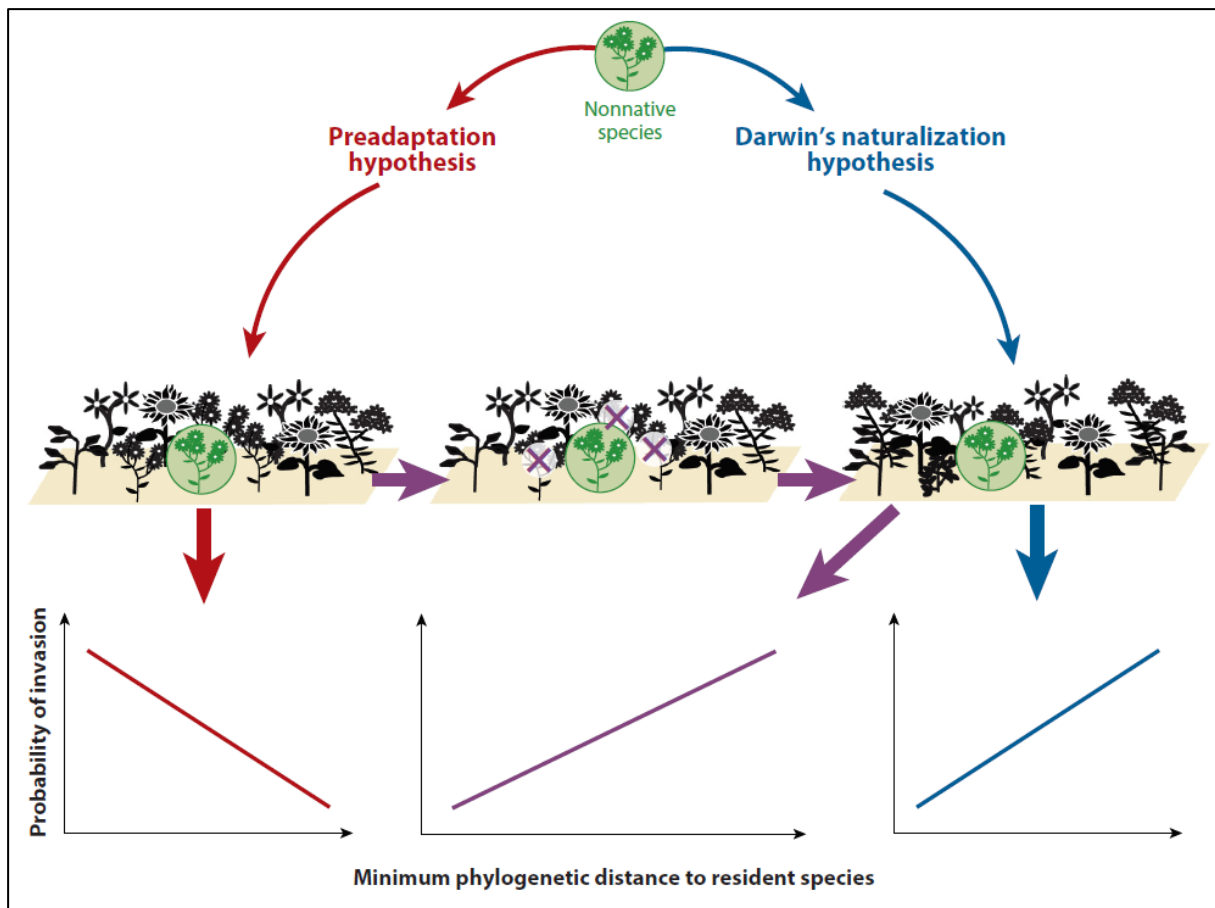


Figure 2 - Schematic view of Darwin's Naturalization Conundrum. The Preadaptation Hypothesis explains invasion success by the phylogenetic closeness between the alien and the native species while Darwin's Naturalization Hypothesis (DNH) states that alien species have more chance invading an ecosystem without any phylogenetically close species. A third explanation shows patterns toward DNH but because of the extinction of the phylogenetically close species, which scenario is toward the Preadaptation Hypothesis. Scheme proposed by Cadotte et al. (2018).

Other explanations and theories also exist to explain the observed distribution patterns of alien and invasive species that are not based on the competition between local and alien species with small phylogenetic distances between them (Cadotte & Colautti, 2005). For example, the Enemy Release Hypothesis (ERH), formalized by Ryan Keane and Michael Crawley in 2002, explains the invasion success of certain species by the absence of specialized predators in the newly colonized environment. This hypothesis states that if native and alien species are closely related, predators, pests and diseases of the former are likely to switch to the latter. In contrast, if native and alien species are remotely related, alien species may be free of pests and diseases, giving to alien species a competitive advantage over native species (Keane & Crawley, 2002). Although the application of the theory depends on whether predators or parasites are specialists or generalists (Colautti et al., 2004), the ERH was, for example, supported for pathogens-linked diseases (Parker et al., 2015).

As the niche conservatism concept has been increasingly challenged (Wiens & Graham, 2005), the assumption that phylogenetic distance can be used as a proxy for ecological niche similarity has also been questioned (Marx et al., 2016). Researchers studying the invasion process and patterns have thus increasingly developed a multidimensional approach where the phylogenetic relatedness of native and alien species is not the only predictor of the DNC

anymore but where life-history traits analyses were included to take environmental filtering into account (Gallien & Carboni, 2017; Lemoine et al., 2015, 2016; Marx et al., 2016; Pinto-Ledezma et al., 2020). The results of such studies show the importance of environmental filtering in the naturalization process of alien species (Catford et al., 2019; Lemoine et al., 2015; Marx et al., 2016; Pinto-Ledezma et al., 2020), with phenotypic similarity tending to be more important than phylogenetic distance to explain invasion potential. This is especially true with abundance data rather than with presence/absence data only because abundant species (native and alien together) tend to be more phenotypically similar than rare species (Kraft & Ackerly, 2010; Lemoine et al., 2015, 2016).

In the context of insular biogeography, studies focusing on this particular topic showed similar results as to the ones conducted in mainland. However, the invasion process and underlying mechanisms might probably be different between islands and mainland (Richardson & Pyšek, 2006), and some historical examples can show how the results vary even between island analyses. Daelher (2001), for instance, failed to evidence that alien, invasive species are significantly more distant to native species than alien, non-invasive species in the Hawaiian flora. In contrast, Schaefer et al. (2011) found that invasive species are more distant than non-invasive alien species to the native flora in the Azores, thus supporting the DNH. As a third example, Marx et al. (2016) showed that invasive and native species of the San Juan archipelago tend to be more closely related than what a random distribution would display, but that the life-history traits were significantly different between the two groups.

The INVASION project, in which the present study is embedded, attempts at identifying the drivers of biological invasions in the Canary Islands.

The Canary Islands are an archipelago composed of eight islands (Lanzarote, La Graciosa, Fuerteventura, Gran Canaria, Tenerife, La Gomera, La Palma, El Hierro) and is part of the group of archipelagos called Macaronesia (*The Happy Islands*), along with the Azores, Madeira and Cape Verde Islands (Fig. 3). The Canary Islands are the only Macaronesian archipelago that

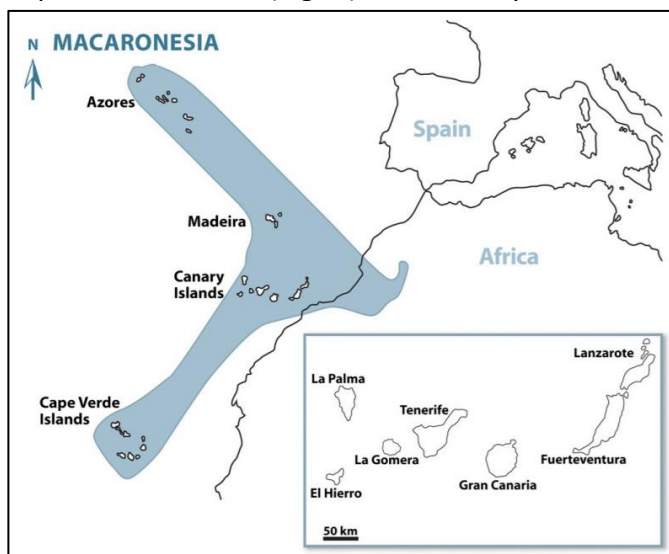


Figure 3 - Map of Macaronesia in shaded and detail of the Canary Island archipelago representing the main islands (La Graciosa missing). Retrieved from Mort et al. (2015).

had an aboriginal population at the European Conquest time, the first records dating back to 1400 before Common Era (CE). This region was also the first discovery in the Age of Discovery, when the Portuguese sailed to those islands in 1336CE. The human impact on the vegetation can be traced back to the beginning of colonization by the aborigines, including the introduction of alien species like goats that grazed abundantly on native endemic species (Arévalo et al., 2011) and the cut of pine trees to build houses

and weapons (del Arco Aguilar et al., 1992). Among the eight islands, Tenerife is the highest with 3750m above sea-level and is covered by six different ecosystems. Tenerife is particularly interesting to study as it is the island with the maximal extension of pine forest ecosystem, which covered 25% of the island at the beginning of the Castilian conquest in the 15th century. This ecosystem has been heavily exploited, leading to the drastic reduction of its surface to only 12% of the island in the beginning of the 19th century. Thanks to reforestation efforts from 1940 to nowadays, the pine forest went back to a belt-shape around the Mount Teide from scattered vegetation nuclei. The pine forest was restored but also extended to other ecosystem zones, where the original vegetation was replaced by *Pinus* species considered more economically profitable. Not only the endemic *Pinus canariensis* was planted, but also alien species like *Pinus radiata* or *Pinus sylvestris* (del Arco Aguilar et al., 1992; del Arco Aguilar & Rodríguez Delgado, 2018; de Nascimento et al., 2020).

Nowadays, tourism has become the most important economic sector of the Canary Islands and more specifically on Tenerife where the majority of the population lives. In 2018, no less than 13.7 million people travelled to the Canary Islands (González Gorrín, 2019). This particular context makes the Canary Islands, with their 965 alien species from which 150 invasive (*Biota*, 2021), and more specifically the pine forest ecosystem with its long history of human-mediated reshaping, particularly suitable for testing competing hypotheses on the mechanisms of biological invasions.

This study aims at determining whether biological invasions can be predicted from environmental features and/or characteristics of the native flora, in line with Darwin's hypothesis that some communities would, due to their remote similarities with alien species, be more prone to biological invasions than others. We first determine whether environmental variation impacts on the naturalization of alien, non-invasive and invasive species, i.e., whether some habitats are more prone to facilitate naturalization than others (**Q1**). In a second time, we determine whether the probability of invasion can be predicted from the taxonomic composition (**Q2**) and life-history traits (**Q3**) of native communities, i.e., whether some communities are, due to their taxonomic composition and/or life-history traits, more prone to biological invasions than others.

2. Material and method

2.1 Field sampling and environmental plot characterization

The sampling period took place between February and May 2021 on the island of Tenerife, Canary Islands, Spain. The sampling protocol was designed in the context of a broader project studying the impacts and patterns of invasive species in different ecosystems and at different spatial scales. This thesis focuses on the pine forest ecosystem of Tenerife Island at the finest scale measured in the larger study.

Twenty localities across the pine forest were visited (Fig. 4). In each one, an area of 400m² (20x20m) was subdivided into four 100m² (10x10m) plots. Two of those four plots were randomly selected. In each plot, a complete inventory of the vascular plant flora was carried out and the percentage cover of each species recorded. Diameter at breast height (DBH) was measured for all trees and bushes. Each species was characterized by measurements of the height and largest and smallest widths of five individuals. A leaf sample was collected from five different individuals (when available) per species for further processing. Each plot was further characterized by its altitude (Garmin® Oregon 750), slope and slope orientation (aspect). The coverages in rocks and naked soil were also estimated.

Climatic data at each plot were retrieved from CHELSA (Climatologies at High resolution for the Earth's Land Surface Areas), specifically developed by Karger et al. (2017) for environmental and ecological studies (version 2.1, a downscaling at 5m resolution), using R 4.0.3 (R Core Team, 2020) and the 'raster' package (v3.4-13; Hijmans, 2021). The data are composed of nineteen variables describing the temperatures and precipitations during different periods of the year (more information in Appendix 1) (Karger et al., 2017, 2018).

2.2 Characterization of the life-history traits of native species

The life-history traits included in the present study are the following: the specific leaf area (SLA), the leaf dry matter content (LDMC), the DBH of trees and bushes, the plant volume, seed dispersal modes, and growth form. Part of these traits were measured on the field or in the laboratory (SLA, LDMC, volume, DBH) while the missing information was retrieved from bibliographic sources and online databases (dispersal mode, growth form).

The SLA measure is often used as a proxy for the growth rate or the maximum photosynthetic rate: low values are related to oligotrophic environment and high defense investment toward resource stress while high values are related to eutrophic environments (Cornelissen et al., 2003). The LDMC is related to plant tissue density, with high values linked to stiff resistant leaves, but usually correlated to the SLA even if it doesn't inform on the same plant properties (Cornelissen et al., 2003).

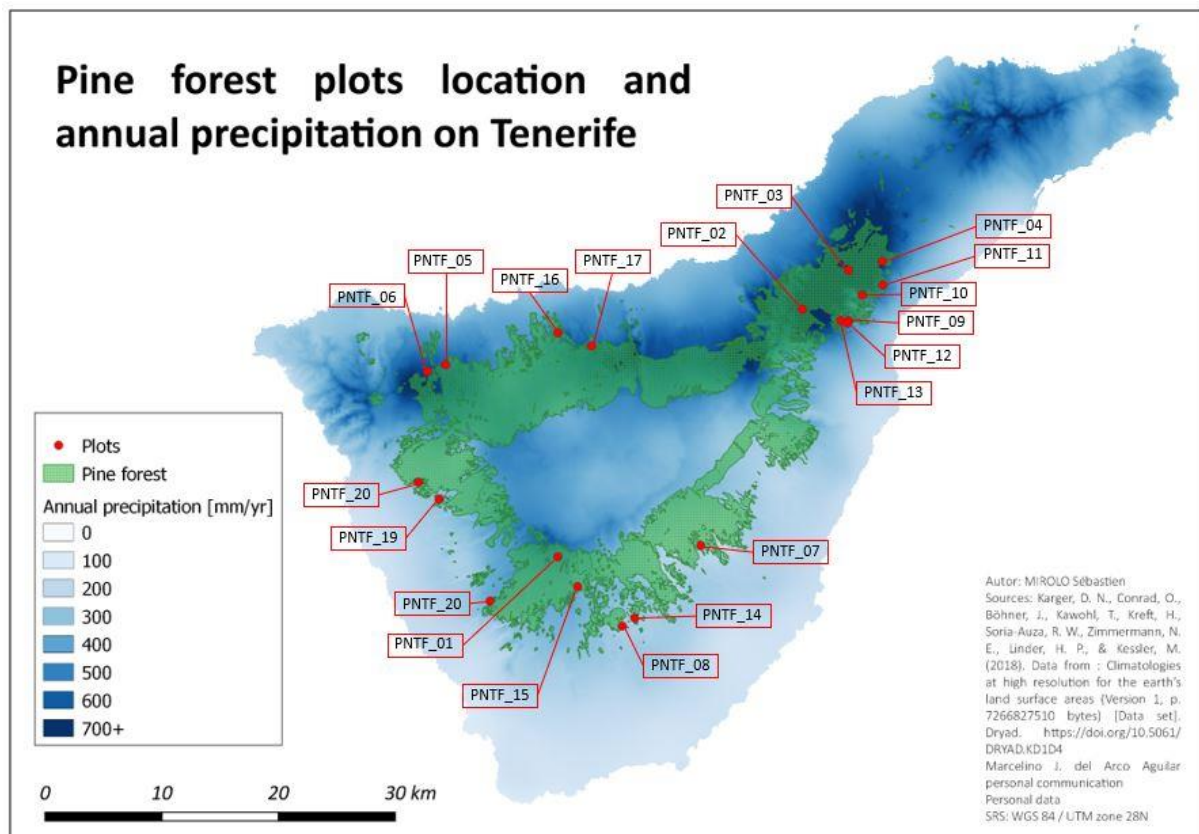


Figure 4 – Map of Tenerife representing the annual precipitation [mm/yr] at the background (blue gradient) and the pine forest ecosystem (green zone). The plot investigated in the present study are represented by the red dots. PNTF = "Pinar Tenerife".

2.2.1 Trait measurements

The leaves were saturated with water by wrapping them in wet paper for 48h in a refrigerator. The saturated weight was measured at 10^{-3} g precision using an analytical balance (Shimadzu Analytical ATX324; Shimadzu, Kyoto, Japan). After scanning of the leaves (Epson® Perfection V600 Photo, middle dusting removal; Brother® DCP-J562DW, middle dusting removal), the images were processed using the cellSens Standard 3.1 software of Olympus® Corporation. Surface area, perimeter and shape factor¹ were recorded. The leaves were then placed in an oven at 65°C for at least seven days before weighting the dry weight of the samples.

The raw data were transformed as follows:

- The specific leaf area (SLA) was calculated by dividing the surface area [mm²] by the dry weight [mg] (Cornelissen et al., 2003).
- The leaf dry matter content (LDMC) was calculated by dividing the dry weight [mg] by the water-saturated weight [g] (Cornelissen et al., 2003).
- The volume of the plant was calculated by multiplying the two widths and the height of each individual.
- The data were then all averaged by species or genera for the non-identified ones and arranged into matrices with the plots as rows and the different species as columns.

¹ Area relative to the area of a circle with an equal perimeter.





2.2.2 Literature survey

Growth form, seed dispersal mode, endemism and origin status were determined from the literature.

Endemism and nativeness were determined from the Canarian biodiversity databank (Acebes & Beltrán-Tejera, 2003; *Biota*, 2021), which includes the following categories: endemic and non-endemic species (E and NE respectively), native (“Nativo Seguro”, NS), likely native (“Nativo Probable”, NP), likely alien (“Introducido Probable”, IP), alien non-invasive (“Introducido Seguro No Invasor”, ISN) and alien invasive (“Introducido Seguro Invasor”, ISI). Here, the “likely native” and “native” categories were merged, as were the “likely alien” and “alien” categories. Five categories of growth forms were identified after simplification of the nineteen categories of Cornelissen et al. (2003), i.e., “Herbs”, “Shrubs”, “Trees”, “Vines” and “Ferns”. Those categories were assigned to each species from the descriptions provided in “*Flora canaria*” (Schönfelder & Schönfelder, 2018).

