

TDV-optimization exemplified: Application to coastal cliff vegetation in Cabo Verde

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Abstract

Aims: We illustrate the application of Total Differential Value (TDV) optimization – a vegetation classification technique – and introduce methodological innovations for identifying syntaxa at different ranks and their diagnostic species. This approach produced a new syntaxonomic synthesis for the coastal cliff vegetation of the Cabo Verde archipelago. **Study area:** Cabo Verde archipelago. **Methods:** We analysed 167 relevés sampled on coastal cliffs using a five-step approach: (1) Initial characterization of communities based on dominant species using formal logic rules. (2) Analysis of each physiognomic group for patterns of differential species using TDV-optimization, supporting the identification of preliminary associations. (3) Validation of associations by confirming the presence of differential species across them. (4) Application of TDV-optimization to the synoptic table to establish preliminary higher-rank syntaxa. (5) Validation of higher-rank syntaxa with characteristic species by assessing species fidelity across all 484 known relevés from Cabo Verde using the Differential Value (DiffVal) index. **Results:** The five-step classification procedure revealed 17 physiognomic-floristic units at the association level, supported by differential species. TDV-optimization successfully identified higher-rank syntaxa – two alliances, one order, and one class – based on exclusive species and with clear biogeographic and ecological interpretations. Partial DiffVal scores proved useful for distinguishing characteristic species at higher ranks. **Conclusions:** Based solely on presence-absence data, TDV-optimization and the DiffVal index proved effective for vegetation classification at different scales, revealing co-occurrence/co-absence patterns. The identified syntaxa emphasize Cabo Verde's distinctness from Mediterranean and Eurosiberian communities, confirming its affinity with the *Warm deserts and semi-deserts* subbiome and its biogeographical placement within the *Tropical Sahara* region. Further research should expand knowledge of Cabo Verdean and other African vegetation and numerically validate its syntaxonomy to support evidence-based conservation policies.

Taxonomic reference: Plants of the World Online database (POWO 2025), except for *Campylanthus glaber* subsp. *spathulatus* (Brochmann et al. 1997), *Fagonia latifolia* (Pinto Basto 2002), *Launaea arborescens* subsp. *melanostigma* and *Tetraena vicentina* (Rivas-Martínez et al. 2017), and *Lotus bollei* (Chevalier 1935).

Syntaxonomic references: Mucina et al. (2016); Rivas-Martínez et al. (2017) for the endemic Cabo Verde vegetation.

Abbreviations: DiffVal = Differential Value; IAP = Internal Assignment Precision; pDiffVals = partial values used in the calculation of DiffVal; TDV = Total Differential Value.

Keywords

Cabo Verde, classification, coastal cliffs, Differential Value index, phytosociology, plant community, *Polycarpaceo lycioidis-Limonietea braunii*, syntaxonomy, TDV-optimization, vegetation

Introduction

The exploration of the flora of Cabo Verde dates back to the 19th century, with pioneering works by Webb (1849) and Schmidt (1852), followed by Andrade (1908), Chevalier (1935), and later contributions by Lobin (1986), Hansen and Sunding (1993), and the *Flora de Cabo Verde* project (Martins et al. 1995–2002). Several studies have highlighted Cabo Verde's remarkable endemic flora (Gomes et al. 1995; Brochmann and Rustan 1987; Brochmann et al. 1997; Duarte 2008), as well as the assessment of its threatened categories (Leyens and Lobin 1996; Romeiras et al. 2016). More recent syntheses (Arechavaleta et al. 2005; Gomes et al. 2023) and additional taxonomic studies (Duarte et al. 1999; Romeiras et al. 2011, 2015; Marrero and Almeida Pérez 2012; Sukhorukov and Nilova 2016; Sukhorukov et al. 2018; Gardère et al. 2021) have further expanded knowledge of the flora of this volcanic archipelago.

In the drier areas of the Cabo Verde archipelago, savannoid, pre-desertic and desertic floristic elements of Saharan, Sahelian, and Afrotropical origin are particularly common (Barbosa 1968; Duarte et al. 2005; Costa et al. 2017a, 2017b; Rivas-Martínez et al. 2017).

Since the late 20th century, several works have addressed the vegetation of the archipelago (Diniz and Matos 1986, 1987, 1988a, 1988b, 1993, 1994a, 1994b, 1999a, 1999b; Duarte and Moreira 2002; Duarte et al. 2005). However, phytosociological approaches have only been published recently (Gomes et al. 2012; Costa et al. 2014, 2017a, 2017b; Neto et al. 2023), and among these, only Rivas-Martínez et al. (2017) published relevés.

