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Shifts in grasses diversity patterns between two contrasting 40-year climate periods in tropical dry islands

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Abstract

Grasses are one of the most successful and dispersed plant families worldwide and their environmental and economic values are widely acknowledged. They dominate the landscape of Cabo Verde, the southernmost and driest archipelago of Macaronesia, and are relevant natural resources for local populations, but a comprehensive evaluation of their distribution patterns is still lacking. In this study, we aim to evaluate the potential effects of climate change using the long-term data concerning grass distribution in Cabo Verde and the widely recognized climatic variability of this archipelago, which entails a huge irregularity in spatial and temporal rainfall. We identified two contrasting climatic periods (wet, from 1929 to 1968, and dry, from 1969 to 2007) and gathered all the information available from the bibliography, herbaria, and fieldwork concerning spontaneous grass species recorded in Cabo Verde during those two periods, which amounted to 107 taxa. This information was then used to disclose the patterns of grass diversity as related to climatic and topographic variables (altitude and windward vs. leeward aspects). Different altitudinal shifts in the distribution patterns of grass species assemblages and an assemblage specific to the wet period were revealed by comparing the two climatic periods. The role of exposure in delimiting the altitudinal distribution of the various assemblages was highlighted; the trade winds clearly determine the distribution of grass assemblages. We detected shifts in the distribution of grass assemblages according to the climatic periods (related to the macroclimate) and local topographic factors (associated with mesoclimates). Also, functional traits (i.e., annuals vs. perennials, C3 vs. C4 grasses, and tropical vs. temperate species) were found to vary between wet and dry periods, as well as with altitude and with slope aspect. Understanding species distributions and the role of the climatic variability of Cabo Verde is crucial to predicting how climate change will affect them and thus to support effective management and conservation actions.

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KEYWORDS
Africa, Cabo Verde, climate variability, drought, environmental adaptations, functional traits, Macaronesia, Poaceae

INTRODUCTION

Climate fluctuations and climate change have strong implications on vegetation patterns, potentially leading to species shifts. Biodiversity is predicted to alter expressively in response to climate change globally (Harter et al., 2015). Accordingly, the displacement of plants to higher elevations and latitudes than those to which they adapted is among one of the predicted consequences of climate change (Davis & Shaw, 2001). As species move toward higher latitudes and altitudes, populations at the leading edge of the species range are expected to expand and occupy new territory (Van der Putten, 2012). This results in a reduction of population sizes and extinctions at the contracting edge (Walther, 2003). Thus, climate change might reduce species populations that cannot spatially track the climate to which they are currently adapted (Davis & Shaw, 2001) and increase their extinction risk (Thomas et al., 2004).

Large-scale studies focusing on climatic adaptations of plants are of paramount interest, and it is increasingly important to obtain reference data that improve our knowledge of the biological systems and thus support better predicting models.

Island ecosystems disproportionately contribute to global biodiversity, and their vascular plant diversity, especially in terms of species richness and endemism, surpasses that of mainland regions. Moreover, approximately 35% of the 34 biodiversity hotspots identified by Conservation International in 2005 are either islands or possess a significant island component (Kier et al., 2009; Patiño et al., 2016). Nevertheless, island ecosystems face the greatest global threats. They are especially vulnerable to environmental and natural disasters (e.g., volcanic activity, hurricanes, sea level rise, and climate change) (Harter et al., 2015); also, their usually limited area and anthropogenic pressures exacerbate species vulnerability (Romeiras, Catarino, Filipe, et al., 2016).

Due to their altitudinal gradients and small size, most islands provide good models to understand the effects and responses to climatic drivers (Weigelt et al., 2016). Studies performed in oceanic archipelagos of the Macaronesian region (i.e., Azores, Madeira, Selvagens, Canary Islands, and Cabo Verde) have contributed to understanding how spatial isolation, differential availability of ecological opportunities, topographic complexity, and climatic variables are important drivers of ecological specialization and diversification (Florencio et al., 2021 and references therein). In particular, altitudinal gradients of species distribution have shed light on the mechanisms and environmental variables that can affect community assemblies (e.g., Fernández-Palacios & de Nicolás, 1995; Irl et al., 2015; Steinbauer et al., 2012, 2016).

The archipelago of Cabo Verde encompasses the southernmost islands of Macaronesia, characterized by a dry tropical climate. Here, the desertification processes driven by the scarcity and irregularity of rainfall, worsened by human activities, strongly affect the vegetation cover (Monteiro et al., 2020; Neto et al., 2020).

Modeled distributions of species under several scenarios of climate change were recently addressed using the Cabo Verdean native trees as a case study (Varela et al., 2022, 2023); this approach proved to be an essential tool to understand the future responses and to guide conservation plans in these islands. Moreover, paleoecological research on the dryland soil stratigraphic sequences in Santo Antão (Castilla-Beltrán et al., 2019), São Nicolau (Castilla-Beltrán et al., 2020), Brava (Castilla-Beltrán et al., 2021), and Fogo (Castilla-Beltrán et al., 2023) provided an essential historical view of long-term ecological change in these islands of Cabo Verde.

The knowledge of the general patterns of terrestrial Cabo Verdean plant diversity is still insufficient (Romeiras et al., 2019), with a clear taxonomic bias in data availability. Most contributions concentrate on endemic species (e.g., Romeiras et al., 2015; Vitales et al., 2023) and, to a lesser extent, on native flora (Neto et al., 2020) or particular islands (e.g., Santiago, Duarte et al., 2005).

Together with Asteraceae, Euphorbiaceae, Fabaceae, Malvaceae, Solanaceae, and Cyperaceae, the Poaceae is one of the largest families in Cabo Verde, occurring in all habitats (from wetter to drier) (Brochmann et al., 1997). Grasslands are the predominant landscape in the archipelago, especially in xeric environments where short-lived or perennial herbaceous grasses, sometimes with some scattered shrubs or small trees, are the major plant elements (Neto et al., 2020; Rivas-Martinez et al., 2017).

In Cabo Verde, and besides their invaluable environmental role, grasses are a relevant natural resource for the local economy because most of them are used as forage and pasture, and heavily grazed by livestock such as goats, and as food, namely as small grain crops (Duarte et al., 2022). In countries with low incomes, such as Cabo Verde, the valuation of the plant genetic resources is essential to promote sustainable development, and both Poaceae (Rocha et al., 2021) and Fabaceae (Brilhante et al., 2021) stand among the most important local native resources.

The ability of grasses to colonize, persist, and transform environments seems to favor their success. With their mostly herbaceous habit, high dispersal ability, and meristems protected from injuries, such as defoliation by herbivores, fire, frost, or drought (Fish et al., 2015; Linder et al., 2018; Woodward et al., 2004), the Poaceae are one of the most successful and dispersed families of angiosperms around the globe; they can be found in a variety of ecosystems, covering 31%–43% of the land surface (Beer et al., 2010; Gibson, 2009). Furthermore, they include both C3 and C4 photosynthetic pathways species, thus widening the range of climatic and environmental adaptations and, consequently, the functional diversity of the family (Fish et al., 2015; Linder et al., 2018). Besides their environmental importance, the economic value of grasses is widely acknowledged, mainly as important grain crops (e.g., cereals) and as fodder and forage for livestock (Capstaff & Miller, 2018). The grass family—Poaceae (=Gramineae)—comprises about 12,080 species from about 824 genera, and accounts for 10% of the vascular plant species richness (Bánki et al., 2023).

Although Poaceae are abundant, diverse, and ubiquitous in Macaronesia, they have not been largely used in macroecological studies and long-term analyses, probably because of their inconspicuous character, compared with shrubs and trees. On the other hand, the predicted climate changes for West Africa, and particularly the Sahelian belt, indicate a continuous warming and a greater precipitation uncertainty (Sylla et al., 2016), which will also affect these oceanic islands. These changes, globally influencing vegetation cover, will greatly impact grass species, which, due to their herbaceous growth form and, often, short-life cycle, are particularly sensitive to climate changes (Seddon et al., 2016).

To evaluate the impacts of climate variability in Cabo Verde, we used data concerning grass distribution in the islands from about 80 years (1929–2007), during which two distinct climatic periods (a wet one, from 1929 to 1968, and a dry one, from 1969 to 2007) occurred. We expected to find significant differences in the distribution patterns of grass assemblages between the two climatic periods. Additionally, we hypothesized that this trend would be influenced by altitude and slope aspects, as these topographic factors have long been reported most relevant in shaping plant diversity (e.g., Barbosa, 1968; Brochmann et al., 1997; Neto et al., 2020). As species functional traits are associated with environmental conditions (Tang et al., 2022), we also looked for changes in some functional traits (annuals vs. perennials, C3 vs. C4 grasses, and tropical vs. temperate) to detect differences in the performance of particular functional groups.

To disclose these aspects, we established the main grass assemblages considering the whole archipelago as a "single island model," and we assessed the changes in their distribution patterns that occurred between the two climatic periods. Specific questions were: (1) How did the two contrasting periods (wet and dry) affect the distribution pattern of grass assemblages and how was this pattern influenced by local topographic factors (altitude and slope aspect)? (2) How were the functional traits (i.e., annuals vs. perennials, C3 vs. C4 grasses, and tropical vs. temperate species) affected by the two contrasting climatic periods? How did local topographical factors influence this pattern? The results were expected to help predict the impacts of future climate change and to contribute to the sustainable management of grassland ecosystems in the archipelago.

MATERIALS AND METHODS

Study area

Cabo Verde, the southernmost archipelago of the Macaronesian region, is about 1350 km south of the Canary Islands and approximately 560 km from the coast of Senegal (Figure 1A). It includes 10 islands (all inhabited, except Santa Luzia) and 16 islets. The mountains in the northern islands—Santo Antão, São Vicente, and São Nicolau—and in the southern islands—Santiago, Fogo, and Brava—with altitudes that easily exceed 1000 m, reaching a maximum of 2829 m in Fogo (Appendix S1: Table S1), offer a wide range of habitats in relatively small areas. In contrast, the eastern group—Sal, Boavista, and Maio islands—as well as the northern island of Santa Luzia (including Branco and Raso islets), barely reach a few hundred meters of altitude and are characterized by relatively broad extensions of flat land (Duarte & Romeiras, 2009).