Seed dispersal modes of each species were characterized following the morphological classification from Arjona et al. (2018) and Heleno & Vargas (2015). These two studies describe long distance dispersal syndromes only. Short distance dispersal syndromes were described from Van der Pijl (1982) and added to the present classification. Each species was assigned to one of the following four dispersal syndromes: autochory (AUT), anemochory (ANE), endozoochory (END) and epizoochory (EPI). This assignment was made indirectly from an assessment of the morphology of the diaspores based on the criteria listed in Table 2. Information on diaspore morphology was obtained for 56 species from pictures found in online databases (*Atlas Digital de Semillas de las Islas Canarias*, 2021; *Environmental Weeds of Australia Biosecurity Edition Search*, 2021; *Federal Noxious Weeds Disseminules of the US*, 2021; *Global Plants on JSTOR*, 2021; *Herbario JACA*, 2021; *JACQ - Herbarium Management System*, 2021; *Seed Information Database: Royal Botanic Gardens, Kew*, 2021; *USDA Plants Database*, 2021). For the rest of the species for which no pictures were found, bibliographic sources were compiled (Abbate et al., 2010; Allan et al., 2004; Arditti & Ghani, 2000; Arjona et al., 2018; Bramwell, 1986; Büchi et al., 2021; *CABI - Invasive Species Compendium*, 2021; *Ecological Database of the British Isles*, 2021; *Federal Noxious Weeds Disseminules of the US*, 2021; *Flora canaria. Flora y vegetación de las Islas Canarias*, 2021; *Global Plants on JSTOR*, 2021; *iFlora - Search for species*, 2021; *Plants of the World Online | Kew Science*, 2021; *Royal Botanic Gardens, Kew | Kew*, 2021; *Seed Information Database: Royal Botanic Gardens, Kew*, 2021; *Tela Botanica*, 2021; Castro et al., 2013; Castroviejo et al., 2007; Cook, 1962; Hawksworth & Bull, 2007; Humphries, 1976; Liu, 1986; Pérez de Paz, 1978; Tavşanoğlu & Pausas, 2018; Traveset & Richardson, 2020; *Western Australian Herbarium*, 2021). Each plot was subsequently characterized by the number of species exhibiting each of the four dispersal modes.

Table 2 - Morphological descriptions and examples of the four dispersal modes characterizing the pine forest species of Tenerife Island.

Dispersal Mode	Description of the morphological classification	Examples
Anemochory [ANE]	Any diaspores with wings, plumes and/or pappus. The atrophied pappus and plumes of some Asteraceae were not included in this category. Poaceae awns were considered as promoting anemochory on the condition that they were not stiff.	<p data-bbox="1034 398 1337 430"><i>Ageratina adenophora</i></p> 
Endozoochory [END]	Any diaspores with fleshy and nutritive tissues attracting animals. For seeds with elaiosomes, only the colorful and/or shiny large ones were considered in this category as they are appealing to birds for example.	<p data-bbox="1082 784 1289 815"><i>Ilex canariensis</i></p> 
Epizoochory [EPI]	Any diaspores with morphological structures allowing the clinging on animal fur or feathers, including structures like hooks, spines and sticky substances. Poaceae awns were considered as promoting epizoochory on the condition they were stiff.	<p data-bbox="1056 1120 1315 1151"><i>Erodium cicutarium</i></p> 
Autochory [AUT]	Dispersal mode only dependent on the gravity and the plant capacity directly, like the explosive seed dispersion. No particular morphological aspect of the diaspore is involved. This category includes barochory and ballistochory.	<p data-bbox="1104 1433 1273 1464"><i>Vicia aphylla</i></p> 

2.3 Statistical analyses

All statistical analyses were performed using R software version 4.0.3 (R Core Team, 2020).

Several matrices (topography, climate, taxonomic composition of the native community, and native species traits) were employed to predict the proportion of alien species per plot (Q1)

and the likelihood of the presence of an invasive species in a plot (Q2, Q3) from regression analyses. Since the latter is highly sensitive to multicollinearity and to avoid overfitting due to a high number of predictors, the complex information included in each predictor matrix was summarized using a Principal Component Analysis (PCA) to derive uncorrelated compound variables (the PCA axes) (Abdi & Williams, 2010). A PCA was therefore performed on each of the following data-matrices using the 'FactoMineR' (Lê et al., 2008) and 'factoextra' (v1.0.7; Kassambara & Mundt, 2020) packages: (i) the climatic matrix, including the nineteen CHELSA variables; (ii) the topographical matrix, including altitude, slope, aspect, stone and soil coverages; (iii) the relative coverage of native species x plot matrix; and (iv) each of the life-history trait matrix, i.e., SLA, LDMC, DBH, plant volume, leaf shape factor and dispersal mode. For each PCA, the three first axes were selected.

To avoid any potential issue of multicollinearity among the PCA axes of the different matrices analyzed, a correlation matrix was computed among all the generated PCA axes per regression analysis and one variable was randomly removed out of a pair of variables correlated at $R > 0.7$ ('cor' function). The PCA axes of the SLA, LDMC and leaf shape factor were thus removed to only keep DBH, plant volume and dispersal mode as predictors for the likelihood of the presence of invasive species in a plot (Q3).

To address Q1, we implemented a Linear Model to predict the percentage of alien species within a plot as a function of topographic and climatic predictors. The residuals were tested for normality and homoscedasticity with a Shapiro-Wilk Normality test and a Breusch-Pagan Test of Heterogeneity of Variances ('shapiro.test' function; 'bptest' function, 'lmtest' package (Hothorn & Zeileis, 2002)). Model accuracy was characterized by its R^2 .

To visualize the relationship between variation in climatic conditions and the abundance of invasive species, a clustering analysis was computed based on the CHELSA climatic variables. The 19 variables were first scaled by centering the data and dividing them by the standard deviation. A Euclidian distance matrix was calculated and a dendrogram was built with Ward's method.

To address Q2 and Q3, we implemented Generalized Linear Models (GLM) to predict whether the presence/absence of invasive species in a plot can be predicted from the taxonomic composition (Q2) and life-history traits (Q3) of native species, respectively. The independent variables were the three first axes of the PCA of the native species coverage data matrix and the native species life-history traits matrices. Because the response variable is binomial, the "logit" link function was used. For the same reason, model accuracy was characterized by the Area Under the ROC Curve (AUC) instead of the R^2 ('pROC' package (Robin et al., 2011)) (Hosmer et al., 2000). The "Receiver Operating Characteristic" (ROC) is a technique where the performance of "the receiver" to assign cases into binomial categories can be plotted in a probability curve of the specificity against the sensitivity (1-sensitivity). The Area Under the ROC Curve (AUC) is a classification error metric based on the specificity (true positive rate) and the sensitivity (true negative rate) of a logistic regression model. The AUC is used to measure the effectiveness of the model to classify binomial data. This metric is often used in

ecology for presence/absence data (Fielding & Bell, 1997; Lemoine et al., 2015; Phillips et al., 2009).

In all models, spatial autocorrelation of the dependent variable was tested by measuring Moran's I. This measure characterizes the correlation between a variable and the geographic distance among the localities where it has been measured. Its value ranges between -1 and 1. If the statistic is significantly above or below $\frac{-1}{N-1}$ where N is the number of plots in this particular case, there is a positive or negative spatial autocorrelation, respectively. The null hypothesis that there is no spatial autocorrelation was only rejected for the second GLM analysis (Q1 p-value = 0.11; Q2 p-value = 0.14; Q3 p-value = 0.01). A spatial autocovariate was calculated using the 'autocov_dist' function of the 'spdep' package (Bivand & Wong, 2018) and then added as a predictor to the GLM model to account for spatial autocorrelation. This autocovariate is build based on a function of the response of two neighbors to the explanatory variable through a distance-weighted average approach following Dormann et al. (2007). The presence of invasive species was averaged when two neighbors were close but less weighted for distant plots. The neighbor radius was set to 15km, which means that 15km is the minimal distance for each plot to have a neighbor.

For all GLMs, we contrasted the performance of competing models based on the Akaike Information Criterion (AIC). Starting from the complete model with all predictors, the AIC of models including a progressively decreasing then increasing and/or decreasing number of predictors are computed and compared until the model has an optimal AIC. Based on the 'stepAIC' function ('MASS' package (Venables & Ripley, 2002)), we selected the model with the lowest AIC. To test the significance of the selected model, an analysis of deviance was performed to determine if the GLM model with the selected predictors was more informative than a null model only based on the intercept. The deviance is a goodness-of-fit statistic used to test hypotheses for statistical models, i.e., a statistic that summarizes the discrepancy between the predicted and observed values of a model, particularly for GLM where it is comparable to the residual variance ANOVA test for linear models. The two models are tested under the null hypothesis that the null model is true, which means that the linear predictors are not significantly different from zero. The observed statistic, which is the difference of deviance between the models, follows a chi-square distribution. The number of degrees of freedom is equal to the difference between the number of parameter in the two models (Myers & Montgomery, 1997).

To assess the potential of all regression models to make predictions from observations independent from those used to calibrate them, i.e., make sure that models were not over-fitted, we re-ran each model after leave-one-out cross-validation ('lmtree' (Hothorn & Zeileis, 2002) and 'caret' (v6.0-88; Kuhn, 2021) packages). For each of the n observations (plots), one observation is left-out, the model is re-computed based on the n-1 observations, and the observed and predicted data are compared. A large difference between the R²/AUC of the full model, and of the cross-validated model, points to a poor predicting ability of the model due to overfitting.

3. Results

3.1 Fieldwork results

In total, 135 species (including 13 labelled as “sp”, because scanty material did not allow for certain identification at species level) were recorded, including 4 gymnosperm, 5 fern and 113 angiosperm species. There were 44 endemic species among those found in the plots. From those endemics, the only trees encountered were *Pinus canariensis* and *Arbutus canariensis* and the only fern was *Hemionitis pulchella*. There were also 10 herb and 31 shrub endemic species. Among the ten most frequently sampled species, there were four endemic species: *Pinus canariensis* (40 plots), *Cistus symphytifolius* (12 plots), *Micromeria hyssopifolia* (11 plots) and *Chamaecytisus proliferus* (9 plots). The 122 identified species are listed in Appendix 2 with the species code used in the analyses.

There were 16 species considered as alien, including 8 invasives (ISI category) and 8 non-invasives (ISN and IP category) (Table 3). Two of the eight invasive species are among the ten most encountered species across the forty plots: *Opuntia maxima* (15 plots) and *Ulex europaeus* (7 plots).

Table 3 - Alien species recorded in the pine forest of Tenerife in the present study, with their status according to the Canarian Biodiversity Databank and the number of plots where they were recorded. ISI = “Introducido Seguro Invasor” a.k.a. “Alien Invasive”, ISN = “Introducido Seguro No Invasor” a.k.a. “Alien Non-Invasive”, IP = “Introducido Probable” a.k.a. “Likely Alien”.

Species	Status	Number of plots
<i>Opuntia maxima</i>	ISI	15
<i>Ulex europaeus</i>	ISI	7
<i>Oxalis pes-caprae</i>	ISI	4
<i>Eucalyptus globulus</i>	ISI	4
<i>Cupressus macrocarpa</i>	ISI	2
<i>Eschscholzia californica</i>	ISI	1
<i>Ageratina adenophora</i>	ISI	1
<i>Agave americana</i>	ISI	1
<i>Hyparrhenia hirta</i>	ISN	4
<i>Scorpiurus muricatus</i>	ISN	4
<i>Calendula arvensis</i>	ISN	2
<i>Foeniculum vulgare</i>	ISN	1
<i>Lupinus angustifolius</i>	ISN	1
<i>Ficus carica</i>	IP	2
<i>Stellaria media</i>	IP	2
<i>Carthamus lanatus</i>	IP	1

Species richness per plot ranged between 2 (*Pinus canariensis* and *Chamaecytisus proliferus*) and 21 species (Vilaflor, Pino Gordo), alien species included. The maximum number of alien species on a plot was four, with only six plots without any alien and eight without invasive species. There was an average of 9.32 species per plot with 1.25 alien species representing 14.3% of the species richness per plot.

3.2 Statistical analyses

The selected linear regression model predicting the percentage of alien species per plot as a function of the climatic and topographic variables (**Q1**) (AIC = 175.39) included only PCA3_{Topo}, the third PCA axis of the topographic data (Fig. 5). The residuals were normally distributed (Shapiro-Wilk test p-value = 0.26) and their variances homogenous (Breusch-Pagan test p-value = 0.59). The model was significantly different from the intercept-only model based on the analysis of deviance (p-value = 0.001). The multiple R² and adjusted R² of the model are 0.22 and 0.2 respectively. After the leave-one-out cross-validation, the R² value is of 0.15.

PCA3_{topo} is mainly correlated to two topographic variables: soil coverage and aspect, a.k.a. the percentage of naked soil in a plot and the main orientation of the slope. Both are positively correlated at 0.67 and 0.61 to the axis respectively (see Appendix 3 for detailed information about the PCA analyses). The slope of the linear regression is negative (-4.561), therefore, the relation between the percentage of alien species and the soil coverage and aspect is also negative. The percentage of alien species is inversely proportional to the percentage cover of naked soil in a plot, which means that there are more alien species when soil coverage decreases, thus, when rock or vegetation coverage increases. The aspect is the orientation of the slope in degrees: North corresponds to 0°, East to 90°, South to 180° and West to 270°. Thus, the model predicts that the proportion of alien species increases towards the East and the North.

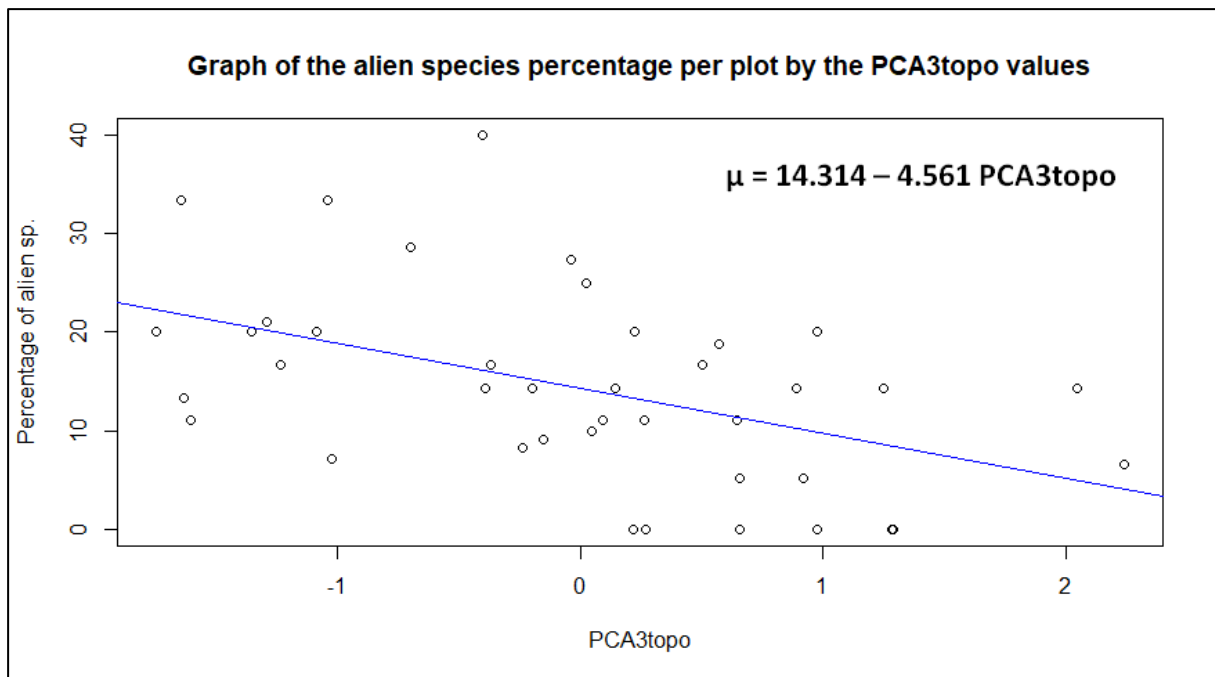


Figure 5 - Graph of the relationship between alien species percentage per plot (μ) in the pine forest of Tenerife depending on the third axis of the PCA of the topographic data (PCA3_{topo}). The regression line is in blue.

No variable was selected in the GLM predicting the presence/absence of invasive species per plot as a function of the native species relative coverage PCA axes (**Q2**). The analysis of deviance showed no significant difference between the complete model and the intercept-only null model (p-value = 0.86).

The selected GLM predicting the presence/absence of invasive species per plot as a function of the life-history traits variables (**Q3**) (AIC = 38.3) included two variables: PCA2_{DBH} and PCA1_{dispersal-mode} (Fig. 6). As there was spatial autocorrelation, an autocovariate (ac) correcting the values was added to the model. The result of the analysis of deviance was significant so the selected model is informative compared to the null model (p-value = 0.02). The model has an AUC of 0.81 before cross-validation and of 0.72 after. The model has an error percentage of 15%, but with a high proportion of false positives, as only three non-invaded plots out of the eight were correctly predicted.

Three species contribute for more than 10% to PCA2_{DBH} and are correlated for approximately 0.7 to it (see Appendix 3 for detailed information about the PCA analyses). From those species, two are typical of substitution vegetation of the laurel forest (*Daphne gnidium* and *Ilex canariensis*) and one is typical of the pine forest (*Cistus symphytifolius*). The selection of this variable means that it is more probable to find invasive species where the three mentioned species are tall.

The PCA1_{dispersal-mode} is mainly representing the anemochory, autochory and epizoochory dispersal modes with correlations from 0.7 to 0.9. The model shows a positive relation between the presence of invasive species and a high value of PCA1_{dispersal-mode}. When there are high percentages of species using anemochory, autochory and to a lesser extent epizoochory (25.7% contribution against 40.4% for anemochory and 33.7% autochory), the plots tend to be invaded.