Rivas-Martínez et al. (2017) presented the first broad overview of Cabo Verde vegetation, publishing 317 relevés assigned to nine vegetation classes: *Adiantetea* (chasmophytic vegetation on moist walls and caves); *Arthrocnemetea franzii* (coastal succulent salt marshes); *Asplenietea trichomanis* (rupicolous vegetation on walls and cliffs); *Cocculopenduli-Sarcostemmetea daltonii* (xeromorphic open micro-woodlands, shrublands, and dwarf-shrub savannas); *Frankenio pseudoericifoliae-Suaedetea caboverdeanae* (halophytic coastal vegetation adapted to mobile sand dunes); *Heteropogonetea contorti* (perennial grassland savannas with scattered shrubs and trees); *Cymbalaria-Parietarietea diffusae* (eutrophic chasmophytic and chomophytic vegetation of shaded rocky walls); *Polygono-Poetea annuae* (ruderal and nitrophilous vegetation disturbed by trampling); and *Tetraenetea simplicis* (ephemeral grassland savannas appearing after sporadic rains).

In this work, we investigate the previously uncharted coastal cliffs and associated platform habitats of Cabo Verde. These environments are colonized by cremnophytes (plants

specialized in growing on cliffs), typically dwarf perennials adapted to strong edaphic salinity from sea spray and to permanent exposure to wind, aerosols, and sea storms, and further constrained by oligotrophic conditions, thin soils, steep slopes, and distinctive topoclimatic features.

As a result, these extreme habitats support a species-poor flora, dominated by chasmophytes (occupying soil accumulations in rock cracks, crevices, and hollows) and chomophytes (growing on thin soil layers on rock surfaces), mainly represented by chamaephytes, nanophanerophytes, and hemicryptophytes, with therophytes occurring occasionally. These plant communities are typically permanent and relatively stable over time (Brullo et al. 2017).

A syntaxonomic synthesis of the coastal cliff vegetation of the Cabo Verde archipelago is presented, illustrating the application of Total Differential Value optimization (TDV-optimization; Monteiro-Henriques 2025) within a multi-step approach to identify associations, higher-rank syntaxa, and their respective differential and characteristic species.

Study area

The Cabo Verde archipelago is located in the Atlantic Ocean, approximately 500 km west of the Senegalese coast, between 14°N and 18°N latitude and 22°W and 26°W longitude (Figure 1). Covering a total area of 4,033 km², it comprises ten main islands and several islets.

Geology

The genesis of the Cabo Verde Islands is associated with intra-plate volcanic processes (Ernst and Buchan 2003). Several authors (e.g., Holmes 2008; Ramalho 2009), who support their origin from mantle plumes (hotspots), propose the existence of an underwater ridge connecting the Cabo Verde and Canary archipelagos, as well as a strong similarity in the nature and composition of their volcanic episodes.

Hotspot activity began around 19–22 Ma ago, creating a large submarine crustal uplift zone – known as the Cabo Verde Rise – where the islands are located (McNutt 1988; Plesner et al. 2003; Holm et al. 2008; Ramalho 2009). Volcanic activity has persisted to the present day.

The islands collectively form a westward-open arc and are divided into two main groups – northern and southern – based on the prevailing NE trade winds: the windward group comprises Santo Antão, São Vicente, Santa Luzia, São Nicolau, Sal, and Boa Vista, whereas the leeward group includes Maio, Santiago, Fogo, and Brava.