Due to its location off the African Sahelian area, Cabo Verde is part of an arid and semiarid climatic region. Three main wind systems influence the climate of the archipelago (Correia, 1996) (Figure 1A): (1) the NE trade winds, blowing between 400 and 1500 m of altitude throughout the year, but especially between December and May (Varela-Lopes & Molion, 2014), are important for fog formation, the source of most of the water intercepted by vegetation; (2) the dry hot eastern winds (Harmattan) that, from October to June, occasionally blow from the southern Sahara Desert, increasing the dryness and bringing dust and sandstorms, especially

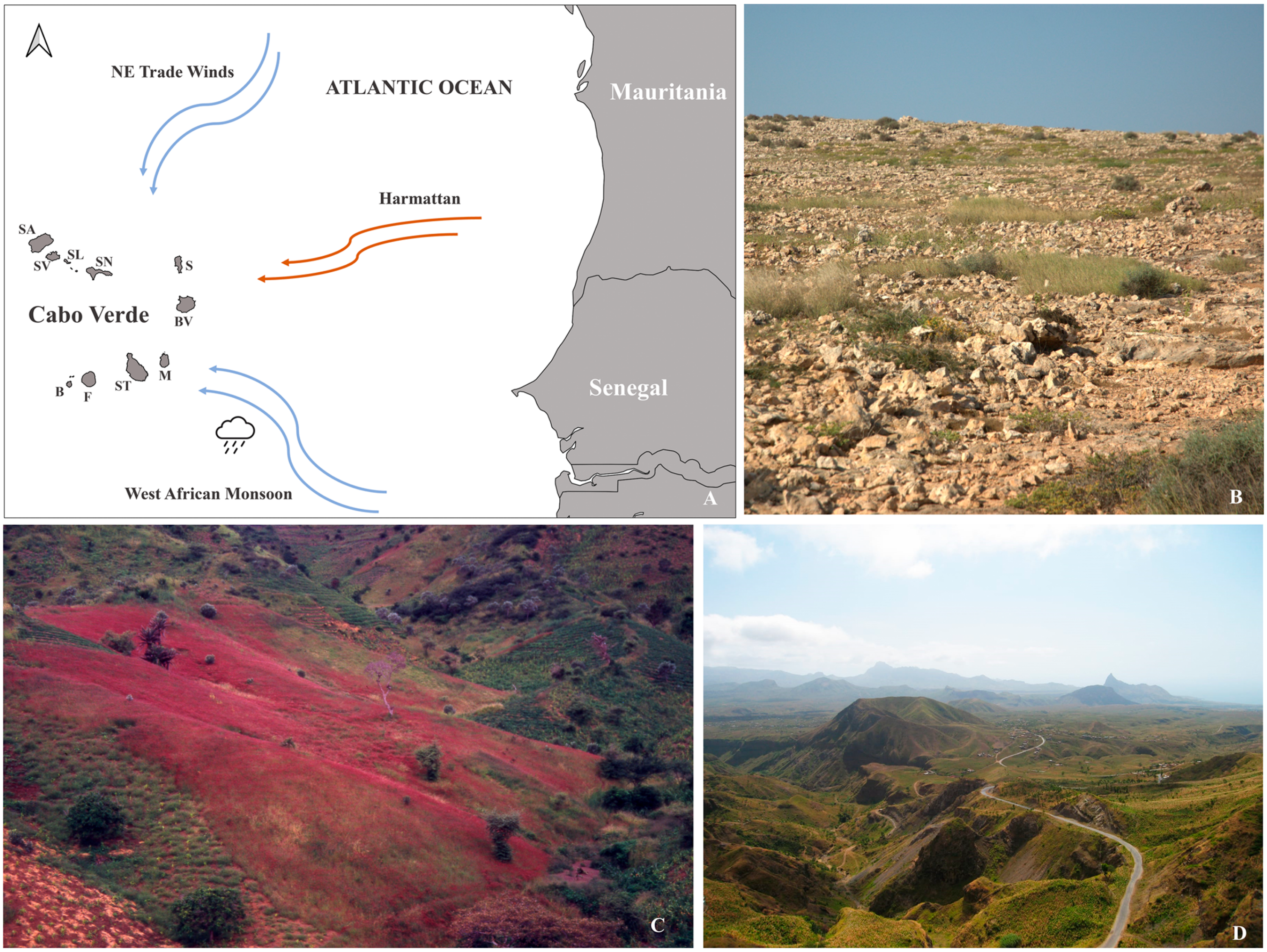

FIGURE 1 Cabo Verde archipelago. (A) Geographic location of the archipelago, illustrated with the three main wind systems that influence the climate of the islands. B, Brava; BV, Boavista; F, Fogo; M, Maio; S, Sal; SA, Santo Antão; SL, Santa Luzia; SN, São Nicolau; ST, Santiago; SV, São Vicente. (B) Grass communities of arid lowlands areas of the island of Boavista. (C) *Melinis repens* community in the island of Santiago. (D) Grass communities of medium-altitude areas on the island of Santiago, alternating with cultivated areas, namely rainfed. Photo credits: Maria C. Duarte.

to the eastern islands of lower altitude; and (3) the South-southwest winds (West African Monsoon), usually blowing between July and October, and carrying most of the rain that falls on the archipelago. The alternation and prevalence of these main wind systems throughout the year clearly define two different periods: (1) a dry season (November–June) and (2) a wet season (July–October) (Varela-Lopes & Molion, 2014).

These climatic factors and the particular orography (mainly altitude and exposure to prevailing winds) of each island enable a variety of mesoclimates that are reflected in the high diversity of habitats and ecological conditions and, consequently, in the distribution of the approximately 750 spontaneous vascular plant taxa (native or introduced) that occur in this archipelago (Duarte et al., 2022) and, also, in the wide diversity of plant communities found in these islands, including the predominant grasslands, which range from the xeric in the arid lowlands to the more mesic in high-altitude areas (Figure 1B–D), woodlands, and shrublands in the more humid mountainous zones (Romeiras et al., 2015). The growing human population on the islands, which increased threefold in the last decades—184,999 in 1950 to 598,682 in 2023 (Macrotrends, 2023)—exerts strong anthropogenic pressure on plant communities, posing major challenges for the conservation of natural resources (Romeiras, Catarino, Gomes, et al., 2016). Agriculture, the main economic activity and involving 34.8% of the total population (Ministério da Agricultura e Ambiente, 2015), is practiced traditionally, so the varied spontaneous flora present, especially rich in grasses, is widely used as fodder.

Selecting wet and dry periods

The climatic variability of Cabo Verde is widely recognized. Cyclical drought periods have been known since, at least, the 1580s, from records reporting severe famines due to crop shortages (Amaral, 1991; Patterson, 1988), and they are expected to become more severe (Climate Change Knowledge Portal, 2022).

As this archipelago is highly influenced by the Sahel zone, the climatic data from Western Africa can be considered a proxy for Cabo Verde (Nicholson, 2018). The Standardized Precipitation Index for 12 months (SPI-12), widely used to classify wet and dry periods (Caloiero et al., 2018; Sanogo et al., 2015), was used to define two climatic periods: (1) a wet period, from 1929 to 1968, with positive values of SPI-12 (SDs above the mean); and (2) a dry period, from 1969 to 2007, with negative values (SDs below the mean) (Figure 2A).

Dataset

The species occurrence data that fall into the two periods mentioned above (Figure 2B) were gathered for comparative analyses. These data were mainly compiled from: (1) herbarium specimens housed in the following

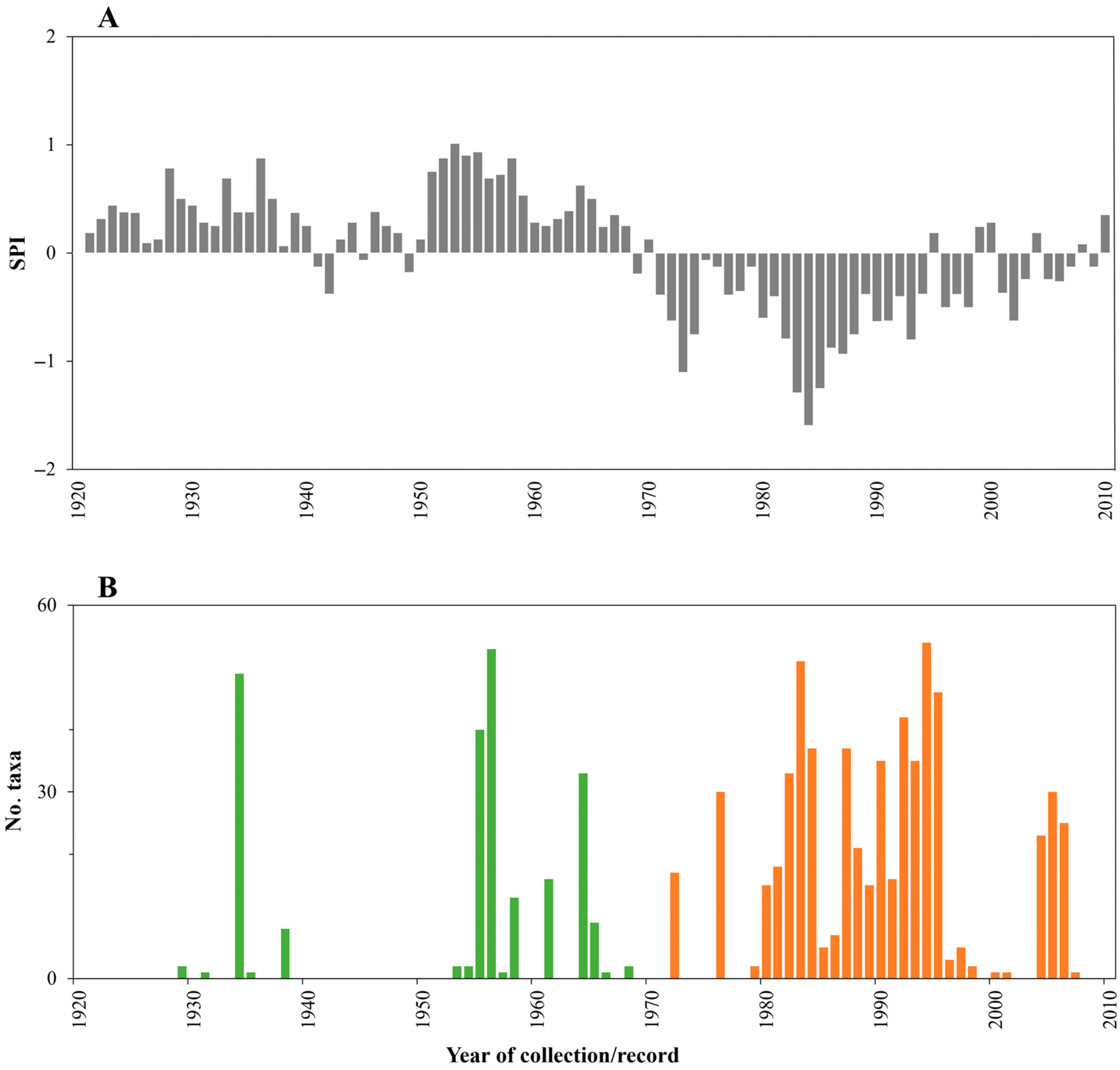

FIGURE 2 Selection of wet and dry periods for the present study. (A) Standardized Precipitation Index for 12 months (SPI-12) in the Sahel, between 1921 and 2010 (adapted from Sanogo et al., 2015). Positive values of SPI-12 (SDs above the mean) indicate a wet period; negative values (SDs below the mean) indicate a dry period. (B) Number of Poaceae taxa collected in Cabo Verde; values are shown for a wet period (1929–1968, green bars) and a dry period (1969–2007, orange bars).