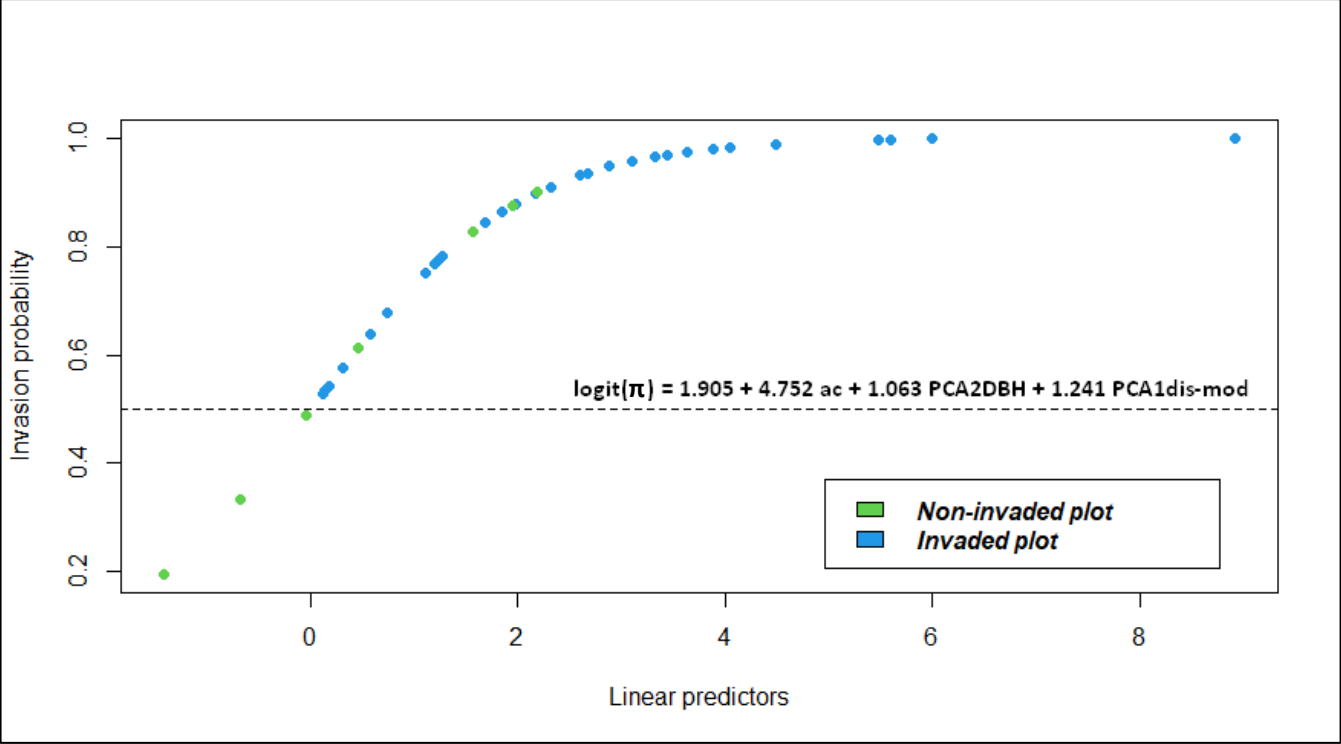


Figure 6 - Graph of the probability for a plot of Tenerife pine forest to be invaded depending on the combination of selected predictors. In green the plots non-invaded, in blue the plots invaded. The dotted line represents the 50% chance to be invaded for a plot: above it is predicted to be an invaded one, and under a non-invaded one. π : probability of invasion for a plot. ac: autocovariate accounting for spatial autocorrelation. PCA2DBH: second axis of the PCA of the DBH data. PCA1dis-mod: first axis of the PCA of the dispersal mode data.

3.3 Cluster analysis

On the dendrogram computed with the clustering analysis, we can see two distinct groups based on the climatic data (Fig. 7). The two sides of the island were displayed in blue for the North and in red for the South. The invaded plots were colored in green leaving the non-invaded ones in black, evenly distributed on the dendrogram.

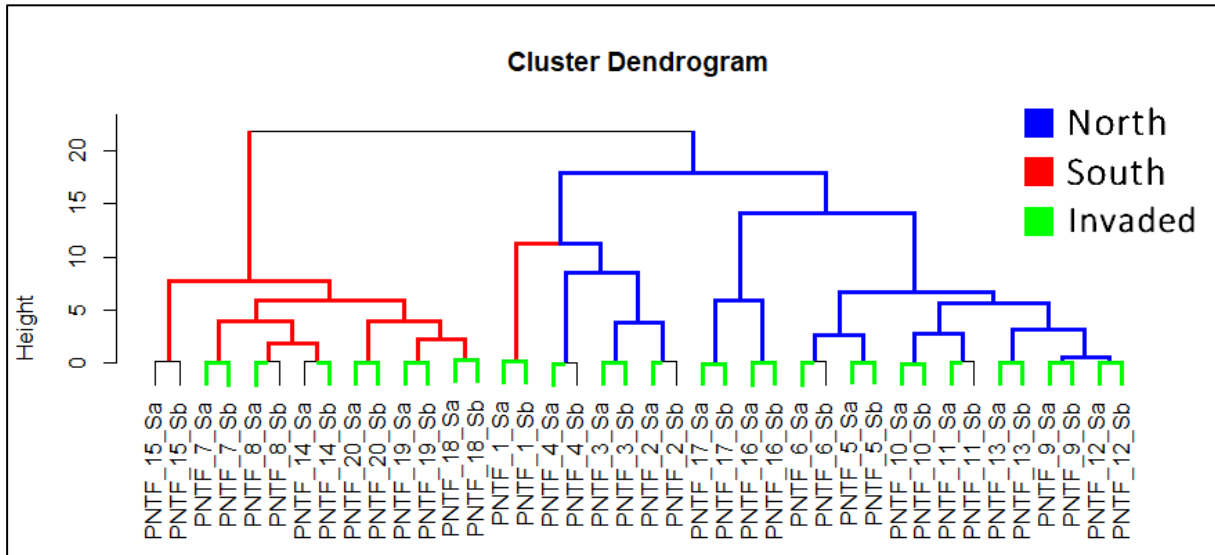


Figure 7 - Cluster dendrogram of the investigated plots of Tenerife pine forest depending on their climatic characteristics, with the Ward's method. In blue the plots from the North of the island, in red the plots from the South of the island, in green the plots with invasive species.

4. Discussion

In line with our **first question**, the relative abundance of alien species in Canarian pine forests was significantly related to environmental variables, supporting mounting evidence that environmental filtering is one of the strongest constraints determining variation in the vulnerability to introduced species of some communities as compared to others (Catford et al., 2019; Lemoine et al., 2015; Pinto-Ledezma et al., 2020). More specifically, the proportion of alien species could be predicted from topographic features, including soil coverage and the general orientation of the slope. In fact, the relative abundance in alien species increases with decreasing soil cover and aspect. The soil cover variable reflects the percentage of naked soil of a plot, where no vegetation was growing and where no rocks were covering the ground, which was another measured variable. The aspect variable is the orientation of the general inclination of the plot slopes in degrees, where the North represents 0°, the East 90°, the South 180° and the West 270°.

In general, it has been shown that invasive species tend to be more present in disturbed habitats than native species, because these environments are less prone to competition, which could prevent alien to establish during the first colonization stages (Kowarik, 2008). Disturbance can be defined as “a change in conditions which interferes with normal functioning of a biological system” (Andel et al., 1987). In a natural pine forest ecosystem, the normal soil condition would be a thick layer of pine needles with few species and mainly shrubs (del Arco Aguilar et al., 1992). Disturbance in this ecosystem is reflected by a naked soil without needles or a great coverage of herb species. In a Mediterranean grassland ecosystem, Caño et al. (2008) experimentally showed that an alien species in its invaded ranges benefits more from increasing naked soil availability than the same species in its native range. In the present study, the model shows that, as opposed to such an expectation, the proportion of invasive species increases with decreasing naked soil cover. We can suggest two hypotheses to explain this unexpected result. First, alien colonization would require facilitation from native communities, enhancing for instance micro-climate conditions (Cavieres, 2021). Second, alien species may shift niche upon colonization in the invasive range (Broennimann et al., 2007). Although niche shift upon invasion may be much less frequent than previously thought (Petitpierre et al., 2012), González-Moreno et al. (2015) reported an ecological niche shift towards disturbed habitats in the invasive herb *Oxalis pes-caprae*, which was also encountered in Tenerife pine forest.

The relevance of the orientation in the model, which reflects the local topography of the plot, is more difficult to interpret. A preference for N-facing slopes, as suggested by the model, cannot be interpreted in terms of climatic conditions because none of the climatic variables were selected in the model. This conclusion was also supported by the clustering analysis of the plots depending on their climatic conditions. In this analysis, two main groups were resolved that almost perfectly corresponded to their North vs South exposure. The North face of Tenerife is more climatically homogenous during the entire year than the South face. Due to high elevation of the Mount Teide and to Trade winds, all humidity contained in the air falls

on the ground as the temperature decreases due to altitude leaving only dry air to the other side of the geological barrier (Fig. 8). This phenomenon of Foehn wind is more pronounced during summer and is moreover enhanced by the vegetation that developed in response to this particular condition: the laurel forest absorbs a great part of the air fog humidity, phenomenon known as “horizontal rain”. Despite such striking differences, no differences in plots vulnerability to alien species were observed. One could have expected a higher percentage of alien species in the South face of Tenerife, where the weather tends to be more desertic than in the North where it is quite homogenous and humid (del Arco Aguilar & Rodríguez Delgado, 2018), because ecosystems exposed to harsh and variable climatic conditions are more prone to invasion (Kowarik, 2008; Traveset & Richardson, 2020). In fact, Lemoine et al. (2015) showed that climatic filtering is a major factor shaping alien species assembly. We suggest that, while variations in climatic conditions do not affect alien species richness per plot, this factor may affect the composition of alien communities. In fact, we observed that *Ulex europaeus* is predominantly distributed in the North, whereas *Opuntia maxima* prevails in the South.

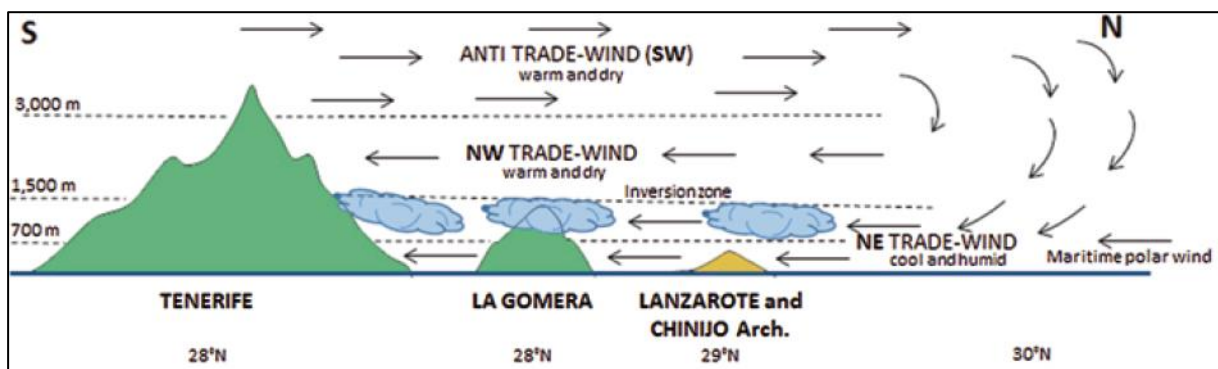


Figure 8 - Schematic view of the Canary Islands climate. The Trade winds go SW in high altitude and inverse at the northern subtropical ridge, thus blowing NE. They accumulate humidity and cool down at the contact of the Canarian current near sea surface. The humidity generates clouds at the inversion zone where warm and dry and cool and humid air masses meet. Scheme from del Arco Aguilar & Rodríguez Delgado (2018).

Contrary to what was expected for the **second question**, the presence of invasive species was not significantly predicted by the native community composition of the Canarian pine forest. The GLM analysis did not select any variables from the native species abundance data PCA, displaying no significant difference from a random assignment of the presence of invasive species. In contrast, Lemoine et al. (2015) demonstrated the prime importance of abundance data to interpret the patterns between native and invasive plant species within a vegetal community. In line with Kraft & Ackerly (2010), we suggest that, while the taxonomic composition of the native community may not necessarily determine the opportunity of alien species to establish, the life-history traits of native species may be more important in the context of the niche pre-emption hypothesis as species sharing the same traits, regardless of their taxonomic identity, may be prone to competitive interactions.

In agreement with this hypothesis, our model predicting the probability of plot invasion depending on the life-history traits of native species exhibited a good predictive power with an AUC of 0.72 after cross-validation (**Q3**). This suggests that some native communities are, due to their life-history architecture, more prone to invasions than others, as if some combinations of life-histories in the native flora would hamper the chances of alien colonization. In our model, DBH of *Daphne gnidium*, *Ilex canariensis* and *Cistus symphytifolius*, as well as anemochory, autochory and epizoochory, were selected as predictors of invasion probability.

DBH of the three species mentioned above can be seen as an indirect measure of forest age and dynamical stage. Large specimens of *Daphne gnidium* and *Ilex canariensis*, characterize the fayal-brezal, which is a typical substitution formation that grows where a laurel forest has been cut down. These species can also occur in humid pine forest still as a substitution to other typical laurel forest species (*Myrica faya*), thus, reflecting human disturbance, and hence, increased opportunities for alien colonization (del Arco Aguilar & Rodríguez Delgado, 2018).

The selection of the proportion of species dispersing through anemochory, epizoochory and autochory as predictors of invasion is more difficult to interpret. In fact, anemochory and epizoochory are long-distance dispersal modes, whereas autochory is a dispersal mode promoting dispersed mainly under the mother-individual or close to it. The only category not explained by PCA1_{dispersal-mode} is endozoochory. We tentatively suggest that this result might emerge from the fact that the three plots that are correctly predicted by the model as being non-invaded are extremely species-poor and lack in particular any endozoochorous species. While dispersal traits themselves may not be directly involved here, the fact that the less species-rich plots are the less prone to invasions ones is intriguing, either supporting the facilitation hypothesis (see above), or suggesting that these sites exhibit some (unmeasured) environmental features that prevent plant colonization, including alien ones.

Only the plant volume variable stayed in the final analysis to avoid multicollinearity with the highly correlated other life-history traits variables (SLA, LDMC, leaf shape factor). The fact that no phenotypic trait was selected by the model is intriguing as environmental filtering has been identified as one of the key drivers of the invasion success and community assembly in general (Catford et al., 2019; Marx et al., 2016; Pinto-Ledezma et al., 2020). This may show a general trend of the pine forest ecosystem that makes all native species displaying similar characteristics that allow them to grow there. In other words, the life-history traits could possibly be homogenous in this particular environment. Relatively few species inhabit this ecosystem compared to other Canarian ones like the laurel forest. Indeed, we recorded 9.3 species on average per plot in the pine forest, whereas there are on average 20.6 species per plot in the laurel forest (data from INVASION project). Moreover, the pine needles render the soil acidic and can make a deep layer, filtering-out a number of species and contributing to the low species richness and, possibly, homogeneity of the phenotypic architecture of the native vegetation.

Finally, it is worth noting that, even though the AUC of our predicting model does not drastically decrease and remains >0.70 following cross-validation, which does not point to overfitting issues, it is characterized by high rates of false positives. This means that plots displaying the features that are characteristic for invaded plots, are not invaded yet. This may suggest that the colonization of the Tenerife pine forest is an ongoing process as many sites display the environmental and biotic features that characterize sites that are vulnerable to invasion.

5. Conclusion

Our results call for further investigation to test competing hypotheses that emerged upon the analysis of the present data. First, the decreasing abundance of alien species on naked soils is intriguing, and we interpreted it in terms of either facilitation upon establishment and/or niche shift. An experiment with different growing conditions could be set up to measure the fitness of invasive species with or without pine forest native species, to determine whether establishment of aliens is facilitated by native species. The depth of the pine needles layer can also be included in the experimental protocol to investigate its impact compared to a naked soil. For the niche shift hypothesis, the same method as Petitpierre et al. (2012) could be considered. This involves modelling the niche of an alien species in its native and invasive range, and partition its total niche into (i) the niche portion that is occupied in both ranges; (ii) the niche portion that is occupied in the native range, but not the invaded one (unfilling, pointing to an ongoing invasion process); and (iii) the niche portion that is occupied in the invaded range, but not the native one, i.e., which points to niche expansion. An accurate estimation of the niche of alien species in Tenerife, potentially integrating niche expansion, could then be projected onto the entire island to identify locations more prone to invasion than others and establishing a monitoring system.

The spatial scale is of utmost importance in invasion biology, as patterns may strongly vary across scales (Cadotte et al., 2018). A comparison between islands among and between ecosystems would be of great interest to deeper investigate the mechanisms of invasion.

Finally, it could also be interesting to integrate a phylogenetic dimension to the analyses to determine whether, in agreement with Darwin's hypothesis, the invasion potential of alien species decreases proportionally to their phylogenetic relatedness with native species (niche pre-emption hypothesis), or if, conversely, invasive species are phylogenetically and phenotypically similar to native species, pointing to the niche preadaptation hypothesis.

6. Appendices

Appendix 1 – CHELSA variables

Table 4 - Codes and meaning for the nineteen climatic variables of CHELSA maps. Retrieved from <https://chelsa-climate.org/bioclimate/>

CODE	VARIABLE
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Appendix 2 – Species encountered

Table 5 - List of the species encountered in the Canarian pine forest of Tenerife along with the code used in the analyses. sp_ID = species code. The species *Argyranthemum vincentii* is currently under revision to act it's a different species from *Argyranthemum foeniculaceum*.