Herbaria: Instituto de Investigação Científica Tropical, University of Lisbon (LISC), which holds the main collections from this geographical region; University of Coimbra (COI); Muséum National d'Histoire Naturelle, Paris (P); and Royal Botanic Gardens, Kew (K); local collections (e.g., Herbarium of the Parque Natural do Monte Gordo (PNMG), São Nicolau Island); (2) online databases such as the GBIF website that provide data on herbarium specimens and field observations (GBIF.org, 2020); (3) published works (namely Duarte, 1998; Duarte et al., 2005; Rivas-Martinez et al., 2017); and (4) unpublished data, including collected specimens and field observations dating from 1992 to 2006, done by the authors in Cabo Verde (mainly M. C. Duarte along with other collectors such as I. Gomes and J. C. Costa).

To merge data from different sources, we unified species taxonomy and nomenclature using the online Plants of the World database (POWO, 2023). Works like Sánchez-Pinto et al. (2005) and Rivas-Martinez et al. (2017) were used to clarify any taxonomical issue on a case-by-case basis. The complete list of occurrences is available on Dryad (Duarte et al., 2024; https://doi.org/10.5061/dryad.47d7wm3jh).

For each occurrence (herbarium specimens or field observations), the following data were collected: (1) year of collection, to classify each occurrence according to the defined climatic periods (wet or dry); (2) sampling location, to georeference the occurrence and obtain the respective coordinates; and (3) altitude and aspect (when not explicitly stated, estimated from the coordinates).

The georeferencing of the occurrences was carried out following Chapman and Wieczorek (2006) and performed using 1:25,000 and 1:150,000 topographic maps of Cabo Verde, and Google Earth Pro 7.3.2.5491 (Serea, 2018). Species occurrences were mapped using QGIS version 3.10.5 software (QGIS Development Team, 2020), and the geographic boundaries of Cabo Verdean islands were obtained from *Infra-estrutura de Dados Espaciais de Cabo Verde* (IDE-CV, 2020). Their altitude was obtained and, additionally, their aspect was determined using the compass and sun visualization tools of Google Earth Pro 7.3.2.5491 (Serea, 2018). Occurrences were classified according to the two main aspect-related classes (windward and leeward).

Only individuals with taxonomic identification at least to the species level were considered, and occurrences omitting the place of collection or with imprecise or misleading coordinates were removed, as well as duplicated records.

The occurrence data were then filtered using three criteria: (1) according to the climatic period (wet or dry); (2) according to six 300-m altitude classes (altitudes above 1500 m, only occurring in Santo Antão and Fogo islands, were included in a single class); (3) according to two main exposure classes: windward (coded as "NE"), to assess the effects of the prevailing and very influential NE trade winds; and leeward (coded as "0"), including all the aspects not directly influenced by trade winds. A total of 24 climatic period/altitude/aspect categories (hereafter simply referred to as categories) were considered (Appendix S1: Table S2).

For each species, occurrences were reduced to one occurrence per category (i.e., only the presence or absence is considered for each species in each of the 24 categories), to reduce biases due to different collecting efforts and sampling methodologies of various collectors over space and time.

This study included species reported in all types of communities, such as grasslands, rocky escarpments, woodlands, forests, or agricultural areas.

Information on life history (annual vs. perennial) and photosynthetic pathway (C3 vs. C4) was retrieved from Grass Base (Clayton et al., 2006 onward), Schmidt et al. (2011), Fish et al. (2015), and Soreng et al. (2017). Preferred ecology, regarding water requirements (xerophyte vs. mesophyte), was mainly compiled from the abovementioned sources. The world climate regions of Sayre et al. (2020) were used to categorize taxa according to the global bioclimatic domains (tropical, subtropical, warm temperate, cool temperate, boreal, and polar) and two classes were considered: (1) tropical (including subtropical taxa) and (2) tropical/temperate (including subtropical and warm and cool temperate taxa).

Data analysis

The occurrence data from the 10 islands were merged, to consider the whole archipelago as a "single island model" (i.e., considering a single theoretical island).

To explore the role of the climatic period and topography on the distribution of grasses, we ordered the similarities among the 24 considered categories. The principal coordinates analysis (PCoA) was used and the Sørensen coefficient (Sørensen, 1948), which ignores double zeros, was chosen as a similarity index. Multivariate analyses were performed using Canoco version 5.0 software (Ter Braak & Šmilauer, 2012). The relationship between the PCoA axes and altitude was determined using linear regression.

A hierarchical cluster analysis was performed to explore these similarities and to produce hierarchically structured clusters; the Sørensen (or Dice) index was also used as the dissimilarity measure and the centroid clustering method was selected.

To display and evaluate changes in the distribution of the functional traits in each climatic period and altitude/aspect category, we used bar charts.

After testing for normality, we used two-tailed paired sample *t* tests to assess the statistical significance of the differences in species' functional traits between the wet and dry climatic periods. For each trait, we also analyzed the two main exposure classes separately.

Statistical analyses were performed using IBM SPSS Statistics (version 27) software (SPSS Inc., Chicago, IL).

RESULTS

For the two analyzed climate periods, a total of 3138 individual records, corresponding to 107 taxa of Poaceae (Table 1), were compiled. This corresponds to about 88% of the total number of Poaceae species reported to Cabo Verde. Most species occur along a wide range of altitudes and in both climatic periods (Figure 3), 87% of which (93 taxa) were found at altitudes below 600 m (including the flat islands of Santa Luzia, Sal, Boavista, and Maio, most of São Vicente Island, and the lower altitudinal belts of the mountainous islands). The majority (75% of the total number of taxa present during the targeted climatic periods) is native, including four endemic species (*Aristida cardosoi*, *Eragrostis conertii*, *Hyparrhenia caboverdeana*, and *Urochloa caboverdiana*). Most are annual (64 taxa, 60% of the total), display C4 photosynthetic pathway (88 taxa, 82% of the total), and occur in tropical/subtropical biogeographic regions (66 taxa, 62% of the total) (Table 1).

Impacts of climatic variability and topography on the distribution of grasses

To explore the role of the climatic period and topography in the distribution of grasses, we analyzed the grass species present in each one of the considered 24 categories and their relationships with the factors under analysis—period, altitude, and aspect (Figure 4 and Appendix S1: Figure S1). Five distinct clusters were identified:

1. Cluster 1 (xerophytic assemblage)—including, almost exclusively, dry period categories (W1_0 is the exception), altitudes <1200 m on windward slopes, and altitudes <900 m on leeward slopes; this cluster includes records from all islands, and xerophytic species reach here the highest value (37% xerophytes and 63% mesophytes, see Appendix S1: Table S3);
2. Cluster 2 (moderate-/medium-altitude mesophytic assemblage)—including only wet period categories at altitudes <1500 m on windward slopes, and between 300 and 900 m on leeward slopes; this cluster includes records from Santo Antão, S. Nicolau, S. Vicente, Santiago, Fogo, and Brava, with the representativeness of xerophytes reduced by about half and mesophytic species largely dominating (19% xerophytes and 81% mesophytes);
3. Cluster 3 (medium-/high-altitude mesophytic assemblage)—mainly including categories on leeward slopes >900 m and <1200 m from both climate periods; on windward slopes, the lower limit varies according to the climatic period: >1200 m, in the dry period, and >1500 in the wet period; this cluster includes records from Fogo (mainly), Santo Antão, Santiago, and Brava, and mesophytic species are almost exclusive (9% xerophytes and 91% mesophytes);
4. Cluster 4 (medium-altitude mesophytic assemblage)—categories on leeward slopes with altitudes between 1200 and 1500 m; this cluster includes only records from Santo Antão, and only mesophytes are present;
5. Cluster 5 (high-altitude mesophytic assemblage)—categories on leeward slopes with altitudes >1500 m, from both climate periods, and on windward slopes between 1200 and 1500 m of altitude; this cluster includes records from Santo Antão (mainly) and Fogo, and only mesophytes are present.

The results revealed a pronounced effect of altitude, as confirmed by the significant correlation of the scores of the first PCoA axis with elevation ($R^2 = 0.715$; $p < 0.001$).

When comparing pairs of categories with similar altitude/exposure but from different climatic periods, the distances in the PCoA diagram between pairs of medium–low altitudes (e.g., D2_0/W2_0 and D3_NE/W3_NE) are usually larger than those between pairs from greater altitudes such as W5_0/D5_0 (Figure 4). These differences reveal not only the effect of the climatic period but also its generally less pronounced effect at higher altitudes.

On the other hand, when comparing pairs of categories from the same climatic period and altitude but with contrasting aspects, shifts in the grass assemblages increase with altitude: for example, in the PCoA diagram, the distance between pairs such as W5_NE/W5_0 or D6_NE/D6_0 is larger than those between pairs from lower altitudes such as W1_NE/W1_0 or D2_NE/D2_0 (Figure 4). These differences reveal not only the pronounced effect of the aspect but also its smaller effect in the lowlands.

According to these results, a theoretical model of the distribution of clusters can be depicted highlighting the differences between wet and dry periods (Figure 5A,B).

To explore the composition of grass species in each cluster, species distribution along the PCoA1 axis (centroids, see Appendix S1: Figure S2) and their

TABLE 1 Poaceae occurring in Cabo Verde islands in the two considered climatic periods. Species presence on an island is indicated by an asterisk (*).

					Distribution in Cabo Verde											
Taxa	**S**	**World dist.**	**LH**	**PP**	**SA**	**SV**	**SL**	**SN**	**S**	**BV**	**M**	**ST**	**F**	**B**	**NO**	**Alt (m)**
Acrachne racemosa (B. Heyne ex Roth) Ohwi	N	Tropical, subtropical	A	C4		*		*		*	*	*			28	2–500
Aira caryophyllea L. (=*Aira caryophyllea* subsp. *caryophyllea*)	I	Tropical, warm temperate	A	C3									*		1	1400
Andropogon gayanus Kunth (=*Andropogon gayanus* var. *tridentatus* Hack./*Andropogon tridentatus* Roxb.)	N	Tropical, subtropical	P	C4	*			*				*	*	*	90	29–1250
Anthephora cristata (Döll) Hack. ex De Wild. & T. Durand	I	Tropical	A	C4								*			2	32–85
Aristida adscensionis L. (=*Aristida swartziana* Steud.)	N	Tropical, subtropical	A	C4	*	*	*		*	*	*	*	*		76	2–1808
Aristida cardosoi Cout.	E	Tropical	A	C4	*	*	*	*	*	*	*	*	*	*	52	10–1776
Aristida funiculata Trin. & Rupr. (=*Aristida funiculata* var. *paradoxa* (J.A. Schmidt) Henrard/*Aristida paradoxa* J.A. Schmidt)	N	Tropical	A	C4	*	*	*	*	*	*	*	*	*		49	2–1050
Arthraxon lancifolius (Trin.) Hochst.	N	Tropical	A	C4	*	*		*				*	*	*	37	43–1250
Arundo donax L.	I	Tropical, subtropical	P	C3	*	*		*	*	*	*	*	*	*	28	19–928
Avena sativa L. (=*Avena fatua* subsp. *macrantha* (Hack.) Malzev/*Avena sativa* subsp. *macrantha* (Hack.) Rocha Afonso)	I	Subtropical	A	C3	*							*			3	85–1365
Bothriochloa bladhii (Retz.) S.T. Blake (*Amphilophis insculpta* var. *vegetior* (Hack.) Stapf/*Bothriochloa intermedia* (R.Br.) A. Camus)	N	Tropical, subtropical, warm temperate	P	C4	*	*		*		*	*	*		*	20	15–1200
Bothriochloa insculpta (Hochst. ex A. Rich.) A. Camus	N	Dry tropical	P	C4	*	*	*	*	*			*			58	35–1037
Brachypodium distachyon (L.) P. Beauv. (=*Trachynia distachya* (L.) Link)	I	Tropical, subtropical, warm temperate	A	C3	*			*					*		24	290–1770
Brachypodium sylvaticum (Huds.) P. Beauv.	I	Tropical, subtropical, warm, and cool temperate	P	C3	*							*	*		1	984
Bromus catharticus Vahl (=*Bromus willdenowii* Kunth/*Ceratochloa unioloides* (Willd.) P. Beauv.)	I	Subtropical, warm temperate	P	C3	*	*									2	700–1040
Bromus madritensis L. (=*Anisantha madritensis* (L.) Nevski/*Bromus rubens* subsp. *kunkelii* (H. Scholz) H. Scholz)	I	Subtropical, warm temperate	A	C3		*							*		2	620–710
Bromus rigidus Roth	I	Subtropical, warm temperate	A	C3		*							*		2	700–1400
Cenchrus biflorus Roxb.	N	Tropical, subtropical	A	C4					*	*	*	*			9	3–45
Cenchrus ciliaris L.	N	Tropical, subtropical, warm temperate	P	C4	*	*	*	*	*	*	*	*	*	*	137	10–1880
Cenchrus echinatus L.	I	Tropical, subtropical	A	C4	*			*		*	*	*			10	6–1320

TABLE 1 (Continued)

Taxa	S	World dist.	LH	PP	Distribution in Cabo Verde										NO	Alt (m)
					SA	SV	SL	SN	S	BV	M	ST	F	B		
Cenchrus pedicellatus (Trin.) Morrone subsp. *pedicellatus* (=*Pennisetum pedicellatum* subsp. *pedicellatum*)	N	Tropical	A	C4	*	*		*			*	*	*		35	43–928
Cenchrus pedicellatus subsp. *unispiculus* (Brunken) Morrone (=*Pennisetum pedicellatum* subsp. *unispiculum* Brunken)	N	Tropical	A	C4	*	*		*			*	*	*		32	13–1000
Cenchrus setosus subsp. *hordeoides* (Lam.) Zon (=*Cenchrus polystachios* subsp. *atrichus* (Stapf & C.E. Hubb.) Morrone/*Pennisetum polystachion* subsp. *atrichum* (Stapf & C.E. Hubb.) Brunken/*Pennisetum atrichum* Stapf & C.E. Hubb.)	N	Tropical, subtropical	P	C4	*							*			3	566–985
Cenchrus setosus Sw. subsp. *setosus* (=*Pennisetum polystachion* subsp. *setosum* (Swartz) Brunken)	N	Tropical, subtropical, warm temperate	P	C4	*	*		*			*	*	*	*	45	11–1655
Chloris gayana Kunth	N	Tropical, subtropical	P	C4	*	*									1	710
Chloris pilosa Schumach. (=*Chloris pilosa* var. *nigra* (Hack.) Vanden Berghen)	N	Tropical, subtropical	A	C4	*	*			*		*	*	*		49	10–1205
Chloris pycnothrix Trin. (=*Chloris humilis* Kunth)	N	Tropical, subtropical	A	C4	*	*		*				*	*	*	21	50–1218
Chloris virgata Sw.	I	Tropical, subtropical, warm temperate	A	C4	*	*	*	*	*	*	*	*	*	*	121	5–1538
Cymbopogon citratus (DC.) Stapf	I	Tropical	P	C4								*			1	307
Cynodon dactylon (L.) Pers.	N	Tropical, subtropical, warm temperate	P	C4	*	*	*	*	*	*	*	*		*	113	1–1538
Dactylis smithii Link (=*Dactylis glomerata* subsp. *smithii* (Link) Stebbins & D. Zohary/*Dactylis smithii* subsp. *hylodes* P.F. Parker)	N	Tropical	P	C3	*			*			*				2	135–1240
Dactyloctenium aegyptium (L.) Willd.	N	Tropical, subtropical, warm temperate	A	C4	*	*	*	*	*	*	*	*	*	*	146	1–1195
Dichanthium annulatum (Forssk.) Stapf (=*Dichanthium papillosum* Stapf/*Dichanthium annulatum* var. *papillosum* (Hochst. ex A. Rich.) de Wet & Harlan))	N	Tropical, subtropical	P	C4	*	*			*	*	*	*	*		25	13–1760
Dichanthium foveolatum (Delile) Roberty (=*Dichanthium foveolatum* var. *foveolatum*)	N	Tropical	P	C4	*	*	*		*	*	*	*			39	2–1875
Diectomis fastigiata (Sw.) P. Beauv. (=*Andropogon fastigiatus* Sw.)	N	Tropical, subtropical	A	C4	*							*	*		5	65–725
Digitaria ciliaris (Retz.) Koeler (=*Digitaria adscendens* (Kunth) Henrard)	N	Tropical, subtropical, warm temperate	A	C4	*						*	*	*	*	60	1–999

(Continues)

TABLE 1 (Continued)

Taxa	S	World dist.	LH	PP	Distribution in Cabo Verde										NO	Alt (m)
					SA	SV	SL	SN	S	BV	M	ST	F	B		
Digitaria eriantha Steud.	I	Subtropical, warm temperate	P	C4	*							*			1	300
Digitaria horizontalis Willd.	N	Tropical, subtropical	A	C4	*	*					*	*	*	*	21	23–1100
Digitaria nodosa Parl.	N	Tropical	P	C4	*							*	*		9	35–1210
Digitaria nuda Schumach.	N	Tropical	A	C4	*			*			*	*	*		90	7–1040
Digitaria sanguinalis (L.) Scop.	I	Tropical, subtropical, warm temperate	A	C4	*							*	*		1	598–870
Echinochloa colonum (L.) Link	N	Tropical, subtropical, warm temperate	A	C4	*	*		*			*	*			41	6–1538
Eleusine indica (L.) Gaertn. (=*Eleusine indica* subsp. *indica*)	N	Tropical, subtropical, warm temperate	A	C4	*	*		*		*		*	*	*	72	10–1037
Elionurus royleanus Nees ex A. Rich.	N	Tropical	A	C4	*	*		*	*	*	*	*			15	5–615
Enneapogon desvauxii P. Beauv. (=*Enneapogon brachystachyus* (Jaub. & Spach) Stapf)	N	Tropical, subtropical, warm and cool temperate	P	C4	*	*	*	*	*	*	*	*			15	5–500
Enteropogon prieurii (Kunth) Clayton (=*Chloris prieuri* Kunth)	N	Tropical	A	C4	*				*	*	*	*		*	36	3–1037
Enteropogon rupestris (J.A. Schmidt) A. Chev.	N	Tropical	P	C4	*		*				*	*			6	30–150
Eragrostis aethiopica Chiov.	I	Tropical, subtropical	A	C4								*			3	345–980
Eragrostis barrelieri Daveau (=*Eragrostis insulatlantica* A. Chev.)	N	Tropical, subtropical, warm temperate	A	C4	*	*		*				*	*		51	50–2100
Eragrostis cilianensis (All.) Vignolo ex Janch.	N	Tropical, subtropical, warm temperate	A	C4	*	*		*	*	*	*	*	*	*	53	1–1538
Eragrostis ciliaris (L.) R.Br. (=*Eragrostis pulchella* Parl.)	N	Tropical, subtropical	A	C4	*	*		*	*	*	*	*	*	*	39	2–1780
Eragrostis conertii Lobin	E	Tropical	P	C4	*	*		*				*	*		5	530–860
Eragrostis minor Host	N	Tropical, subtropical, warm temperate	A	C4	*	*					*				2	22–28
Eragrostis viscosa (Retz.) Trin. (=*Eragrostis amabilis* (L.) Wight & Arn./*Eragrostis tenella* (L.) P. Beauv. ex Roem. & Schult.)	I	Tropical, subtropical	A	C4	*							*			6	20–623
Eriochloa barbatus (Trin.) S. Yadav & M.R. Almeida (=*Eriochloa fatmensis* (Hochst. & Steud.) Clayton)	N	Tropical, subtropical	A	C4	*							*			4	15–95
Festuca myuros L. (=*Vulpia myuros* (L.) C.C. Gmel.)	I	Tropical, subtropical, warm temperate	A	C3	*										4	100–1350
Gastridium ventricosum (Gouan) Schinz & Thell.	I	Subtropical, warm temperate	A	C3									*		4	1245–1780
Hackelochloa granularis (L.) Kuntze (=*Mnesithea granularis* (L.) de Koning & Sosef)	N	Tropical, subtropical	A	C4							*	*			5	20–1037
Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult.	N	Tropical, subtropical, warm temperate	P	C4	*	*	*	*	*			*	*	*	138	25–1808

TABLE 1 (Continued)