Genera	species	Authority	sp_ID
<i>Adenocarpus</i>	<i>foliolosus</i>	(Aiton) DC.	Ade_fol
<i>Adenocarpus</i>	<i>viscosus</i>	(Willd.) Webb & Berthel.	Ade_vis
<i>Aeonium</i>	<i>arboreum</i>	(L.) Webb & Berthel.	Aeo_arb
<i>Aeonium</i>	<i>spathulatum</i>	(Hornem.) Praeger	Aeo_spa
<i>Aeonium</i>	<i>urbicum</i>	(C. Sm. ex Hornem.) Webb & Berthel.	Aeo_urb
<i>Agave</i>	<i>americana</i>	L.	Aga_ame
<i>Ageratina</i>	<i>adenophora</i>	(Spreng.) R. M. King & H. Rob	Age_ade
<i>Aichryson</i>	<i>laxum</i>	(Haw.) Bramwell	Aic_lax
<i>Allium</i>	<i>canariense</i>	(Regel) N. Friesen & P. Schoenfelder	All_can
<i>Andryala</i>	<i>pinnatifida</i>	Aiton	And_pin
<i>Arbutus</i>	<i>canariensis</i>	Veill. in Duhamel	Arb_can
<i>Argyranthemum</i>	<i>adauctum</i>	(Link) Humphries	Arg_ada
<i>Argyranthemum</i>	<i>frutescens</i>	(L.) Sch. Bip.	Arg_fru
<i>Argyranthemum</i>	<i>vincentii</i>		Arg_vin
<i>Artemisia</i>	<i>thuscula</i>	Cav.	Art_thu
<i>Asparagus</i>	<i>scoparius</i>	Lowe	Asp_sco
<i>Asphodelus</i>	<i>ramosus</i>	L.	Asp_ram
<i>Avena</i>	<i>barbata</i>	Pott ex Link	Ave_bar
<i>Avena</i>	<i>canariensis</i>	R. Baum, Rajhathy & D. R. Sampson	Ave_can
<i>Bituminaria</i>	<i>bituminosa</i>	(L.) C. H. Stirt.	Bit_bit
<i>Brachypodium</i>	<i>distachyon</i>	(L.) P. Beauv.	Bra_dis
<i>Briza</i>	<i>maxima</i>	L.	Bri_max
<i>Bromus</i>	<i>tectorum</i>	L.	Bro_tec
<i>Bystropogon</i>	<i>origanifolius</i>	L'Hér.	Bys_ori
<i>Calendula</i>	<i>arvensis</i>	(Vaill.) L.	Cal_arv
<i>Carduus</i>	<i>tenuiflorus</i>	Curtis	Car_ten
<i>Carlina</i>	<i>salicifolia</i>	(L. f.) Cav.	Car_sal
<i>Carlina</i>	<i>xeranthemoides</i>	L. f.	Car_xer
<i>Carthamus</i>	<i>lanatus</i>	L.	Car_lan
<i>Chamaecytisus</i>	<i>proliferus</i>	(L. f.) Link	Cha_pro
<i>Cistus</i>	<i>monspeliensis</i>	L.	Cis_mon
<i>Cistus</i>	<i>symphytifolius</i>	Lam.	Cis_sym
<i>Convolvulus</i>	<i>althaeoides</i>	L.	Con_alt
<i>Cupressus</i>	<i>macrocarpa</i>	Hartw.	Cup_mac
<i>Daphne</i>	<i>gnidium</i>	L.	Dap_gni
<i>Davallia</i>	<i>canariensis</i>	(L.) Sm.	Dav_can

Descurainia	<i>lemsii</i>	Bramwell	Des_lem
Echium	<i>plantagineum</i>	L.	Ech_pla
Echium	<i>virescens</i>	DC.	Ech_vir
Erica	<i>arborea</i>	L.	Eri_arb
Erodium	<i>chium</i>	(L.) Willd.	Ero_chi
Erodium	<i>cicutarium</i>	(L.) L`Hér. in Aiton	Ero_cic
Eschscholzia	<i>californica</i>	Cham.	Esc_cal
Eucalyptus	<i>globulus</i>	Labill.	Euc_glo
Euphorbia	<i>balsamifera</i>	Aiton	Eup_bal
Euphorbia	<i>berthelotii</i>	Bolle ex Boiss. in DC.	Eup_ber
Euphorbia	<i>lamarckii</i>	Sweet	Eup_lam
Ferula	<i>linkii</i>	Webb	Fer_lin
Ficus	<i>carica</i>	L.	Fic_car
Filago	<i>gallica</i>	L.	Log_gal
Foeniculum	<i>vulgare</i>	Mill.	Foe_vul
Fumaria	<i>bastardii</i>	Boreau	Fum_bas
Galium	<i>scabrum</i>	L.	Gal_sca
Gennaria	<i>diphylla</i>	(Link) Parl.	Gen_dip
Geranium	<i>robertianum</i>	L.	Ger_rob
Hemionitis	<i>marantae</i>	(Bory ex Willd.) Christenh.	Not_mar
Hemionitis	<i>pulchella</i>	Christenh.	All_fra
Hyparrhenia	<i>hirta</i>	(Delile) Llauradó ex G. López	Hyp_sin
Hypericum	<i>calycinum</i>	Choisy	Hyp_gra
Hypericum	<i>canariense</i>	L.	Hyp_can
Hypericum	<i>reflexum</i>	L. f.	Hyp_ref
Hypochaeris	<i>glabra</i>	L.	Hyp_gla
Ilex	<i>canariensis</i>	Poir. in Lamarck	Ile_can
Juniperus	<i>cedrus</i>	Webb & Berthel.	Jun_ced
Juniperus	<i>turbinata</i>	Guss.	Jun_tur
Kleinia	<i>neriifolia</i>	Haw.	Kle_ner
Lamarckia	<i>aurea</i>	(L.) Moench	Lam_aur
Lavandula	<i>canariensis</i>	Mill.	Lav_can
Lotus	<i>campylocladus</i>	Webb & Berthel.	Lot_cam
Lupinus	<i>angustifolius</i>	L.	Lup_ang
Lysimachia	<i>arvensis</i>	(L.) U.Manns & Anderb.	Lys_arv
Lysimachia	<i>linum-stellatum</i>	L.	Lys_lin
Melica	<i>teneriffae</i>	Haeck ex. Christ	Mel_ten
Micromeria	<i>hyssopifolia</i>	Webb & Berthel.	Mic_hys
Micromeria	<i>varia</i>	Benth.	Mic_var
Morella	<i>faya</i>	(Aiton) Wilbur	Mor_fay
Neotinea	<i>maculata</i>	(Desf.) Stearn	Neo_mac
Opuntia	<i>maxima</i>	Mill.	Opu_max
Oxalis	<i>pes-caprae</i>	L.	Oxa_pes

Pallenis	<i>spinosa</i>	(L.) Cass. in Cuvier	Pal_spi
Pericallis	<i>cruenta</i>	(L`Hér.) Bolle	Per_cru
Periploca	<i>laevigata</i>	Aiton	Per_lae
Phagnalon	<i>purpurascens</i>	Sch. Bip. in Webb & Berthel.	Pha_pur
Phagnalon	<i>saxatile</i>	(L.) Cass.	Pha_sax
Pinus	<i>canariensis</i>	C. Sm. ex DC. in Buch	Pin_can
Piptatherum	<i>coerulescens</i>	(Desf.) P. Beauv.	Pip_coe
Polypodium	<i>macaronesicum</i>	A. E. Bobrov	Pol_mac
Pteridium	<i>aquilinum</i>	(L.) Kuhn in Von der Decken	Pte_aqu
Pterocephalus	<i>lasiospermus</i>	Link ex Buch	Pte_las
Ranunculus	<i>cortusifolius</i>	Willd.	Ran_cor
Raphanus	<i>raphanistrum</i>	L.	Rap_rap
Retama	<i>rhodorhizoides</i>	Webb & Berthel.	Ret_rho
Romulea	<i>columnae</i>	Sebast. & Mauri	Rom_col
Rubia	<i>fruticosa</i>	Aiton	Rub_fru
Rubus	<i>ulmifolius</i>	Schott	Rub_ulm
Rumex	<i>lunaria</i>	L.	Rum_lun
Rumex	<i>maderensis</i>	Lowe	Rum_mad
Scilla	<i>haemorrhoidalis</i>	Webb & Berthel.	Sci_hae
Scorpiurus	<i>muricatus</i>	L.	Sco_mur
Scrophularia	<i>glabrata</i>	Aiton	Scr_gla
Sedum	<i>rubens</i>	L.	Sed_rub
Senecio	<i>teneriffae</i>	Sch. Bip. ex Bolle	Sen_ten
Sherardia	<i>arvensis</i>	L.	She_arv
Sideritis	<i>roteneriffae</i>	Negrín & P. Pérez	Sid_oro
Silene	<i>berthelotiana</i>	Webb ex Christ	Sil_ber
Silene	<i>vulgaris</i>	(Moench) Garcke	Sil_vul
Solanum	<i>nigrum</i>	L.	Sol_nig
Sonchus	<i>acaulis</i>	Dum. Cours.	Son_aca
Sonchus	<i>canariensis</i>	(Sch. Bip.) Boulos	Son_can
Sonchus	<i>congestus</i>	Willd.	Son_con
Sonchus	<i>leptocephalus</i>	Cass. in Cuvier	Son_lep
Sonchus	<i>microcarpus</i>	(Boulos) U. Reifenb. & A. Reifenb.	Son_mic
Sonchus	<i>oleraceus</i>	L.	Son_ole
Stellaria	<i>media</i>	(L.) Vill.	Ste_med
Tolpis	<i>barbata</i>	(L.) Gaertn.	Tol_bar
Tragopogon	<i>porrifolius</i>	L.	Tra_por
Ulex	<i>europaeus</i>	L.	Ule_eur
Umbilicus	<i>gaditanus</i>	Boiss.	Umb_gad
Vicia	<i>aphylla</i>	C. Sm. ex Buch	Vic_aph
Vicia	<i>disperma</i>	DC.	Vic_dis
Vulpia	<i>myuros</i>	(L.) C. C. Gmel.	Vul_myu
Wahlenbergia	<i>lobelioides</i>	(L. f.) Link	Wah_lob

Appendix 3 – PCA results

Topographic data PCA

The three first axes of the PCA based on the topographic data per plots (Fig. 9) account for 79.53% of the environmental variance (PCA1: 33.68%; PCA2: 25.78%; PCA3: 20.07%). The first axis is mostly composed of the aspect and the soil and stone coverage, particularly the last one (26.19%, 26.11% and 39,4% contribution respectively). The second axis is more correlated to the slope and the altitude variables (52.68% and 45.44% contribution respectively while the third is also correlated to the aspect and soil cover like the first one, but slightly more (37.02% and 44.39% contribution respectively). Together, the three first PCA axes explain 63.37% of the aspect, 59% of the slope, 61.36% of the altitude, 70.96% of the soil coverage and 45.3% of the stone coverage. On the first axis, the stone coverage (0.81 correlation) and aspect (0.66 correlation) are opposed to the soil coverage (-0.66 correlation). The second axis opposes the slope (0.82 correlation) to the altitude (-0.76 correlation) and the third axis groups the soil coverage (0.66 correlation) to the aspect (0.61 correlation).

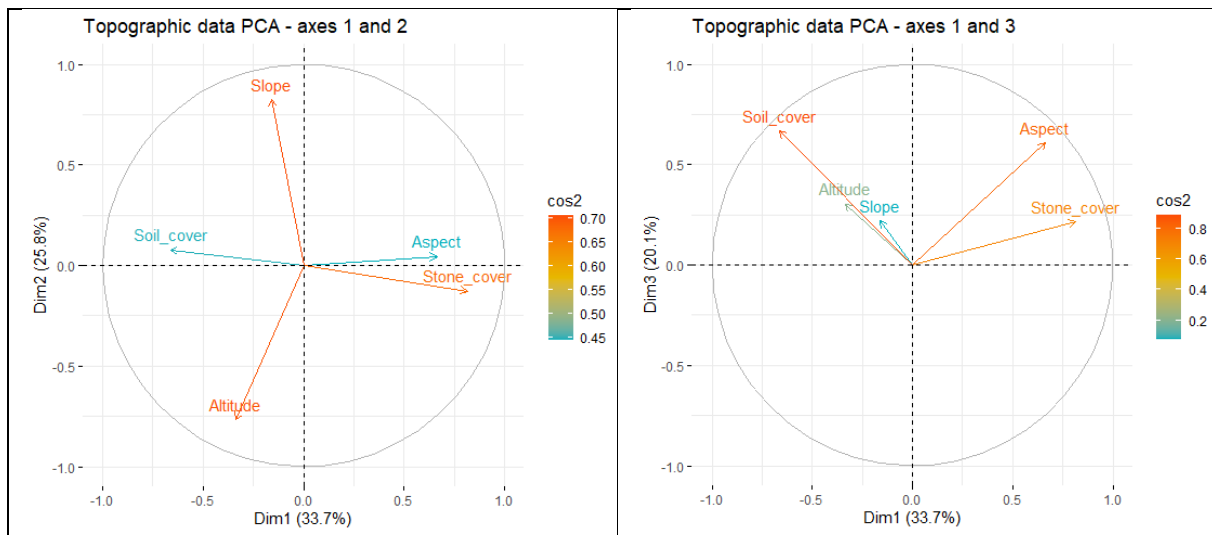


Figure 9 - Correlation circles between the three first axes of the topographic data PCA. The percentages show the percentage of variance explained by the axis. The name of each variable is written on the arrows. The color gradient shows the contribution (\cos^2) of the variables to the axis. 1st (Dim1) and 2nd (Dim2) axes: left; 1st (Dim1) and 3rd (Dim3) axes: right.

The plots that contribute to more than 5% to the first axis are the n.6 (Sa: 29.06%; Sb: 25.72%) and the n.3 (Sa: 7.8%; Sb: 6.42%). Moreover, these four plots are opposed on the axis. The plots n.8 (Sa: 11.58%; Sb: 10.94%), 2 (Sa: 7.82%; Sb: 7.6%) and n.12 (Sa: 6.32%; Sb: 6.32%) satisfy the same condition for the second axis while it is the plots n.5 (Sa: 12.5%; Sb: 10.45%), n.17 (Sa: 7.6%; Sb: 6.44%), n.13Sa (6.76%) and n.7Sa (6.64%) for the third axis (Fig. 10-11). Those plots have high values of the most correlated variables of their respective axis. For example, the plot n.6 (Sa, Sb) has the highest value of stone coverage and the plot n.8 (Sa, Sb) was the steepest one.

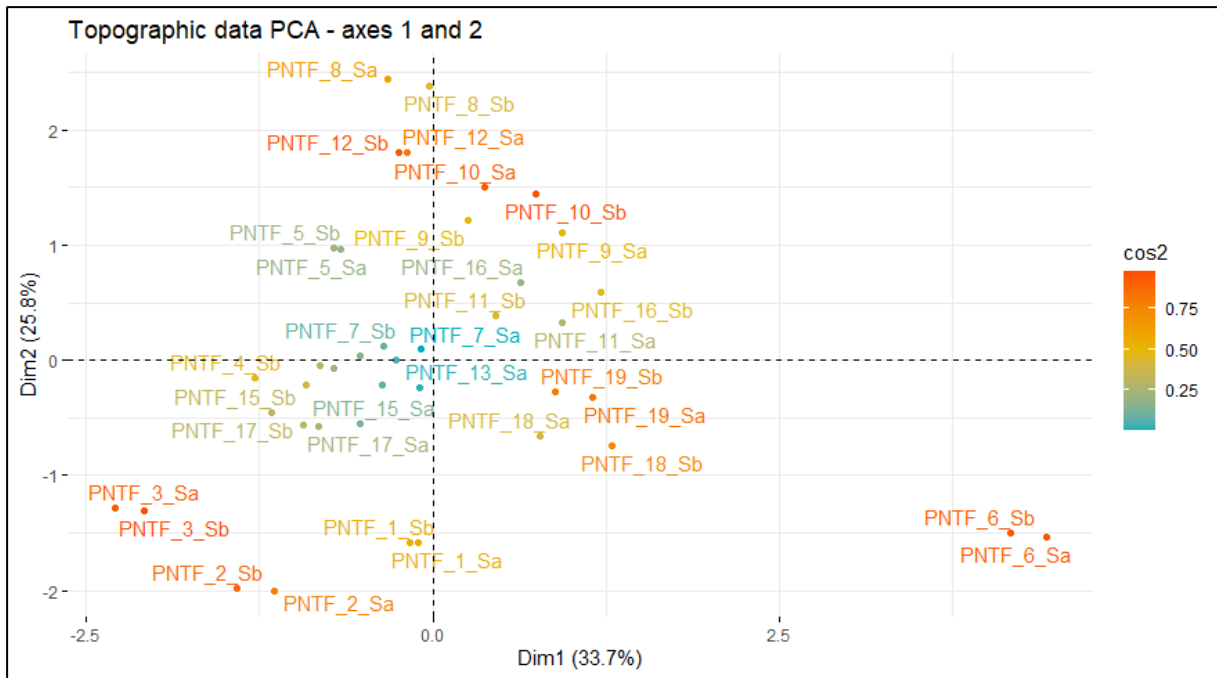


Figure 10 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the topographic data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = “Pinar Tenerife”.

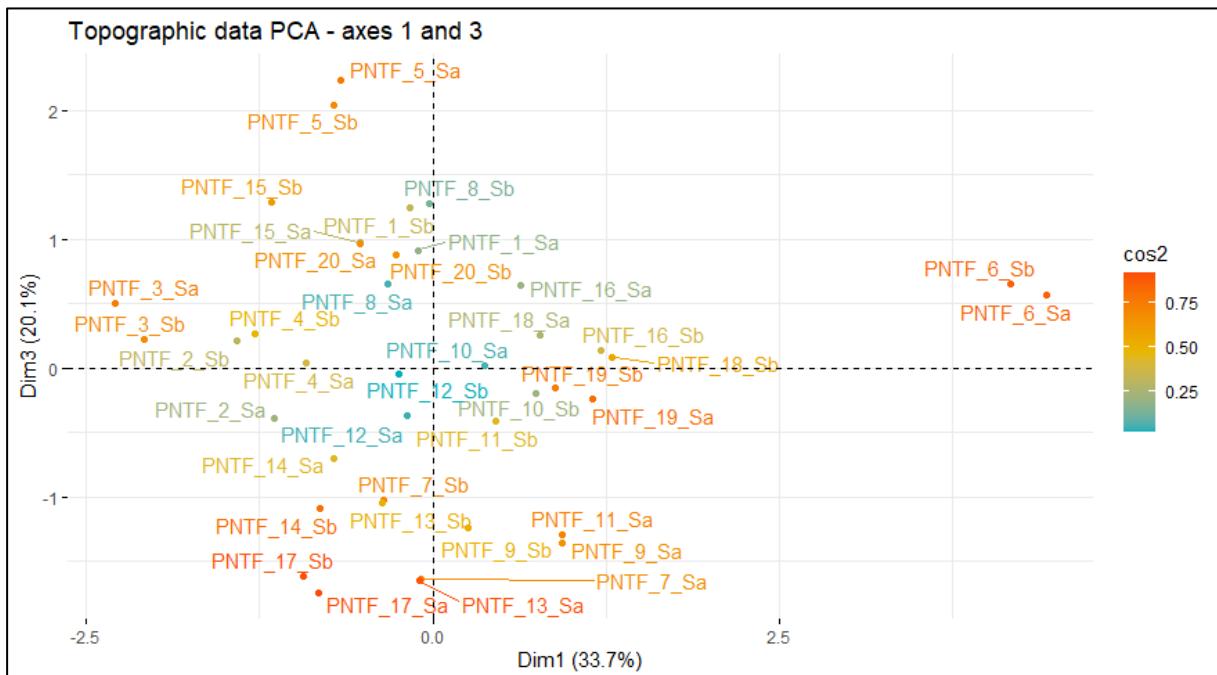


Figure 11 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the topographic data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = “Pinar Tenerife”.

Climatic data PCA

The three first axes of the PCA based on the CHELSA climatic variables per plots (Fig. 12) account for 86.92% of the environmental variance (PCA1: 48.37%; PCA2: 27.53%; PCA3: 11.02%). The variables that contribute the most to PCA1_{climat} are the maximum temperature of the warmest month (bio05, 9.32%), the mean temperature of the warmest quarter (bio10, 8.37%) and the annual precipitation (bio12, 7.78%). For PCA2_{climat}, it is the minimum temperature of the coldest month (bio06, 15.92%), the mean temperature of coldest quarter (bio11, 12.3%) and the mean temperature of wettest quarter (bio08, 11.03%) variables that contribute the most. The third axis is mostly represented by the isothermality (bio03, 19.32%) and the precipitation of the coldest quarter (bio19, 11.47%) variables. The maximum temperature of the warmest month and the mean temperature of the warmest quarter (0.92 and 0.88 correlation) are opposed to the annual precipitation (-0.84 correlation) on the first axis while the minimum temperature of the coldest month, the mean temperature of the coldest quarter and the mean temperature of the wettest quarter are positively correlated to the second axis (0.91, 0.8 and 0.76 correlation respectively). The isothermality and the precipitation of the coldest quarter are also opposed on the third axis (-0.64 and 0.49 correlation respectively).