Taxa	S	World dist.	LH	PP	Distribution in Cabo Verde										NO	Alt (m)
					SA	SV	SL	SN	S	BV	M	ST	F	B		
Heteropogon melanocarpus (Elliott) Benth. (=*Andropogon melanocarpus* Elliott)	N	Tropical, subtropical	A	C4	*	*						*	*		36	70–1425
Hordeum vulgare L.	I	Subtropical	A	C3	*										2	1212–1400
Hyparrhenia caboverdeana Rivas Mart., Lousã, J.C. Costa & Maria C. Duarte (=*Hyparrhenia hirta* (L.) Stapf/*Hyparrhenia hirta* subsp. *caboverdeana*)	E	Tropical	P	C4	*	*		*	*		*	*	*	*	77	12–2760
Imperata cylindrica (L.) P. Beauv. (=*Imperata cylindrica* var. *cylindrica*)	N	Tropical, subtropical, warm temperate	P	C4									*		3	910–1740
Leptochloa panicea (Retz.) Ohwi	I	Tropical, subtropical	A	C4								*			11	20–388
Lolium canariense Steud. (=*Lolium gracile* Parl.)	N	Tropical	A	C3	*			*					*		5	115–890
Melinis minutiflora P. Beauv.	N	Tropical, subtropical	P	C4	*							*			13	97–1440
Melinis repens (Willd.) Zizka (=*Melinis repens* subsp. *repens*/*Melinis repens* subsp. *grandiflora* (Hochst.) Zizka/*Rhynchelytrum villosum* (Parl.) Chiov./*Melinis grandiflora* (Hochst.) Hack.)	N	Tropical, subtropical	A	C4	*	*	*	*	*	*	*	*	*	*	231	6–1760
Oplismenus burmanni (Retz.) P. Beauv.	N	Tropical, subtropical	A	C3	*	*		*				*	*	*	5	100–705
Oplismenus hirtellus (L.) P. Beauv.	N	Tropical, subtropical, warm temperate	P	C3	*			*				*	*		5	386–1275
Panicum laetum Kunth	N	Tropical	A	C4	*								*		1	18
Paspalum scrobiculatum L. (=*Paspalum scrobiculatum* var. *commersonii* (Lam.) Stapf)	N	Tropical, subtropical	P	C4								*	*	*	13	20–956
Paspalum vaginatum Sw.	I	Tropical, subtropical, warm temperate	P	C4								*			1	205
Phragmites australis (Cav.) Trin. ex Steud. (=*Phragmites australis* subsp. *altissimus* (Benth.) Clayton)	N	Tropical, subtropical, warm and cool temperate, boreal	P	C3		*						*			2	6–47
Polypogon monspeliensis (L.) Desf.	N	Tropical, subtropical, warm temperate	A	C3	*										1	112
Polypogon viridis (Gouan) Breistr. (=*Polypogon semiverticillatus* (Forssk.) Hyl.)	N	Tropical, subtropical, warm temperate	P	C3	*	*		*				*			15	40–1215
Rottboellia cochinchinensis (Lour.) Clayton	N	Tropical, subtropical, warm temperate	A	C4	*	*					*	*	*		51	23–995
Schmidtia pappophoroides Steud. ex J.A. Schmidt	N	Tropical, subtropical, warm temperate	P	C4	*	*	*	*		*	*	*			12	20–300
Schoenefeldia gracilis Kunth	N	Tropical, subtropical	A	C4						*		*			2	325–340
Sehima ischaemoides Forssk.	N	Tropical, subtropical	A	C4				*	*	*	*	*			28	12–560
Setaria barbata (Lam.) Kunth	N	Tropical, subtropical	A	C4	*	*		*		*		*	*	*	57	26–1040

(Continues)

TABLE 1 (Continued)

					Distribution in Cabo Verde											
Taxa	**S**	**World dist.**	**LH**	**PP**	**SA**	**SV**	**SL**	**SN**	**S**	**BV**	**M**	**ST**	**F**	**B**	**NO**	**Alt (m)**
Setaria geminata (Forssk.) Veldkamp (=*Paspalidium geminatum* (Forssk.) Stapf)	N	Tropical, subtropical	P	C4								*			3	57–490
Setaria pumila (Poir.) Roem. & Schult. (=*Setaria pallide-fusca* (Schumacher) Stapf & C.E. Hubb./*Setaria helvola* (L.f.) Roem. & Schult.)	N	Tropical, subtropical, warm and cool temperate	A	C4	*	*		*			*	*	*	*	58	1–1350
Setaria verticillata (L.) P. Beauv. (=*Setaria adhaerens* (Forssk.) Chiov.)	N	Tropical, subtropical, warm temperate	A	C4	*	*	*	*	*	*	*	*	*	*	111	5–1538
Sorghum arundinaceum (Desv.) Stapf (=*Sorghum bicolor* subsp. *verticilliflorum* (Steud.) de Wet ex Wiersema & J. Dahlb.)	N	Tropical, subtropical	P	C4									*		1	980
Sorghum bicolor (L.) Moench (=*Sorghum caudatum* (Hack.) Stapf)	I	Tropical	A	C4	*							*	*	*	7	30–1200
Sorghum halepense (L.) Pers.	I	Tropical, subtropical, warm temperate	P	C4	*			*				*		*	25	15–768
Sporobolus helvolus (Trin.) T. Durand & Schinz	N	Tropical	P	C4					*						1	18
Sporobolus minutus Link (=*Sporobolus minutus* subsp. *minutus*)	I	Tropical	A	C4					*		*				3	1–4
Sporobolus molleri Hack.	N	Tropical, subtropical	A	C4	*							*	*	*	4	15–800
Sporobolus robustus Kunth	N	Tropical, subtropical	P	C4	*	*	*		*	*		*		*	17	3–800
Sporobolus spicatus (Vahl) Kunth	N	Tropical, subtropical	P	C4	*	*	*	*	*	*	*	*	*		29	1–69
Sporobolus virginicus (L.) Kunth (=*Sporobolus confertus* J.A. Schmidt)	N	Tropical, subtropical, warm temperate	P	C4		*	*	*	*	*	*				5	5–225
Stenotaphrum secundatum (Walter) Kuntze	I	Tropical, subtropical, warm temperate	P	C4								*	*		1	206
Stipagrostis uniplumis (Licht.) De Winter (=*Aristida papposa* Trin. & Rupr.)	N	Tropical, subtropical, warm temperate	P	C4	*	*				*		*			10	64–975
Tetrapogon cenchriformis (A. Rich.) Clayton	N	Tropical	A	C4					*	*		*			10	15–170
Tetrapogon villosus Desf.	N	Tropical, subtropical, warm temperate	P	C4					*	*		*			2	7–28
Tragus racemosus (L.) All.	N	Tropical, subtropical, warm and cool temperate	A	C4	*	*	*	*	*	*	*	*			15	1–1538
Trichanthecium tenellum (Lam.) Zuloaga & Morrone (=*Panicum tenellum* Lam./*Panicum lindleyanum* Nees ex Steud.)	N	Tropical, subtropical	A	C3								*	*		2	730–1064

TABLE 1 (Continued)

					Distribution in Cabo Verde											
Taxa	**S**	**World dist.**	**LH**	**PP**	**SA**	**SV**	**SL**	**SN**	**S**	**BV**	**M**	**ST**	**F**	**B**	**NO**	**Alt (m)**
Tricholaena teneriffae (L.f.) Link (=*Tricholaena teneriffae* (L.fil.) Link subsp. *teneriffae*)	N	Tropical, subtropical, warm temperate	P	C4	*	*	*	*			*	*	*		43	10–1761
Tripogon multiflorus Miré & H. Gillet	I	Tropical	P	C4	*							*			3	685–830
Tripogonella minima (A. Rich.) P.M. Peterson & Romasch. (=*Tripogon minimus* (A. Rich.) Hochst. ex Steud.)	N	Tropical, subtropical	P	C4	*								*		3	530–893
Urochloa caboverdiana (Conert & C. Kohler) Veldkamp, Potdar & S.R. Yadav (=*Brachiaria lata* subsp. *caboverdeana* Conert & C. Köhler/ *Brachiaria caboverdeana* (Conert & C. Köhler) Rivas Mart., Lousã, J.C. Costa & Maria C. Duarte)	E	Tropical	A	C4		*		*		*	*	*	*		107	7–820
Urochloa deflexa (Schumach.) H. Scholz (=*Brachiaria deflexa* (Schumach.) C.E. Hubb. ex Robyns)	N	Tropical, subtropical	A	C4	*	*		*			*	*	*		9	65–1250
Urochloa maxima (Jacq.) R.D. Webster (=*Panicum maximum* Jacq./ *Megathyrsus maximus* (Jacq.) B.K. Simon & Jacobs)	N	Tropical, subtropical	A	C4	*			*			*	*	*		40	12–1037
Urochloa plantaginea (Link) R.D. Webster (=*Brachiaria plantaginea* (Link) Hitchc.)	I	Tropical, subtropical	A	C4								*			1	900
Urochloa ramosa (L.) T.Q. Nguyen (=*Brachiaria ramosa* (L.) Stapf)	N	Tropical	A	C4	*	*		*		*	*	*	*	*	90	5–1037
Urochloa xantholeuca (Hack.) H. Scholz (=*Brachiaria xantholeuca* (Schinz) Stapf)	N	Tropical, subtropical	A	C4	*	*		*	*	*	*	*	*		17	7–1037

Note: Included are: accepted name (including some synonyms); status in the islands (S) (E, endemic; I, introduced; N, non-endemic native; when there is uncertainty as to whether it is native or introduced, we chose the option that seemed most likely); worldwide native distribution (world dist.); life history (LH) (A, annual; P, perennial); photosynthetic pathway (PP); distribution in the archipelago (SA, Santo Antão; SV, São Vicente; SL, Santa Luzia; SN, São Nicolau; S, Sal; BV, Boavista; M, Maio; ST, Santiago; F, Fogo; B, Brava) total number of occurrences (NO); and altitudinal range (Alt).

respective presence in each of the five clusters were used (Appendix S1: Table S3). Clusters 1 and 2 share a considerable number of species; however, cluster 1 is characterized by the exclusive presence of xerophytic species, such as *Acrachne racemosa*, *Elionurus royleanus*, and *Sehima ischaemoides*, while in cluster 2, species frequently found at higher altitudes, such as *Avena sativa*, *Festuca myuros*, or *Imperata cylindrica*, may be present. These results suggest that, in the wet period, the more xeric species only occur at lowlands and leeward slopes (cluster 1, xerophytic assemblage, Figure 5A), whereas in the dry period, their distribution area significantly expands (Figure 5B). On the other hand, mesophytic species are dominant in the wet period (cluster 2, moderate-/medium-altitude mesophytic assemblage); also, the effects of trade winds in NE slopes, and the unaccounted horizontal precipitation (dew and fog) they provide, may concur to alleviate the effects of low precipitation in the dry period.

In clusters 3–5, including medium- to high-altitude mesophytic assemblages, most of the species present in clusters 1 and 2 are absent, and only a restricted group remains, as is the case of *Eragrostis ciliaris*, *Heteropogon contortus*, and *Cenchrus setosus* subsp. *setosus* (in cluster 3), or *Aristida adscensionis*, *Eragrostis barrelieri*, *Melinis repens*, and *Tricholaena teneriffae* (in clusters 3–5). In these medium- to high-altitude clusters, species not very common in Cabo Verde also occur, such as *F. myuros*, *Gastridium ventricosum*, *Hordeum vulgare*, and *I. cylindrica*, some of them introduced from northern latitudes (cooler), such as Europe and the Mediterranean Basin.

The clusters from the highest altitudes, especially those above 1200 m, are quite variable and show no easily interpretable pattern. Underlying this difficulty may be the fact that the areas are small (only Santo Antão and Fogo islands present a non-negligible area above 1200 m of altitude) and the grass species occurring in altitude, as well as the recorded specimens, are scarce (in total, only 39 species were registered above 1200 m, see Table 1 and Figure 3); moreover, most of the recorded specimens are located on the windward

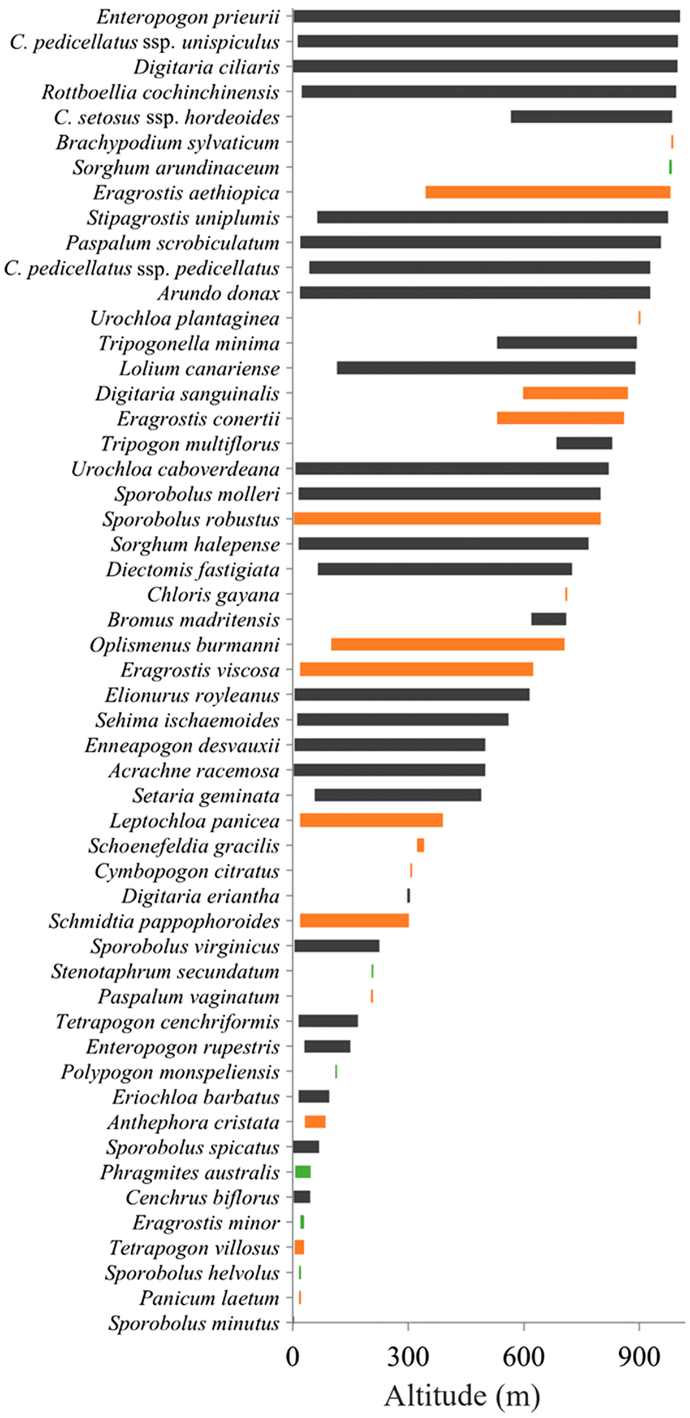

FIGURE 3 Altitudinal distribution of the native and exotic Poaceae taxa in Cabo Verde (including data from wet and dry periods). Taxa are ordered according to their maximum altitude of occurrence and the bars represent their altitudinal ranges. Taxa occurring in dry and wet periods (black bars), only in the dry period (orange bars), and only in the wet period (green bars).

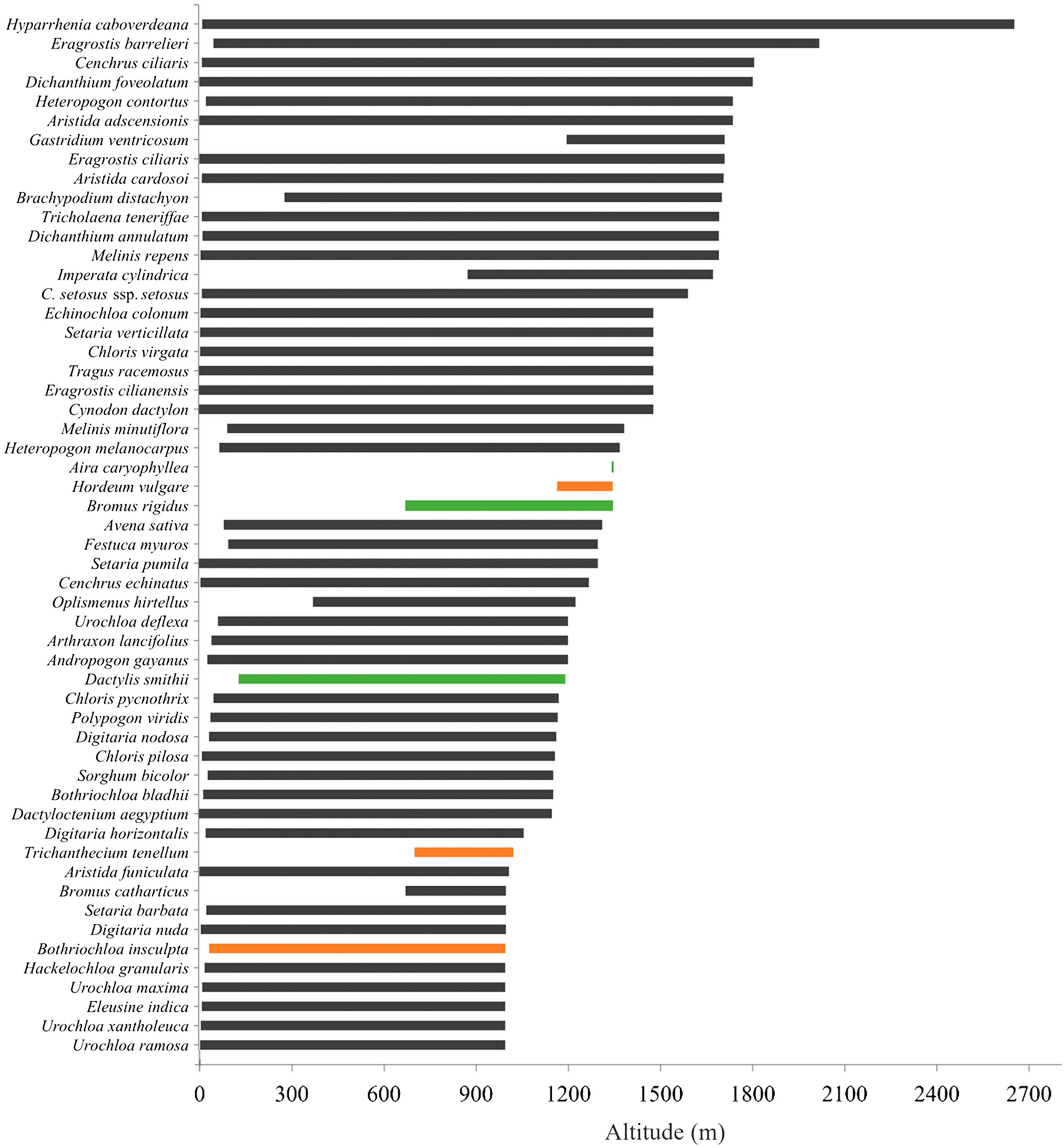

FIGURE 3 (Continued)

slopes, because the leeward slopes, less eroded, are almost inaccessible.

Functional trait distribution

Figure 6 shows the distribution of the considered functional traits in each of the two climatic periods and for the studied altitude/aspect categories; the statistical significance of the differences between periods and categories is shown in Appendix S1: Table S4.

Considering life history (Figure 6A), annuals dominate in almost all altitudinal belts in both periods. The exception is above 1500 m, where perennials roughly equal annuals. Annuals increase significantly in the dry period (paired t test: $p = 0.045$; Appendix S1: Table S4).

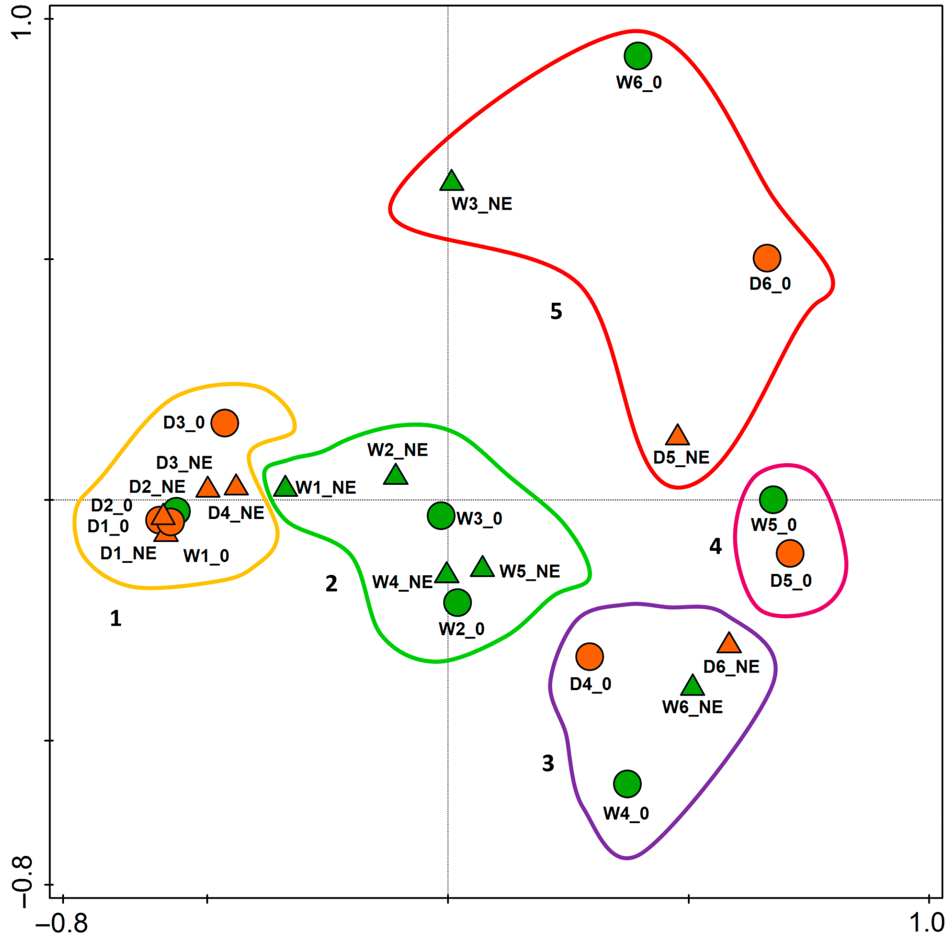

FIGURE 4 Scatter plot of principal coordinates analysis (PCoA) based on grass species assemblages (24 altitude/aspect categories; see Appendix S1: Table S2), with the groups resulting from the cluster analysis marked: dry period (orange symbols); wet period (green symbols). Exposure categories are: triangle, NE; circle, others. Eigenvalues: 0.2125, 0.0999, 0.0849, and 0.0698 for the first, second, third, and fourth ordination axes, respectively. The two first axes accounted for 31.24% of the explained variation (cumulative), with 21.25% and 9.99% for the first and second axes, respectively. Altitude values are significantly correlated with the first PCoA axis ($R^2 = 0.715$; $p < 0.001$). Five groups are highlighted: 1, xerophytic assemblage; 2, moderate-/medium-altitude mesophytic assemblage; 3, medium-/high-altitude mesophytic assemblage; 4, medium-altitude mesophytic assemblage; 5, high-altitude mesophytic assemblage.