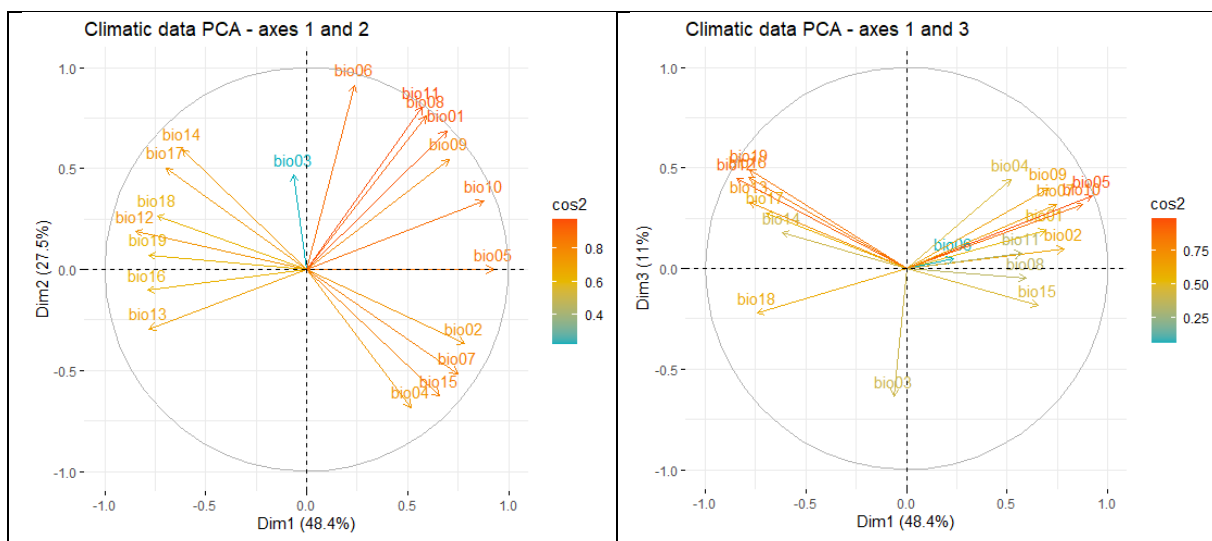


Figure 12 - Correlation circles between the three first axes of the climatic data PCA. The percentages show the percentage of variance explained by the axis. The code of each variable is written on the arrows, see Appendix 1 for more details. The color gradient shows the contribution (\cos^2) of the variables to the axis. 1st (Dim1) and 2nd (Dim2) axes: left; 1st (Dim1) and 3rd (Dim3) axes: right.

The plots that contribute to more than 5% for the three first axes of the PCA are the plots n.3 (Sa, Sb), n.2 (Sa, Sb), n.1 (Sa, Sb) and n.7Sa for the first axis (41.36% together); the plots n.1 (Sa, Sb), n.16 (Sa, Sb) and n.15 (Sa, Sb) for the second axis (56.5% together); the plots n.16 (Sa, Sb), n.17 (Sa, Sb), n.4 (Sa, Sb), n.1 (Sa, Sb) and n.3 (Sa, Sb) for the third axis (71.68%) (Fig. 13-14). Two groups can be differentiated on the Figure 15. More details about those groups can be found in the clustering analysis results section.

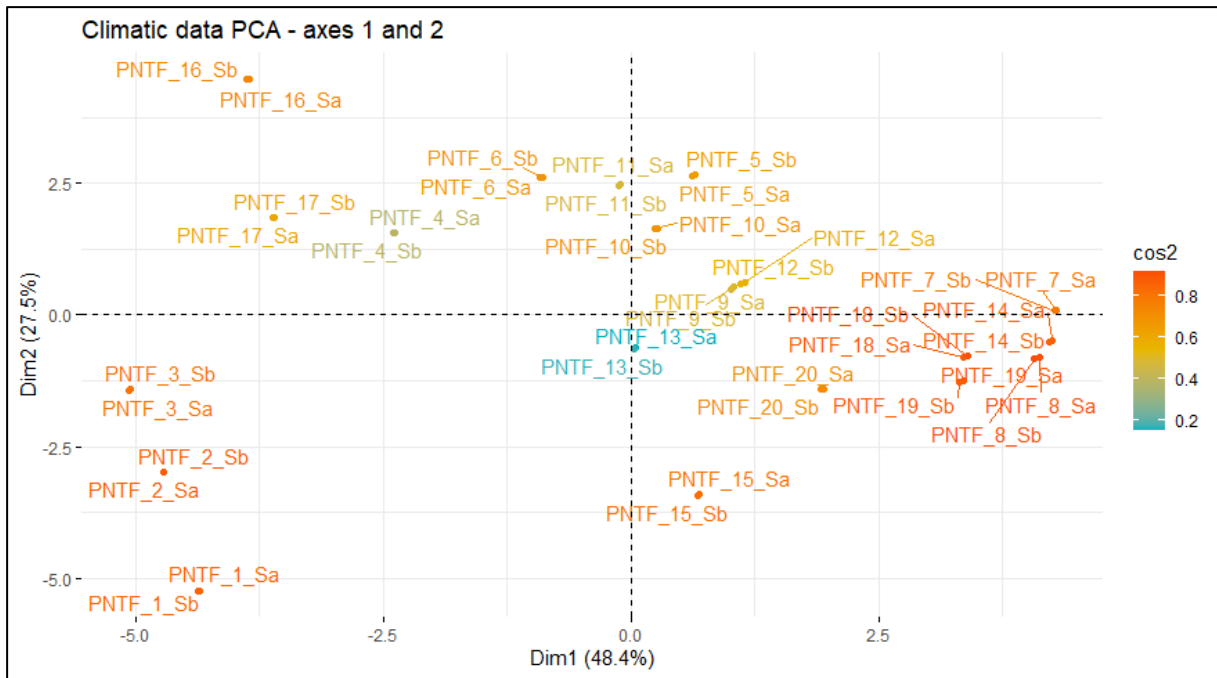


Figure 13 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the climatic data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

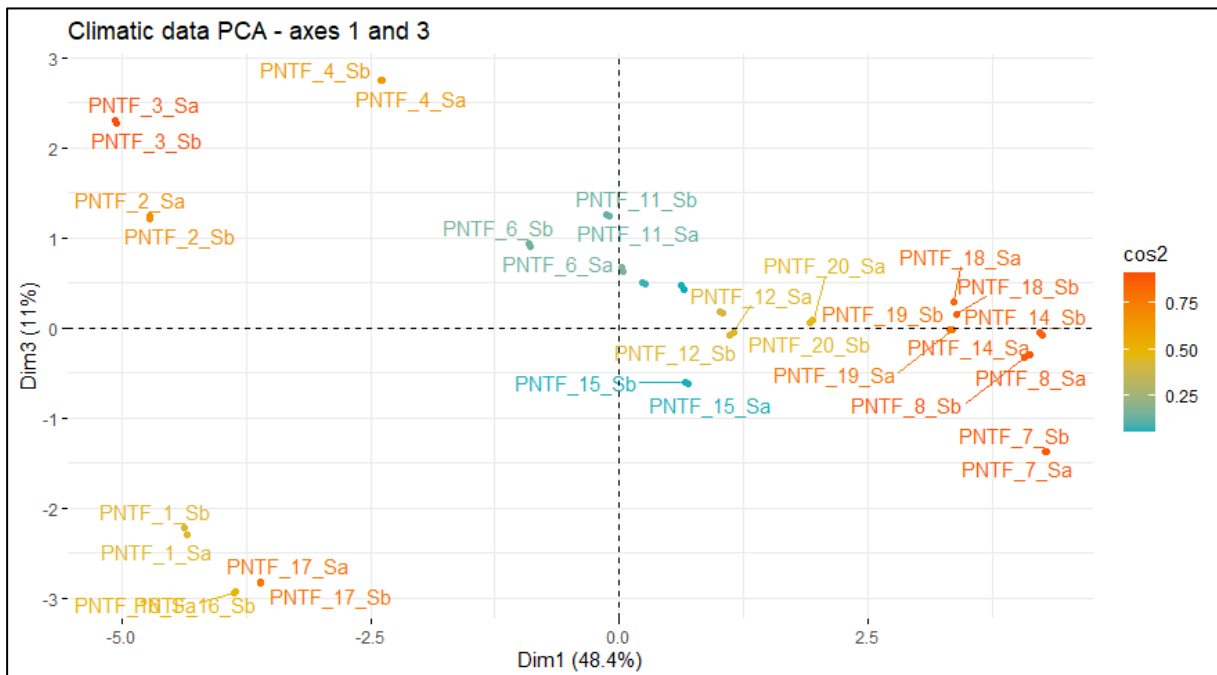


Figure 14 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the climatic data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

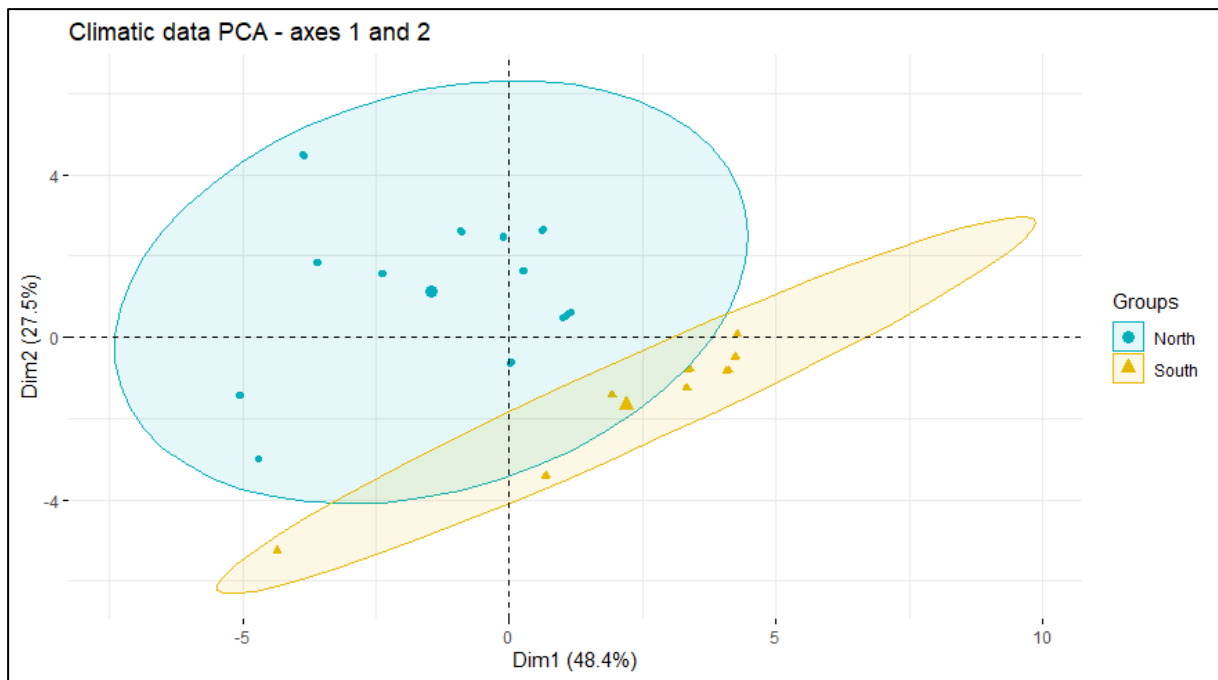


Figure 15 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the climatic data PCA. The percentages show the percentage of variance explained by the axis. The colors indicate the location of the plot on the island: North (blue) or South face (yellow).

Coverage data PCA

The three first axes of the PCA based on the native species coverage per plots (Fig. 16) account for 26.26% of the floristic variance (PCA1: 10.53%; PCA2: 8.88%; PCA3: 6.85%). Ten species contribute for more than 5% in the first PCA axis (*Erodium cicutarium* 8.97%, *Carduus tenuiflorus* 8.97%, *Carlina xeranthemoides* 8.77%, *Piptatherum coerulescens* 8.36%, *Sideritis oroteneriffae* 8%, *Melica teneriffae* 8%, *Hypochaeris glabra* 8%, *Silene berthelotiana* 7.22%, *Argyranthemum adauctum* 6.71%, *Lotus campylocladus* 5.36%). For the second axis, only one species accounts for more than 5% (*Ranunculus cortusifolius* 5.28%) and 36 for more than 1%. Four species satisfy the same condition for the third axis (*Echium virescens* 5.8%, *Bromus* sp. 5.8%, *Adenocarpus foliolosus* 5.8%, *Kleinia neriifolia* 5.41%) and 23 species contribute for more than 1%. The species mentioned here above are positively correlated to their PCA axis except for *Ranunculus cortusifolius* that is negatively correlated to the second axis (between 0.74 and 0.95 for PCA1_{coverage}; -0.67 for PCA2_{coverage}; between 0.6 and 0.62 for PCA3_{coverage}).

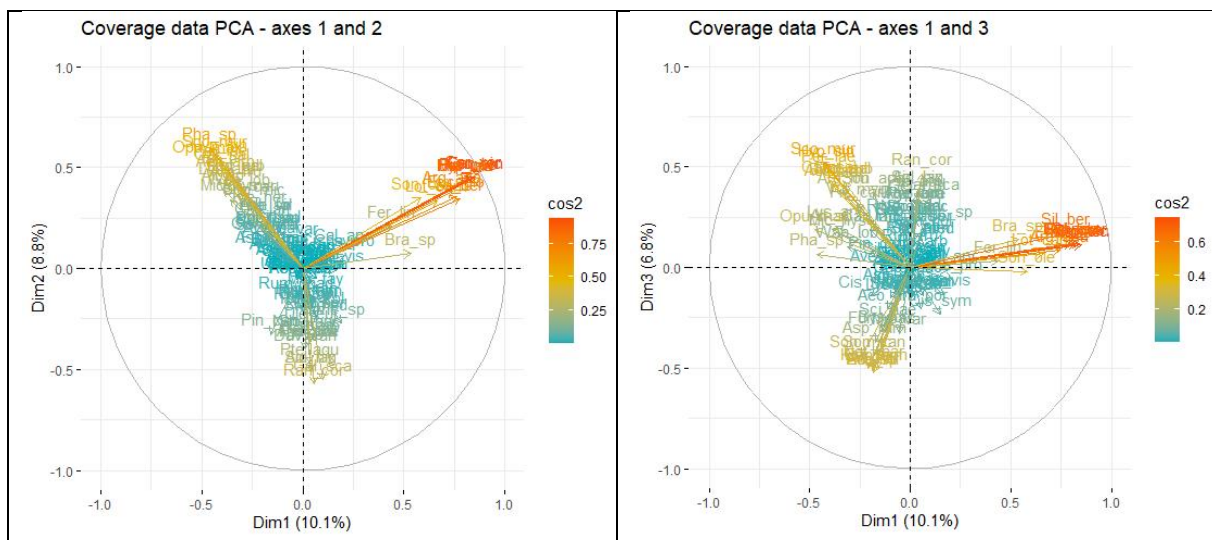


Figure 16 - Correlation circles between the three first axes of the native species coverage data PCA. The percentages show the percentage of variance explained by the axis. The code of each variable is written on the arrows, see Appendix 2 for more details. The color gradient shows the contribution (\cos^2) of the variables to the axis. 1st (Dim1) and 2nd (Dim2) axes: left; 1st (Dim1) and 3rd (Dim3) axes: right.

The plot n.1Sa contributes alone to 78.8% to the first PCA axis, followed by the plot 1Sb with 9.29% and the plot n.8Sa with 2.81%. The plot n.1Sa is also the only one that had the ten species that contribute the most to PCA1_{coverage} together while the other plots only contained part of it. The second axis is represented principally by the plots n.8Sa (29.11%), n.5 (Sa: 16.64%; Sb: 15.65%) and n.12Sa (8.82%). They contribute to 70.22% together. Surprisingly the plots n.8Sa and n.12Sa did not have any *Ranunculus cortusifolius*. The third axis is also mainly represented by the plots n.8Sa (37.2%) and n.12Sa (27.68%) along with others than contribute to more than 5% (n.19Sa, n.12Sb, n.11Sa) (Fig. 17-18). The n.8Sa contains three out of the four most important species for PCA3_{coverage} and the n.12Sa only one of these same four. Most of the plots mentioned in this section are among the top 10 plots with the most species.