If wind exposure is considered (Figure 6A), the overall representation of annuals in the dry period slightly increases in the windward slopes (but not significantly, see Appendix S1: Table S4). Concerning perennials, windward slopes also usually have higher values than leeward slopes, especially at higher altitudes, but no significant differences were detected between the wet and dry periods.

Concerning the photosynthetic pathways (Figure 6B), C4 grasses predominate along the whole altitudinal gradient, with a decrease above 1200 m, where C3 species reach their maximum. In the dry period, the total number of C4 species increases significantly ($p = 0.048$).

The percentage of C4 grasses in windward aspects increases with altitude (especially above 900 m) (Figure 6B); moreover, they show a slight increase in the dry period ($p = 0.050$).

The C3 species are, also, particularly well represented in the windward aspect class, in both climatic periods; they are reduced or even absent in leeward aspects (Figure 6B).

The altitudinal distribution of taxa according to their biogeographic distribution shows that, up to 1200 m, most species are from tropical/subtropical regions, with the tropical/temperate species increasing above 1200 m (Figure 6C). A slight tendency for tropical/subtropical species to increase in the dry period can be pointed out.

Considering wind exposure (Figure 6C), tropical/subtropical species tend to increase in the windward aspect during the dry period ($p = 0.050$), whereas

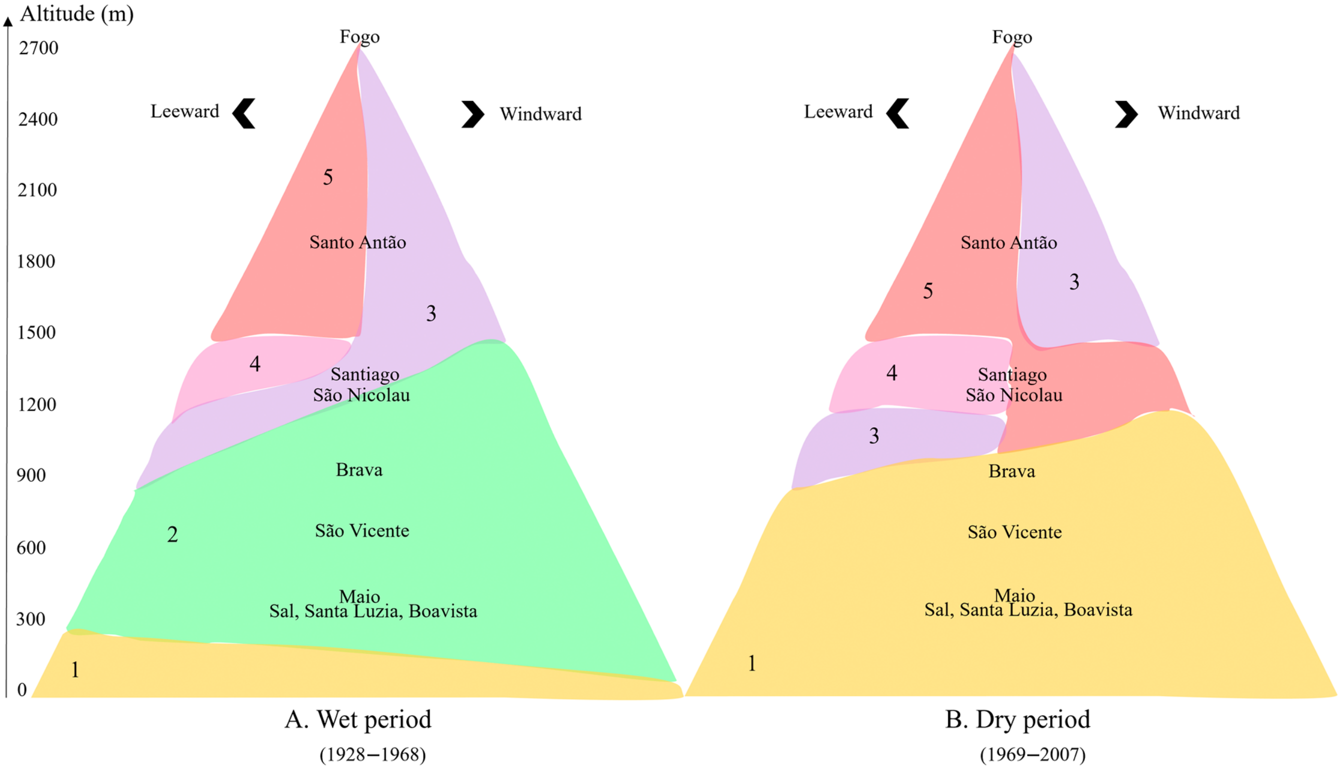

FIGURE 5 Theoretical distribution pattern of grass clusters in the wet (A) and dry (B) periods, according to altitude and exposure. The colors and numbers (1–5) correspond to the groups identified as: 1, xerophytic assemblage; 2, moderate-/medium-altitude mesophytic assemblage; 3, medium-/high-altitude mesophytic assemblage; 4, medium-altitude mesophytic assemblage; 5, high-altitude mesophytic assemblage. The position of the island names indicates its maximum altitude.

tropical/temperate species are favored in the other aspects ($p = 0.036$).

DISCUSSION

Temporal and spatial shifts in grass assemblages: The combined effects of climate and topography

The present study identified temporal (considering two contrasting 40-year periods, wet and dry) and spatial (slope and altitude) shifts in the distribution of grass assemblages in Cabo Verde.

Concerning the temporal shifts, the dry period favored the expansion of the xerophytic assemblage (cluster 1) to higher altitudes, occupying most of the islands' area. In the wet period, this assemblage was replaced, in most of the area, by a mesophytic assemblage (cluster 2), while the xerophyte assemblage remained limited to the lower areas, especially on leeward slopes.

These temporal shifts were clearer in low-altitude areas (as demonstrated when comparing pairs of categories with similar altitude/exposure but from different climatic periods) and not as noticeable in altitude zones above 1200 m (where the three mesophytic assemblages roughly maintained their altitude limits). This suggests that the role of the altitude-associated mesoclimate is more prominent in highlands and may act as a buffer that attenuates the effects of macroclimatic conditions.

Concerning the spatial shifts, the medium- and high-altitude mesophytic assemblages (clusters 4 and 5) occurred preferentially on leeward slopes (in Santo Antão and Fogo, the only islands with non-negligible areas above 1200 m), in both climatic periods. These marked asymmetries in the distribution of assemblages between the windward and leeward slopes, also pointed out by several authors (e.g., Barbosa, 1968; Brochmann et al., 1997), confirmed the importance of moisture-laden NE winds. Thus, the slope aspect contributed not only to changes in the altitudinal limits of the assemblages, both within or between the two climate periods, but also to the presence of particular assemblages, as observed in the higher altitude zones.

These results strengthen the relevance of mesoclimates in Cabo Verde, with local-scale variables, namely altitude and aspect, being responsible for different responses in grass distribution. Similar conclusions were highlighted by