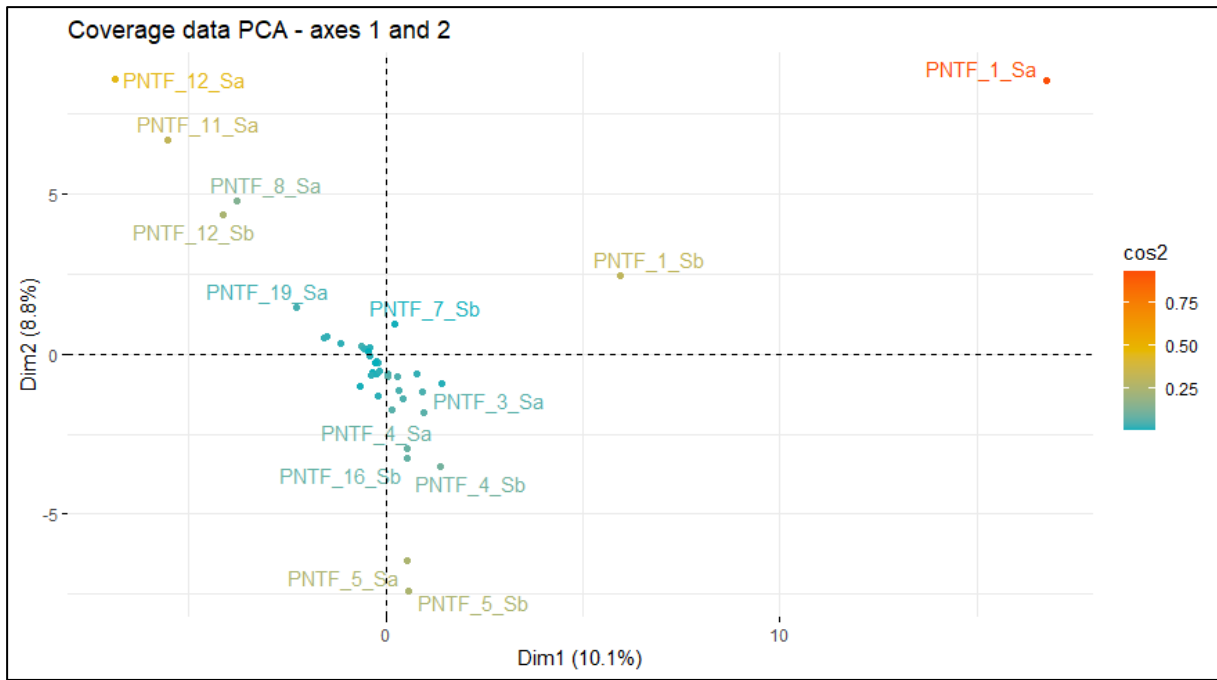


Figure 17 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the native species coverage data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

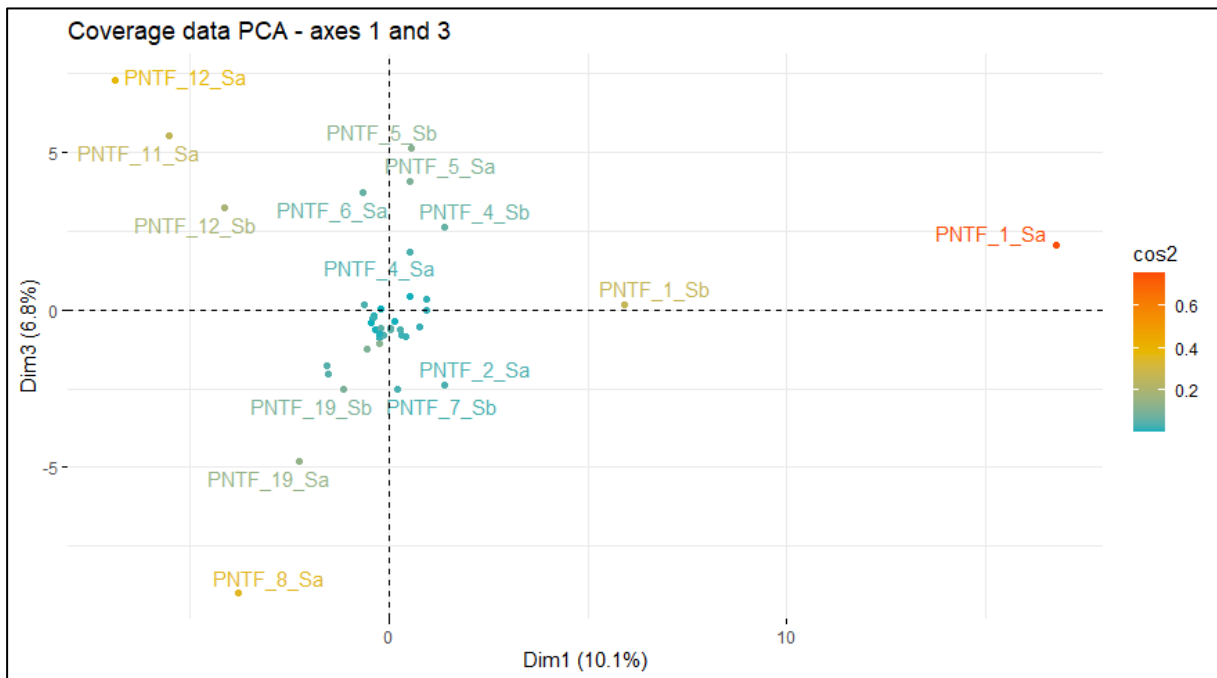


Figure 18 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the native species coverage data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

Dispersal mode data PCA

The three first axes of the PCA based on the native species dispersal mode per plots (Fig. 19) account for 90.35% of the floristic variance (PCA1: 46.89%; PCA2: 25.91%; PCA3: 17.55%). The first axis is made of 40.4% anemochory, 33.72% autochory, 25.71% epizoochory and 0.17% endozoochory contributions. The second axis is dominated by the endozoochory contribution (89.06%) and third axis by the epizoochory (59.03%) and autochory (29.67%) contributions. All variables are positively correlated to PCA1_{dispersal-mode} and PCA2_{dispersal-mode} (ANE: 0.87 correlation to PCA1; AUT: 0.8 correlation to PCA1; EPI: 0.69 correlation to PCA1; END: 0.96 correlation to PCA2). Epizoochory and autochory are opposed on the third axis with -0.64 and 0.46 correlation, respectively.

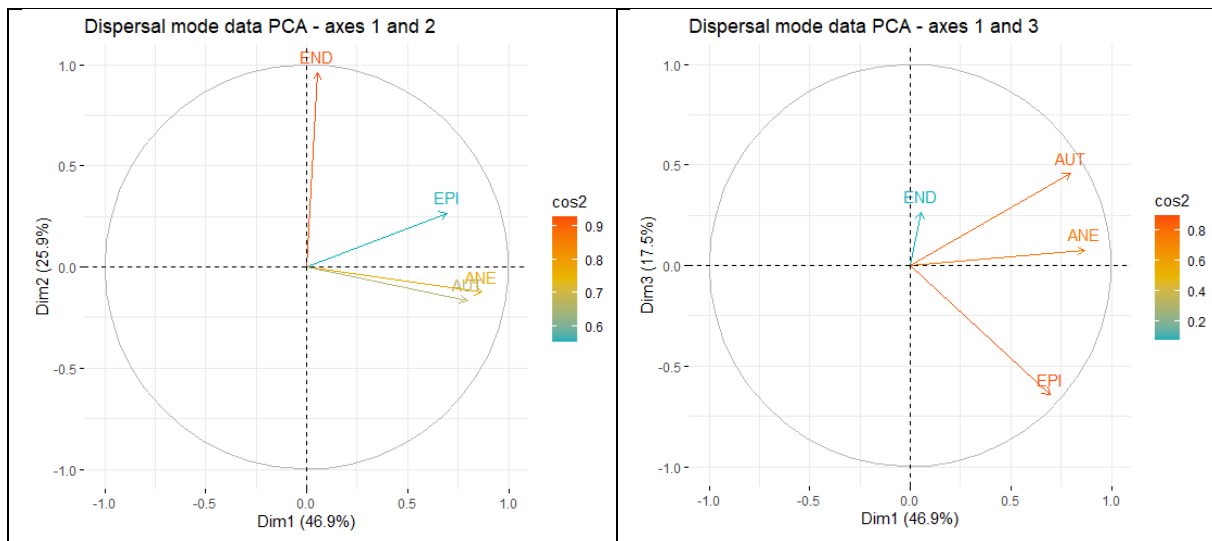


Figure 19 - Correlation circles between the three first axes of the dispersal mode data PCA. The percentages show the percentage of variance explained by the axis. The code of each variable is written on the arrows, see Material and Method section for more details. The color gradient shows the contribution (\cos^2) of the variables to the axis. 1st (Dim1) and 2nd (Dim2) axes: left; 1st (Dim1) and 3rd (Dim3) axes: right.

Here again, the plots that are the most represented are among the top 10 plots with the most species. N.1Sa, n.8Sa, n.12Sa and n.11Sa contribute for more than 5% to the first axis, for example. For the second axis, the repartition is fairer between the plots. The two plots n.5Sa and n.16Sa contribute for 43,62% of PCA2_{dispersal-mode} and are in the same top 10 plots, but the following ones in this selection are not anymore. For the third axis, only the plot n.10Sa is not among the most diverse plots but contributes for 10.54%, just behind the n.8Sa with 14.53% (Fig. 20-21).

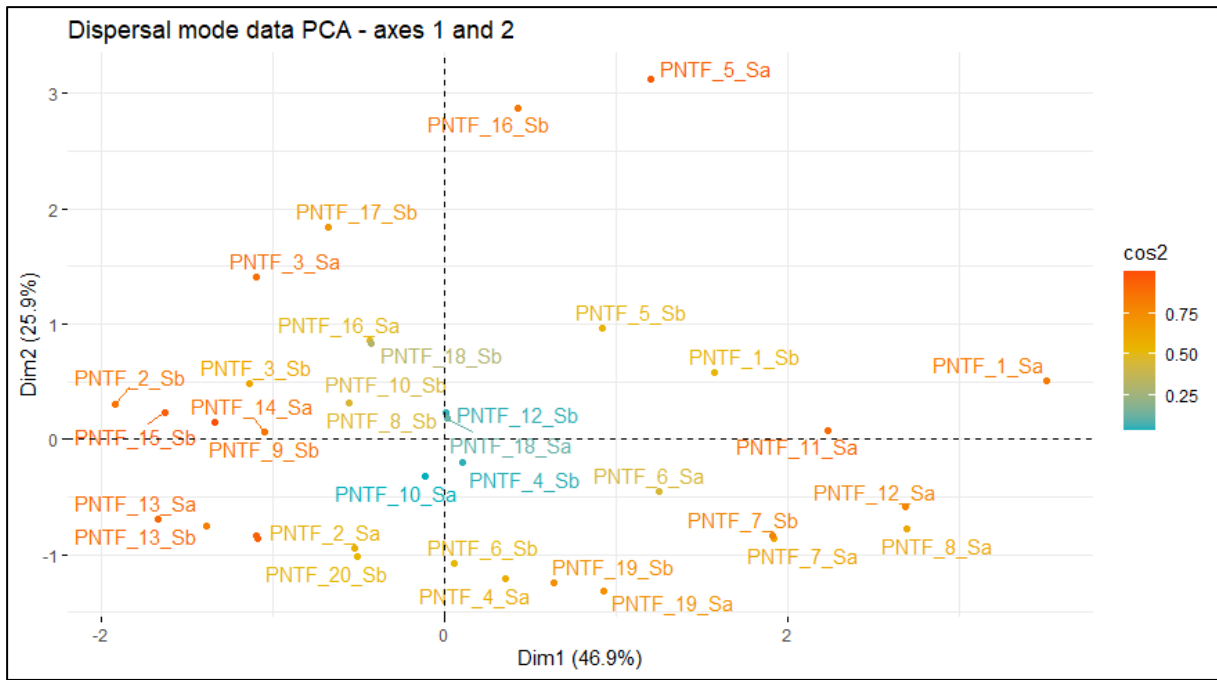


Figure 20 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the dispersal mode data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

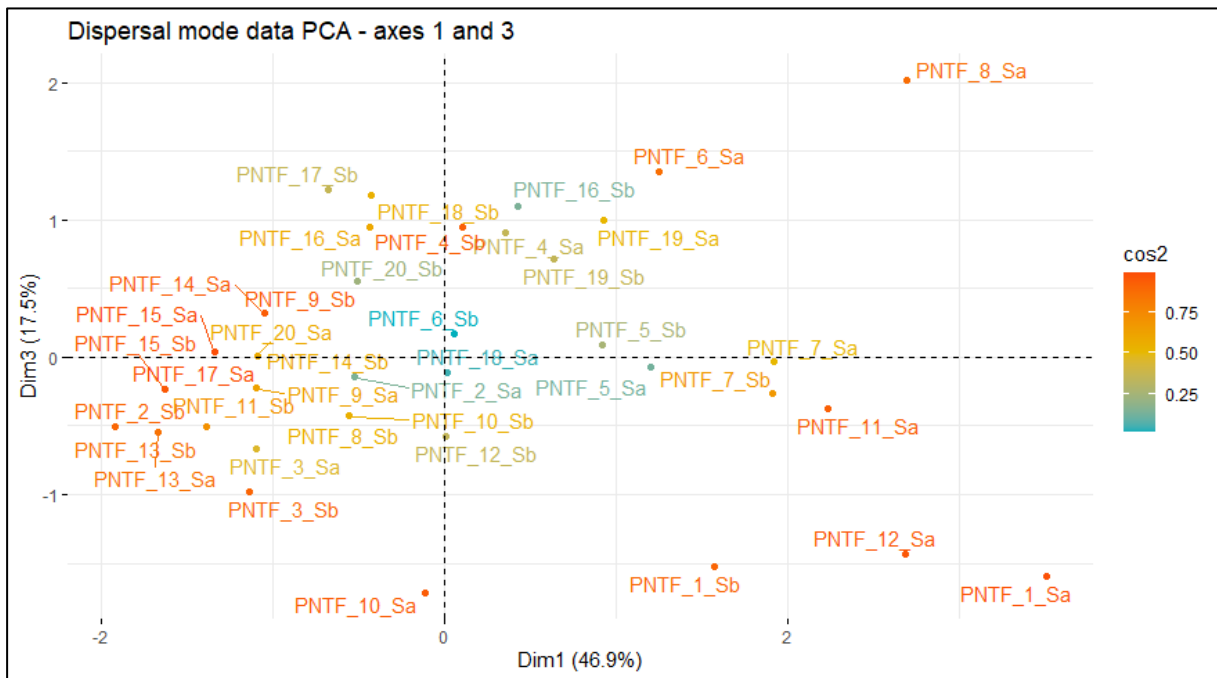


Figure 21 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the dispersal mode data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

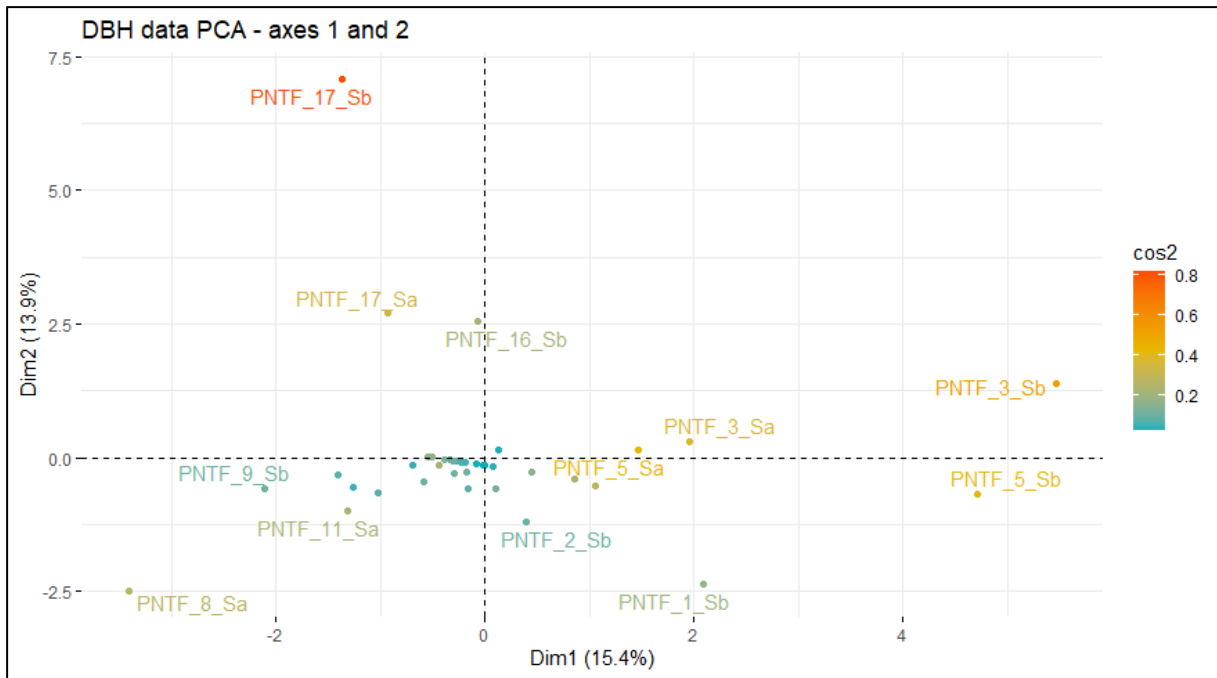


Figure 23 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the DBH data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

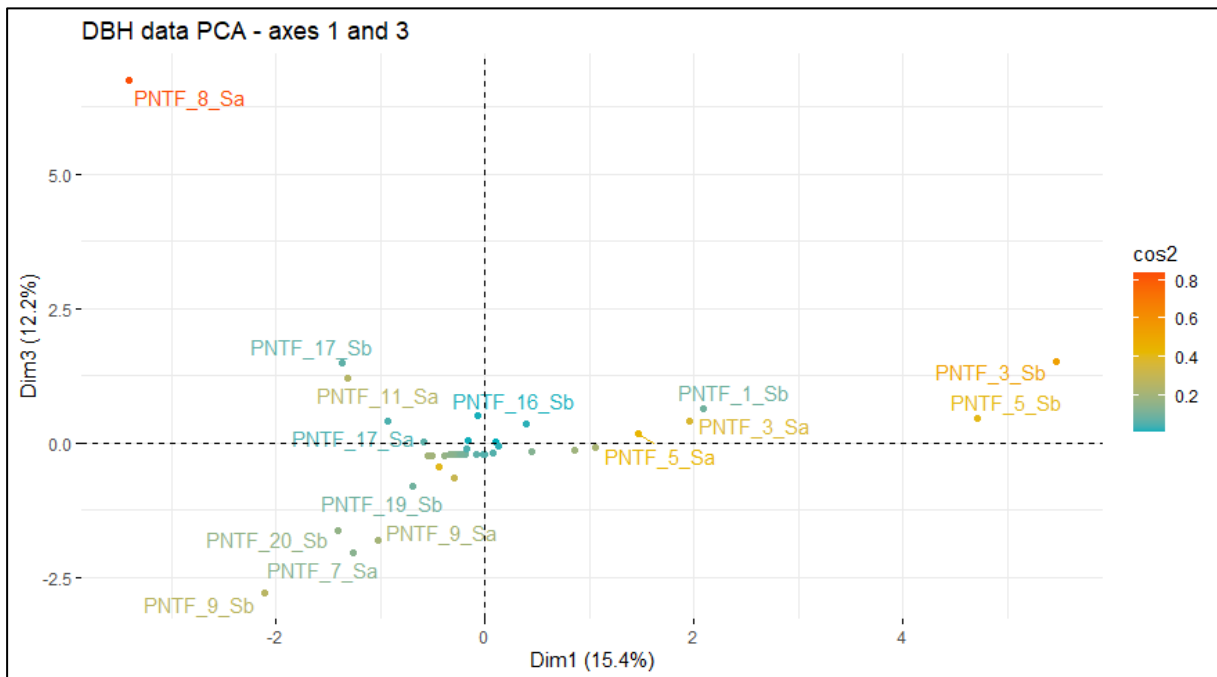


Figure 24 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the DBH data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

Plant volume data PCA

The three first axes of the PCA based on the native species plant volume per plots (Fig. 25) account for 26.44% of the floristic variance (PCA1: 10.18%; PCA2: 9.26%; PCA3: 6.99%). There are nine species with a contribution higher than 5% to the first axis and up to 9.55% (*Erodium cicutarium*, *Carduus tenuiflorus*, *Piptatherum coerulescens*, *Carlina xeranthemoides*, *Hypochaeris glabra*, *Sideritis oroteneriffae*, *Melica teneriffae*, *Silene berthelotiana*, *Brassica* sp.) from which all are positively correlated to this same axis (between 0.71 and 0.94 correlation). The same condition is satisfied by eight species for the second axis, with a maximum at 9.49% (*Ranunculus cortusifolius*, *Aichryson laxum*, *Pteridium aquilinum*, *Solanum nigrum*, *Galium scabrum*, *Erica arborea*, *Sherardia arvensis*, *Neotinea maculata*), and by nine species for the third axis with a maximum at 13.13% (*Avena canariensis*, *Silene vulgaris*, *Artemisia thuscula*, *Senecio teneriffae*, *Trifolium* sp., *Lysimachia arvensis*, *Sonchus oleraceus*, *Raphanus raphanistrum*, *Tragopogon porrifolius*). These species are positively correlated to the second axis between 0.81 and 0.9 and to the third axis between 0.57 and 0.92.

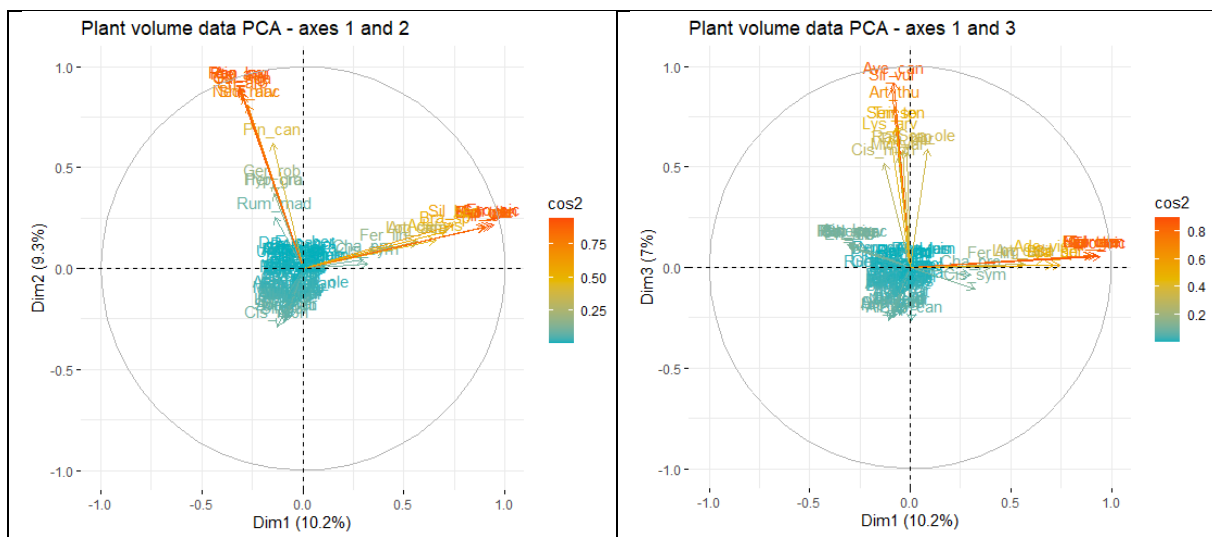


Figure 25 - Correlation circles between the three first axes of the plant volume data PCA. The percentages show the percentage of variance explained by the axis. The code of each variable is written on the arrows, see Appendix 2 for more details. The color gradient shows the contribution (\cos^2) of the variables to the axis. 1st (Dim1) and 2nd (Dim2) axes: left; 1st (Dim1) and 3rd (Dim3) axes: right.

The plot n.1Sa dominates the first axis with 79% contribution, the plot n.5Sa the second axis with 63.46% and the plots n.7 (Sa, Sb) the third axis with 47.7% and 33.07% each (Fig. 26-27). Again, these plots are among the most diverse ones of the sampling and contain all the species the most correlated to their respective axis.

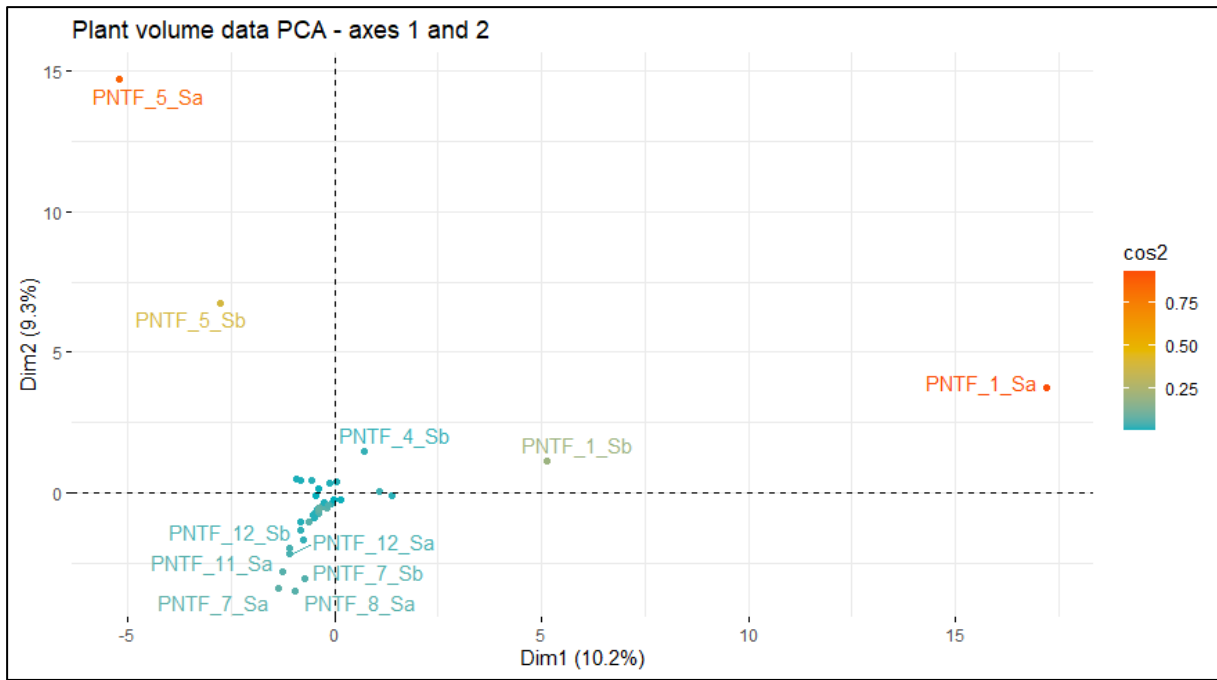


Figure 26 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the plant volume data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

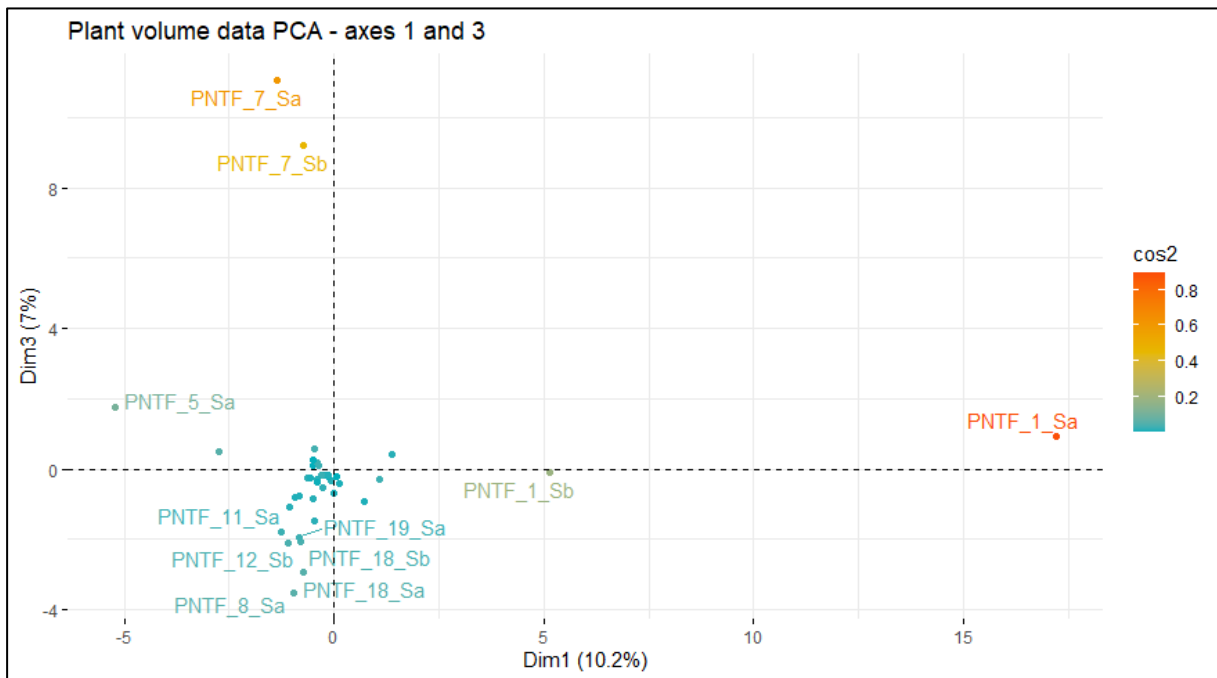


Figure 27 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the plant volume data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

Shape factor data PCA

The three first axes of the PCA based on the native species leaf shape factor per plots (Fig. 28) account for 27.44% of the floristic variance (PCA1: 10.64%; PCA2: 9.31%; PCA3: 7.48%). The species contribution does not exceed 6.2% with *Argyranthemum adauctum* for the first axis and there are only five species with a contribution higher than 5% not including the species already mentioned (*Carduus tenuiflorus*, *Erodium cicutarium*, *Piptatherum coerulescens*, *Carlina xeranthemoides*, *Lotus campylocladus*). Only one species exceeds the 5% contribution for the second PCA axis with 5.11% (*Galium scabrum*) while there are three species for the third PCA axis with between 7.18% and 5.39% (*Trifolium* sp., *Avena canariensis*, *Silene vulgaris*). They are all positively correlated to their respective axis with values between 0.61 and 0.78 for $PCA1_{\text{shape-factor}}$ and $PCA3_{\text{shape-factor}}$ and 0.5 for $PCA2_{\text{shape-factor}}$.

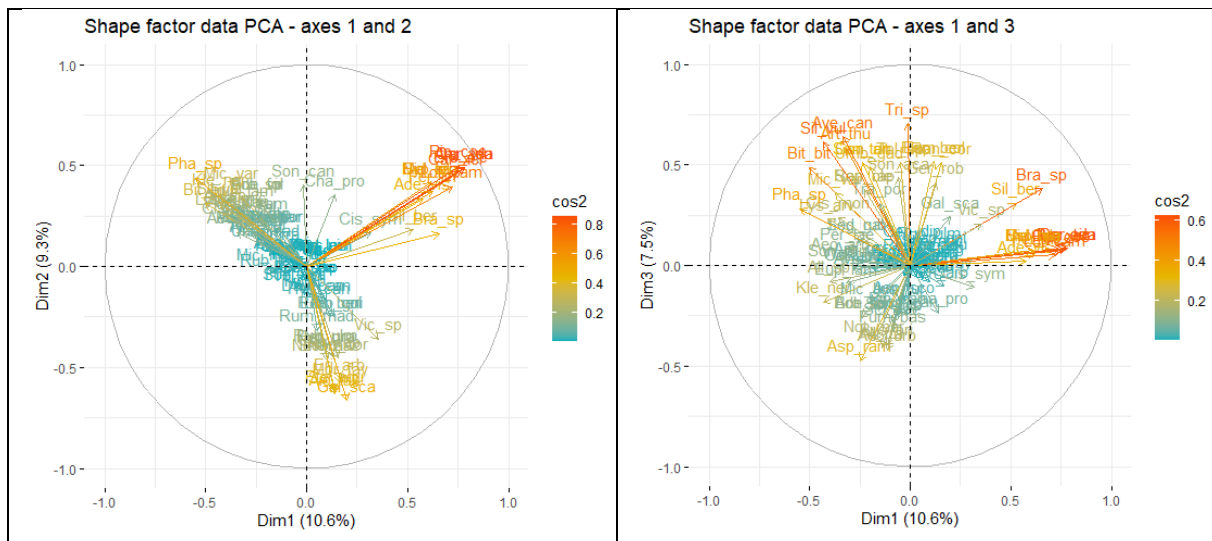


Figure 28 - Correlation circles between the three first axes of the shape factor data PCA. The percentages show the percentage of variance explained by the axis. The code of each variable is written on the arrows, see Appendix 2 for more details. The color gradient shows the contribution (\cos^2) of the variables to the axis. 1st (Dim1) and 2nd (Dim2) axes: left; 1st (Dim1) and 3rd (Dim3) axes: right.

Here too, the plot n.1 (Sa: 36.88%, Sb: 24.46%) dominates the first axis. There are the same number of plots contributing to more than 10% for the second (n.5Sa, n.5Sb, n.1Sa, n.8Sa) and the third (n.7Sa, n.7Sb, n.4Sa, n.4Sb) axes (Fig. 29-30).

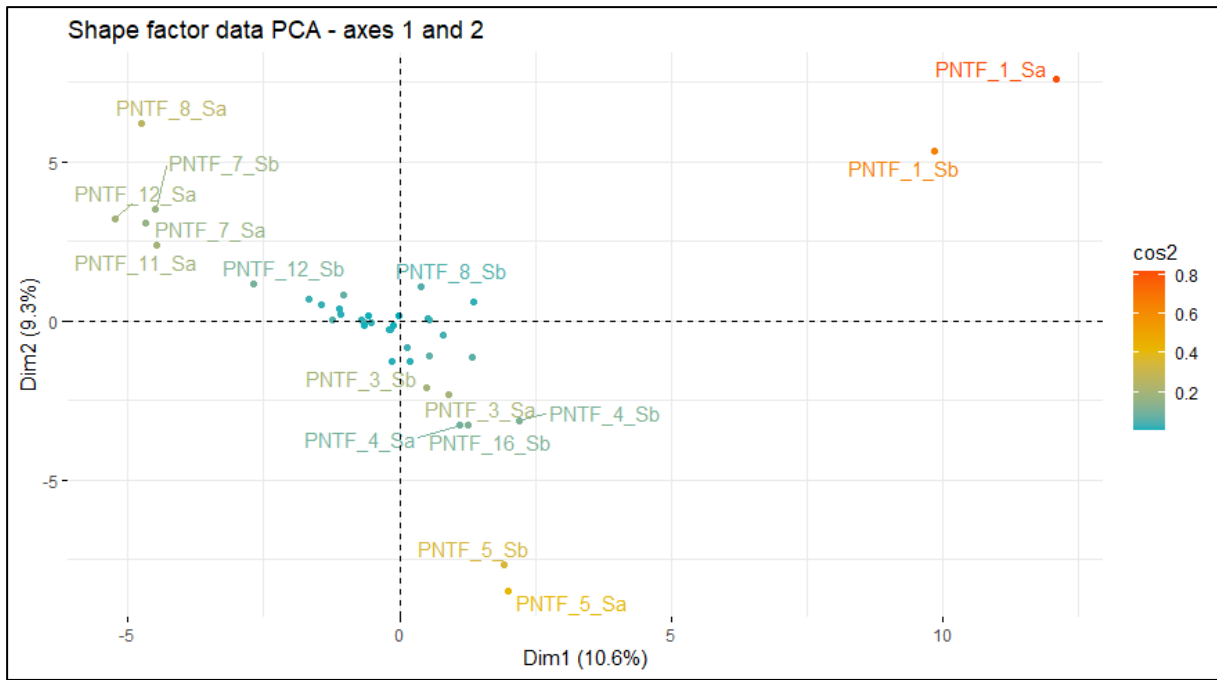


Figure 29 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the shape factor data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

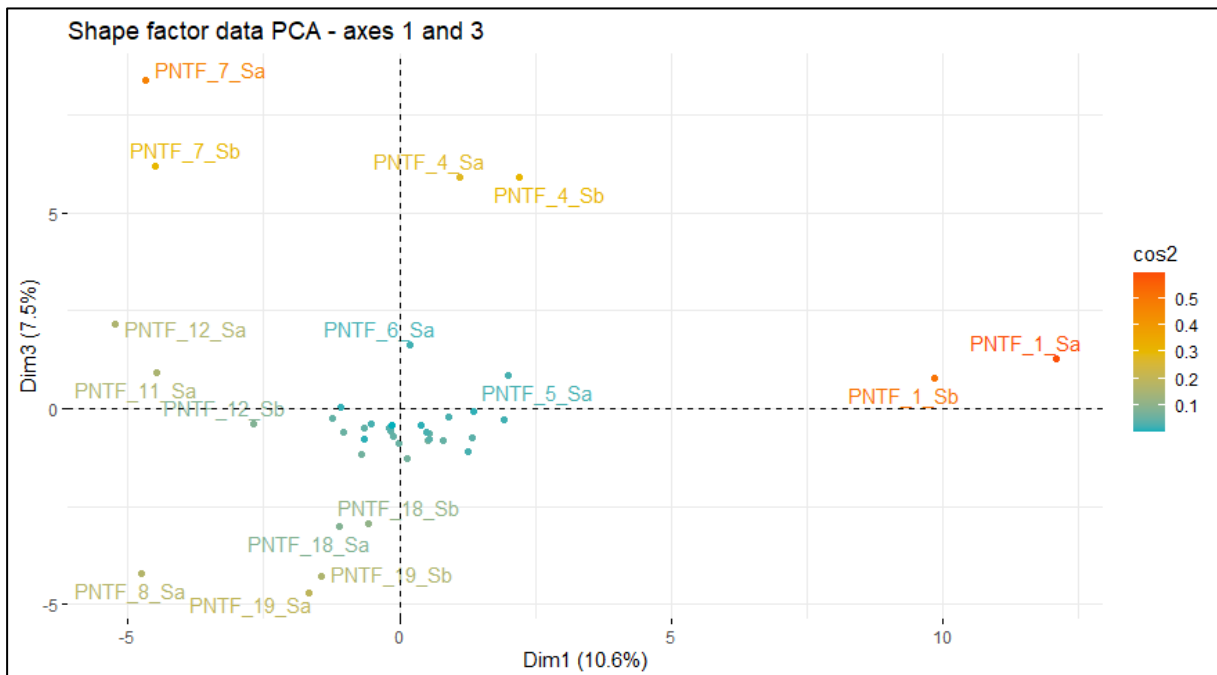


Figure 30 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the shape factor data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

SLA data PCA

The three first axes of the PCA based on the native species' specific leaf area per plots (Fig. 31) account for 29.13% of the floristic variance (PCA1: 11.14%; PCA2: 9.85%; PCA3: 8.14%). The first axis is composed of 44.86% of species contributing for more than 5% each (*Argyranthemum adauctum*, *Carduus tenuiflorus*, *Ferula linkii*, *Piptatherum coerulescens*, *Erodium cicutarium*, *Lotus campylocladus*, *Carlina xeranthemoides*) while no species has a contribution exceeding 4.79% (*Ranunculus cortusifolius*) for the second axis and only three for the third one (8.11% *Artemisia thuscula*, 8.06% *Avena canariensis*, 5.38% *Silene vulgaris*). Those species have positive correlations to their respective axis ranging from 0.74 to 0.86 for the first axis and from 0.64 to 0.78 for the third one. For the second axis, there are five species with a negative correlation higher than 0.6 even if they do not contribute a lot to this axis (*Ranunculus cortusifolius*, *Galium scabrum*, *Aichryson laxum*, *Pteridium aquilinum*, *Solanum nigrum*).