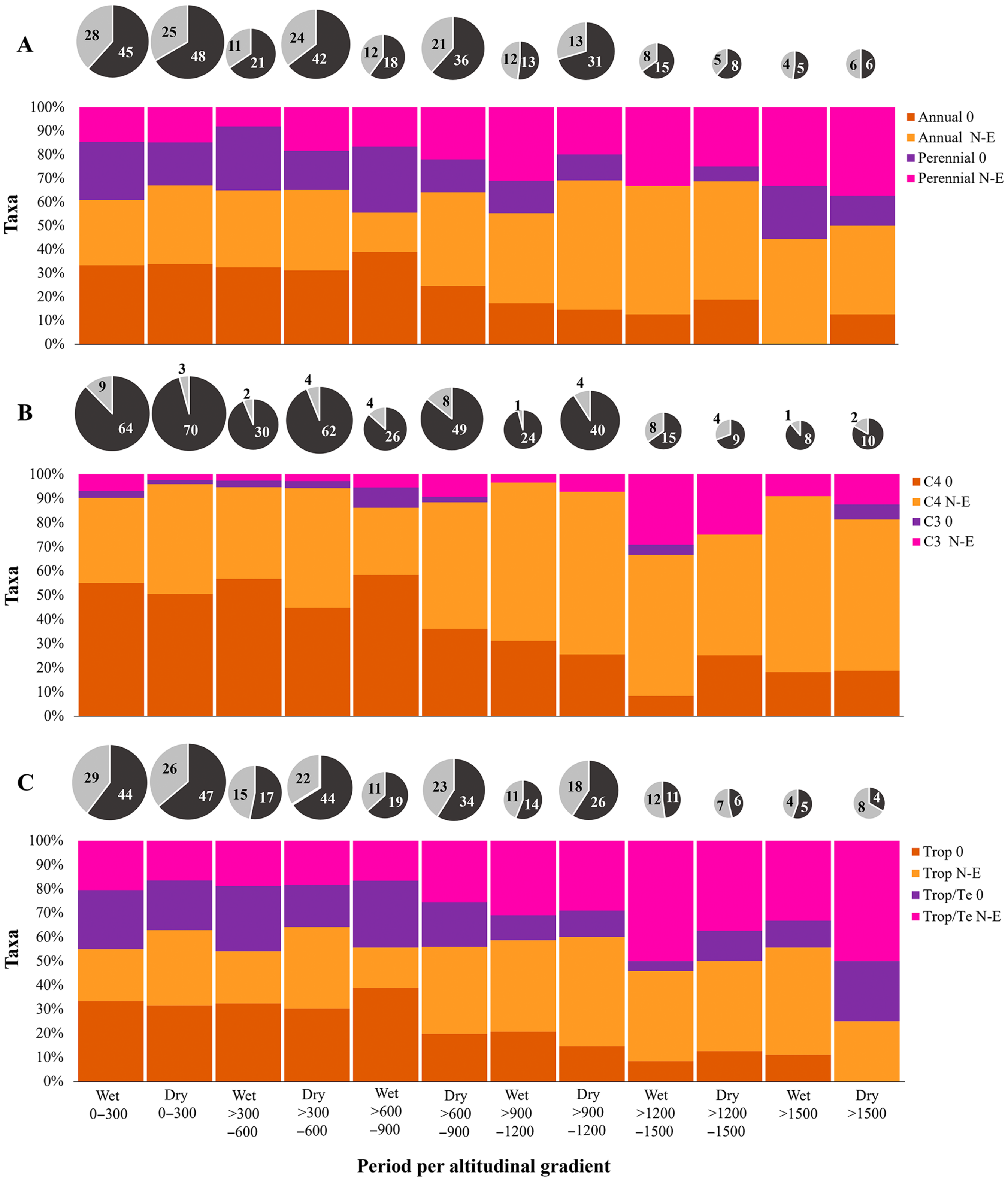

FIGURE 6 Pie charts show the variation in taxa number across altitude classes, in dry and wet periods: (A) annual (black) versus perennial (gray); (B) C4 (black) versus C3 photosynthesis (gray); and (C) tropical/subtropical (black) versus tropical/temperate (gray); the size of the circle is proportional to the number of taxa. Bar charts show the variation in the relative abundance of taxa across altitude and aspect classes (windward, NE; leeward, 0), in dry and wet periods: (A) annual versus perennial; (B) C4 versus C3; and (C) tropical/subtropical (Trop) versus tropical/temperate (Trop/Te).

Maclean et al. (2015), with coastal grasslands in the United Kingdom, and Príncipe et al. (2022), with Mediterranean tree forests, who also emphasize the importance of the local climatic conditions over the macroclimate.

Moreover, the latter work points to the more pronounced effects of local-scale variables in areas where water is a limiting factor, as also seems to occur in this tropical dry archipelago. Water is, in fact, a key-driver in Cabo Verde; it is the increase in dryness, rather than temperature, that most affects plant life. The importance of precipitation is also emphasized in the work of Hanz et al. (2023) who, given the climate changes predicted for the Canary Islands, suggest precipitation (and not temperature) as the factor most affecting the distribution of native species (endemic and non-endemic). This contrasts with studies in other ecosystems, such as the alpine ones, where temperature is often a limiting factor. In these ecosystems, warming and dryness seem to have opposite effects (warming generally reduces abiotic limitations and dryness increases abiotic stress) when alone, but, when combined, dryness overrides any beneficial effects of warming (e.g., on plant development) (De Boeck et al., 2016; Schuchardt et al., 2021, 2023).

For Cabo Verde, climate projections for 2011–2040 indicate a reduction of about 2% in average annual precipitation, increasing the probability of droughts, a reduction in the length of the rainy season, and an increase in mean annual temperature of about 1°C for that period and of 3°C by the end of the century (Ministério da Agricultura e Ambiente, 2021). In this scenario, in which temperatures and aridity are expected to rise at the same time, the combined impacts of these changes on plant life are expected to be more serious than if each of these factors acted alone.

Response of functional traits to contrasting climatic periods and topographies

This study also identified variations in the distribution of functional attributes depending on the climatic period, altitude, and slope aspect.

An overall increase of annuals over perennials was detected in the drier period. Annual growth, a drought escape strategy (Kooyers, 2015), predominates in grasses that occur across the archipelago, except for those present at higher altitudes (above 1500 m) where climatic conditions, generally associated with greater water availability, may favor the establishment of perennial grasses. Annuals are more associated with climatic variability (i.e., irregular, and erratic climate characteristics, as occurs in Cabo Verde), because they survive only during part of the year, avoiding seasonally severe environmental stress (Friedman, 2020; Monroe et al., 2019). The exceptional population growth in recent decades and the consequent increase in human activities, either through agricultural activities or grazing, can lead to water stress (the so-called anthropogenic drought AghaKouchak et al., 2021) and soil erosion and may also favor annual species (Belsky, 1992). In Cabo Verde, soil erosion is one of the most significant impacts of human activities, particularly severe on the mountainous islands of Santiago, Santo Antão, and Fogo, where agricultural areas account for 84.3% of the archipelago's total agricultural area (Monteiro et al., 2020).

As with perennial species, C3 species reach their maximum values at high altitudes, with high water availability regardless of the climatic period. It is interesting to note that among the species collected only during the wet period, about 56% were C3 species; exclusive species of the dry period included only 21% of C3 species. Water availability is a limiting factor for this functional group (Winslow et al., 2003).

C4 species are more widespread, dominating the warmer and drier areas of Cabo Verde. This agrees with the usual worldwide ecological pattern: C4 species tolerate lower water availability and higher temperatures (preferring tropical regions), whereas C3 species are most efficient under high water availability and are particularly well-adapted to mild temperatures (more common in temperate regions) (Parr et al., 2014; Pearcy & Ehleringer, 1984; Woodward et al., 2004). The C4 pathway allows a higher water-use efficiency (Pearcy & Ehleringer, 1984), providing a competitive advantage in more arid environments (Edwards & Still, 2008; Simpson et al., 2020).

At higher altitudes, strongly influenced by the trade winds and with greater water availability, the windward slopes generally have higher percentages of grasses (in both climatic periods and regardless of functional type) than the leeward counterparts. Again, mesoclimates seem to attenuate the effects of the macroclimate.

In Cabo Verde, the presence of C3 grasses can be used as an environmental bioindicator to assess water availability. This is particularly useful, in this archipelago, where significant amounts of water, in the form of horizontal precipitation related to the northeastern trade winds, are not accounted for in precipitation measurements (Amaral, 1991; Duarte et al., 2008).

Species with native distributions in temperate regions are few and occur more frequently in the cooler, high-altitude zones. The low values are due to the fact that dispersal from the African continent to the highlands of the archipelago is difficult, not only because of their small areas, but also because of the considerable distance from possible sources of colonization with ecological similarities in West Africa (e.g., the nearest ones are the Anti-Atlas Mountains in Morocco, 2000 km to the northeast of Cabo Verde, and Mount Loura in Guinea, 1200 km to the southeast). This situation contrasts with that of the Canary Islands, the Macaronesian archipelago closest to Cabo Verde, whose proximity to the African continent has facilitated colonization by species from many different geographic enclaves (Caujapé-Castells et al., 2017).

Species with tropical/subtropical distributions, most of them from West Africa, particularly from the Sahelian region, are much more common. The strong preference of these species for warmer and drier environments may also explain the fact that, as shown in this work, 87% of all the reported grass species are found below 600 m of altitude, the hottest and driest areas, with annual rainfall generally below 300 mm. The physiognomic and structural affinities of the grasslands occurring in the arid lowlands of Cabo Verde with the dry tropical West African graminoid vegetation, including numerous shared taxa, have already been noted (Neto et al., 2020; Rivas-Martinez et al., 2017).

Grassland management and climate change

Grasses and grasslands are extremely important to the Cabo Verdean population, both as food for human consumption (maize is a staple food) and as fodder, so safeguarding their sustainable use is crucial, especially as the degradation of these resources is already significant (Rocha et al., 2021). Climate plays a critical role not only in terms of the area occupied by agricultural activities, as mentioned for West Africa by Ahmed et al. (2016) but also because of the impacts on productivity, as emphasized by Catorci et al. (2021) for the Mediterranean mountain pastures, so climate change projections and their impacts must be taken into account when managing ecosystems.

Considering the important role of climate variability in the distribution of grass assemblages and recognizing the impacts of this variability on the functional attributes of grasses in Cabo Verde, we can foresee shifts in distribution areas as well as variations in functional traits (e.g., an increase in both annual and C4 species). These conclusions can contribute to effective ecosystem management, ultimately guiding conservation efforts, resource utilization, and restoration initiatives in Cabo Verdean islands. In agricultural and livestock systems, for example, measures to cope with climate change could include improving pastures with climate-resilient forage species, using drought-tolerant crops that are better able to cope with heatwaves and droughts, or diversifying crops to ensure food security in the context of the archipelago's climate variability.

CONCLUSIONS

This study successfully used climate variability and available historical data to foresee the impact of climate change on the distribution of grass species. Cabo Verde was selected for the known alternation of dry and wet periods, which can last for decades, and for the orographic characteristics of its islands, which allow an assessment of the role of altitude and aspect, two factors that strongly reflect the impact of regional climatic elements (e.g., trade winds), on the distribution of species.

The present work merged the distribution data from the 10 islands of this archipelago to build a single theoretical island model, allowing the analysis of changes in grass assemblages over space and time. Besides revealing spatial shifts in the distribution of grass assemblages promoted by the alternation of dry and wet periods, the results highlight the relevance of fine-scale data (namely altitude and aspect) in the response of plant communities to climate variability, with the mesoclimate mitigating the effects of the macroclimate.

In addition, the joint effects of the huge population growth of recent decades and the progressively drier climates will intensify the changes associated with species traits, such as the expected increasing success of annuals, C4, and xerophytic taxa, with a profound impact on the use of these resources. This is very important in Cabo Verde, where grasslands are a primary resource for the rural population, and changes in species composition will impact their use.

This approach can also be useful to manage plant resources in other tropical dry archipelagos and thus contribute to ensuring their protection and sustainable use.

Finally, it is worth noting that this work was possible not only due to the great efforts made in recent decades to study the Cabo Verdean flora but also because of the long-term data available (in this case, 80-year-old data). Despite their limitations, historical data have been successfully used here to analyze climate variability, highlighting its potential in this area. Ecological studies including broad temporal and spatial scales depend on an adequate volume of data, and it is therefore imperative to find ways to ensure that such information continues to be collected.

AUTHOR CONTRIBUTIONS

Maria Cristina Duarte and Vanézia Rocha should be considered as co-first authors. Maria Cristina Duarte and Maria M. Romeiras designed the study. Maria M. Romeiras was involved in funding acquisition. Maria Cristina Duarte, Vanézia Rocha, Isildo Gomes, Carlos Neto, José C. Costa, and Maria M. Romeiras conducted the data collection or provided datasets. Vanézia Rocha and Maria Cristina Duarte performed the analysis. Maria Cristina Duarte, Vanézia Rocha, Maria M. Romeiras, Cristina Branquinho, and José María Fernández-Palacios analyzed and interpreted the data. Maria Cristina Duarte and Vanézia Rocha wrote the manuscript with contributions from all the authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Duarte et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.47d7wm3jh.

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SUPPORTING INFORMATION

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