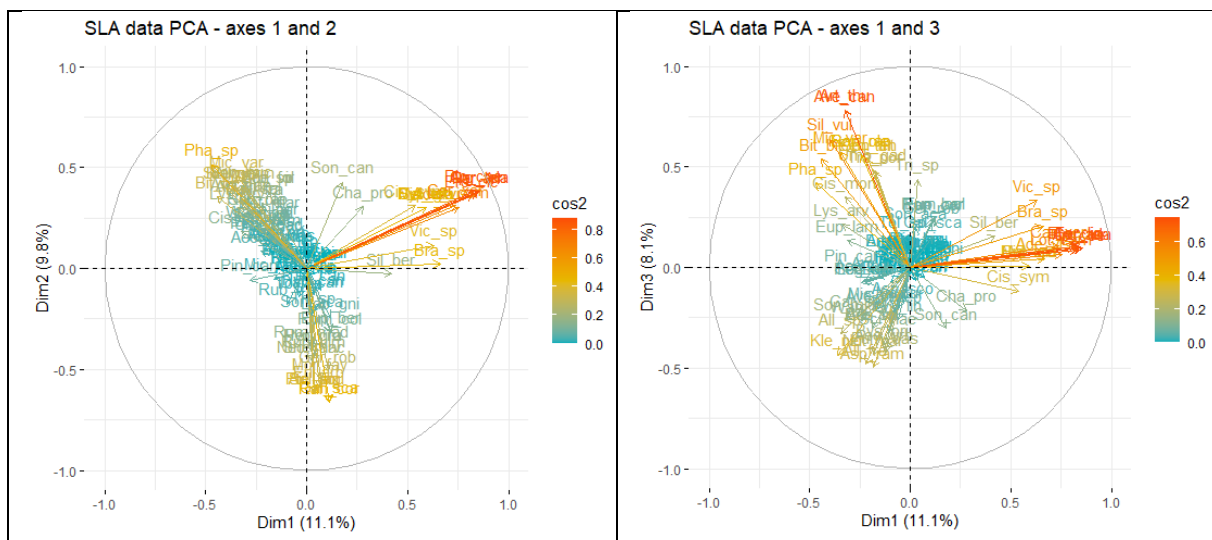


Figure 31 - Correlation circles between the three first axes of the SLA data PCA. The percentages show the percentage of variance explained by the axis. The code of each variable is written on the arrows, see Appendix 2 for more details. The color gradient shows the contribution (\cos^2) of the variables to the axis. 1st (Dim1) and 2nd (Dim2) axes: left; 1st (Dim1) and 3rd (Dim3) axes: right.

The plots n.1Sb and n.1Sa contribute to 37.3% and 34.24% to the first axis. The plots n.5Sa, n.5Sb and n.8Sa contribute to 20.6%, 15.66% and 14.24% to the second axis. The plots n.7Sb, n.7Sa and n.19Sa contribute to 30.49%, 28.33% and 10.31% to the third axis (Fig. 32-33). Almost all those plots are among the top 10 with the most species.

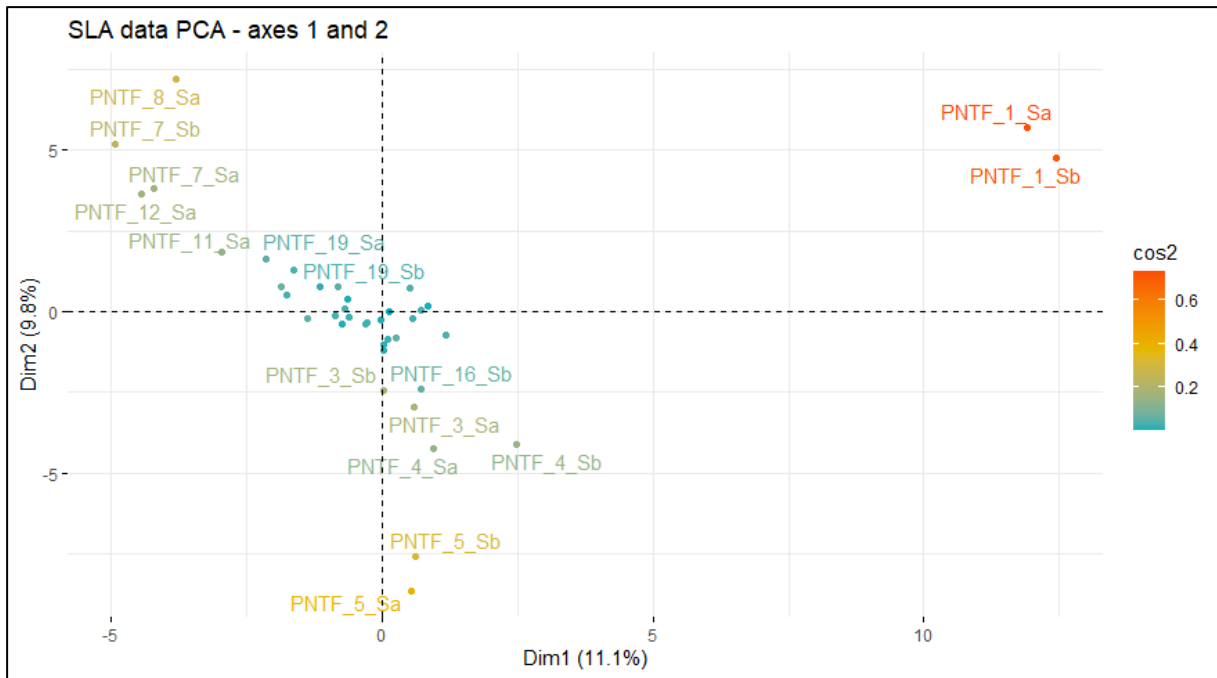


Figure 32 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the SLA data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

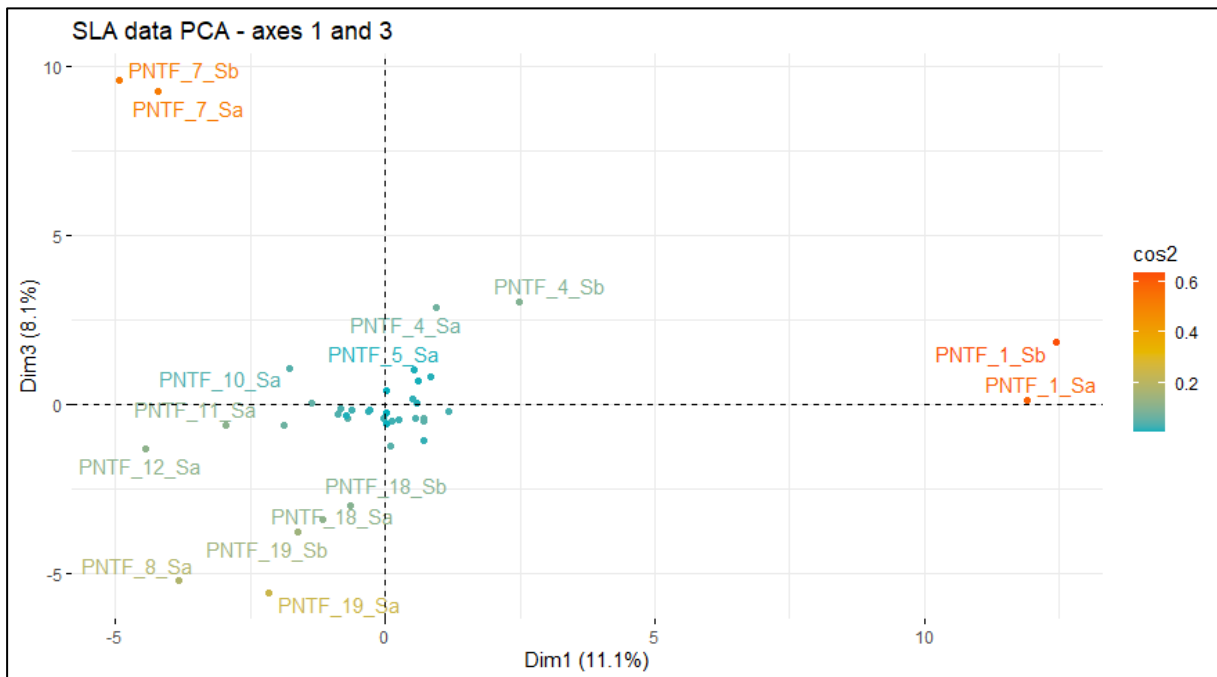


Figure 33 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the SLA data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

LDMC data PCA

The three first axes of the PCA based on the native species leaf dry matter content per plots (Fig. 34) account for 28.1% of the floristic variance (PCA1: 10.78%; PCA2: 9.64%; PCA3: 7.68%). There are eight species with a contribution higher than 5% for the first PCA axis (*Erodium cicutarium*, *Carlina xeranthemoides*, *Ferula linkii*, *Carduus tenuiflorus*, *Argyranthemum adauctum*, *Sideritis oroteneriffae*, *Melica teneriffae*, *Hypochaeris glabra*) and only one for the second axis (*Galium scabrum*) and the third one (*Silene vulgaris*). The eight species are positively correlated with the first axis between 0.76 and 0.84 but *Galium scabrum* is negatively correlated to the second axis (-0.73) while *Silene vulgaris* has a positive correlation of 0.7 with PCA3_{LDMC}.

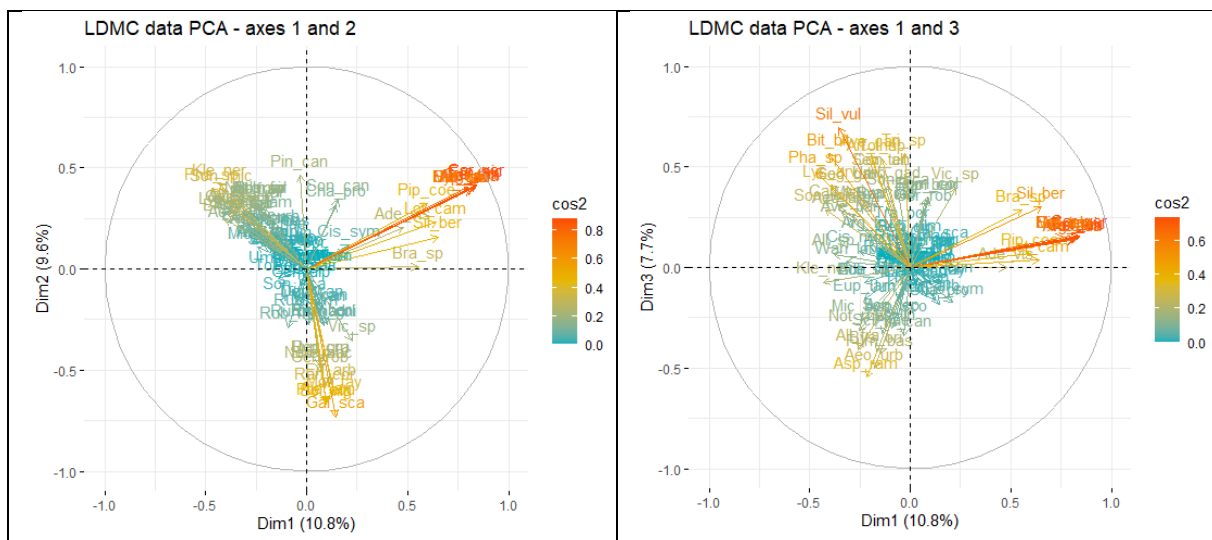


Figure 34 - Correlation circles between the three first axes of the LDMC data PCA. The percentages show the percentage of variance explained by the axis. The code of each variable is written on the arrows, see Appendix 2 for more details. The color gradient shows the contribution (\cos^2) of the variables to the axis. 1st (Dim1) and 2nd (Dim2) axes: left; 1st (Dim1) and 3rd (Dim3) axes: right.

The plots n.1Sa and n.1Sb contribute to 56.76% and 12.53% to the first axis for a total of 69.29%. Four plots are needed to almost reach this percentage for the second axis with 67.94% (n.5Sa, n.5Sb, n.1Sa, n.8Sa) and six plots for the third axis with 70.15% (n.7Sa, n.12Sa, n.19Sa, n.7Sb, n.4Sb, n.18Sb) (Fig. 35-36).

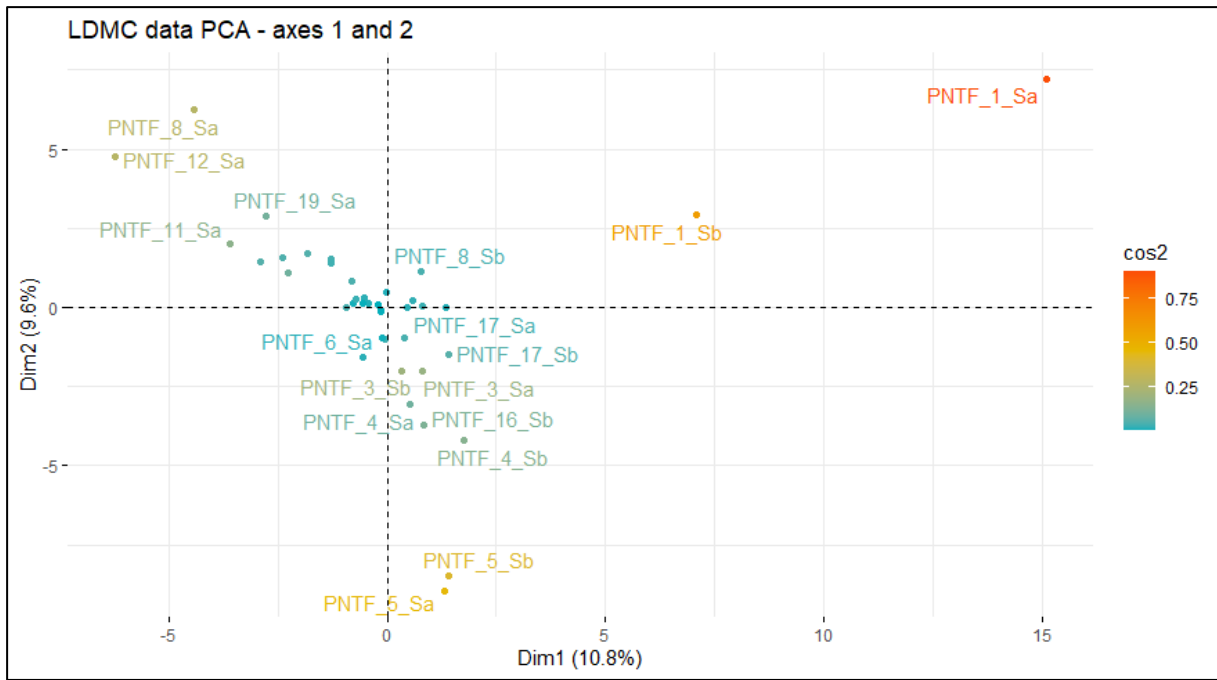


Figure 35 - Coordinates of each plot along the 1st (Dim1) and 2nd (Dim2) axes of the LDMC data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

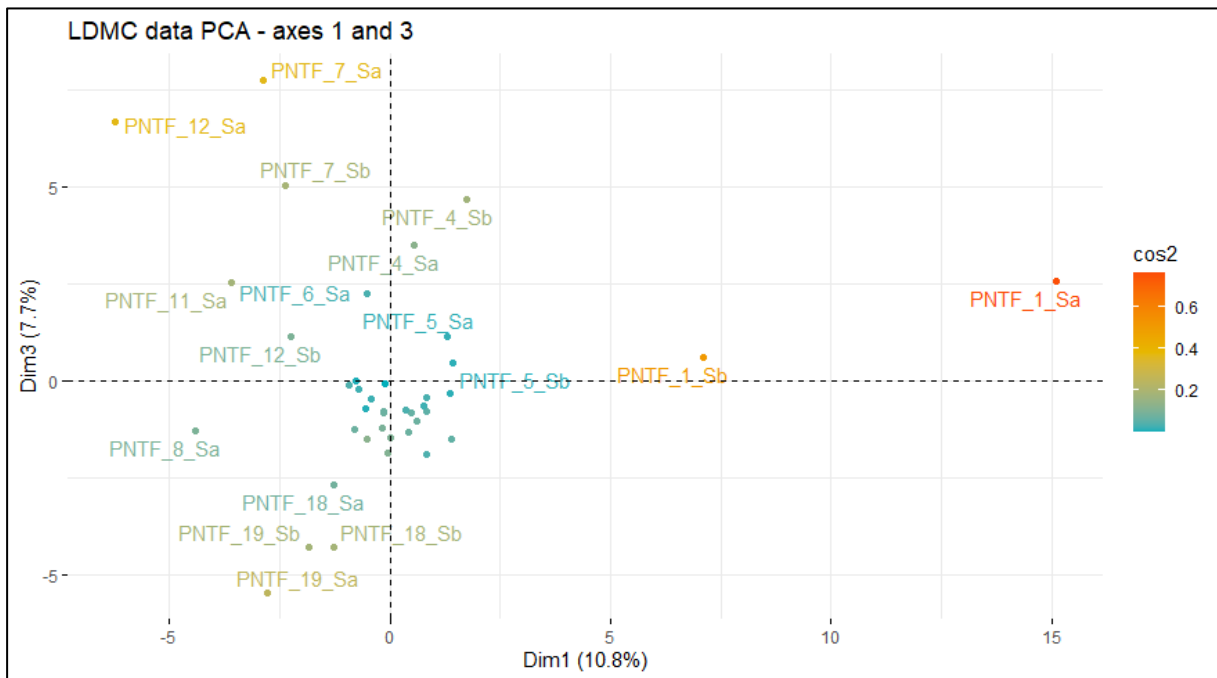


Figure 36 - Coordinates of each plot along the 1st (Dim1) and 3rd (Dim3) axes of the LDMC data PCA. The percentages show the percentage of variance explained by the axis. The color gradient shows the contribution (\cos^2) of the variables to the axes. PNTF = "Pinar Tenerife".

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