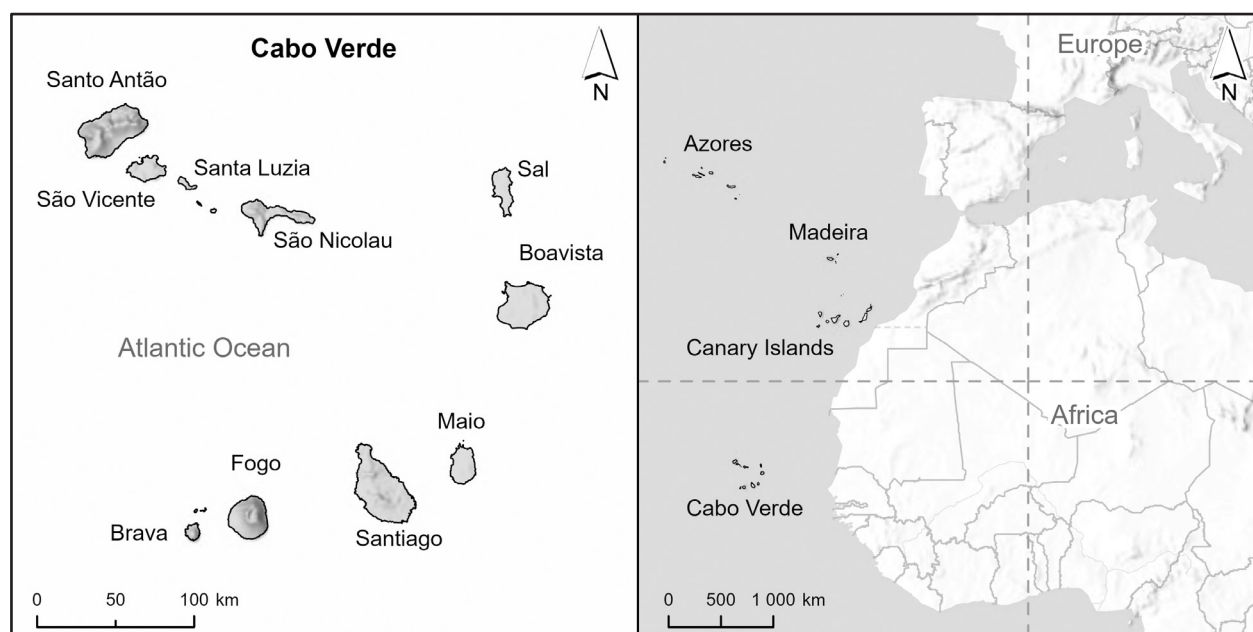


Figure 1. Location of the Cabo Verde archipelago off the coast of West Africa. Basemap information from ESRI.

Our focus was on coastal cliffs and associated platforms covered by sediments predominantly derived from basalt, with variable proportions and grain sizes of basaltic clasts. However, on some islands (São Vicente and Santa Luzia), sandstone cliffs were also sampled. These consist of coralline sands consolidated with limestone cement, unique in terms of geomorphology and flora. These sandstones originated from coral reefs abundant in shallow marine areas – such as the channel between São Vicente and Santa Luzia – which were exposed to subaerial erosion during glacial periods, contributing to accumulations of white calcareous sand, sometimes consolidated.

In the basaltic cliffs, the influence of calcareous sands may also occur, as shallow sandy layers cover rocky platforms or accumulate in crevices. The nature of the rock and the presence of pyroclastic or calcareous materials – namely, remnant skeletal fragments of coral, foraminifera, coralline algae, molluscs, and crustaceans – contribute to a diverse mosaic of habitats.

Climate

Due to its position relative to the Intertropical Convergence Zone, occupying the northern part of its oscillation zone, Cabo Verde experiences a dry tropical climate with two well-defined seasons (rainy and dry) that strongly influence the distribution of its flora and vegetation (Neto et al. 2020). However, island topography contributes to significant spatial variation, depending on altitude and exposure to prevailing winds (see, e.g., Varela-Lopes and Molion 2014). Flatter islands – such as Sal, Boavista and Maio – exhibit a predominantly desertic climate (arid to ultrahyperarid), while the more mountainous islands (Santo Antão, São Nicolau, Fogo, Santiago, Brava) display a semiarid to dry bioclimate, with a clear dichotomy

between north-facing slopes (moister) and south-facing slopes (drier).

According to the Worldwide Bioclimatic Classification System (Rivas-Martínez et al. 2017), the Cabo Verde archipelago falls within a tropical macrobioclimate, encompassing hyperdesertic, desertic, xeric, and pluviseasonal bioclimates. More than 90% of the territory is classified as tropical desertic or tropical xeric (but see also Chevalier 1935; Ribeiro 1954; Amaral 1964; Babau 1983; Alves 1987; Ferreira 1987; Correia 1996; Costa et al. 2017a, 2017b). The coastal areas sampled in our study range from infratropical to thermotropical thermotypes and from ultrahyperarid to arid ombrotypes.

Methods

We employ several vegetation science terms that require precise delineation, as their meanings have fluctuated over time. Precise definitions and concepts used in this work are provided in Suppl. material 1, namely: *characteristic species*; *differential species*; *diagnostic species* (used broadly for species or groups of species with any diagnostic value); *fidelity*; *presence* (distinguished from *constancy* and *Raunkiaer's frequency*); *stand*; *tabular classification* (a clustering technique in phytosociology for partitioning relevés into vegetation units); and *side-by-side tabulation* (arranging data in tabular form to enable comparisons between columns, for example in studies of species fidelity).

For sampling relevés, we followed the minimal area concept (or nested-plot technique) as illustrated by Mueller-Dombois and Ellenberg (1974, pp. 45–54), using flexible plot shapes as noted by Westhoff and van der Maarel (1978, p. 307).

Hereafter, we refer to species and infraspecific taxa collectively as 'species'.

Data sets

We compiled a data set comprising 167 relevés, including seven from Rivas-Martínez et al. (2017) and 160 original relevés collected on coastal cliffs/platforms between 2013 and 2023. The relevés were from the islands of Santo Antão, São Vicente, Santa Luzia, Santiago, Fogo, Brava and Maio. These communities were not observed on islands with mostly low and sandy coastlines (Sal and Boavista). This is hereafter referred to as the *cliff data set*.

The selection of stands and placement of plots adhered to the principle of being “subjective without preconceived bias” (Mueller-Dombois and Ellenberg 1974, p. 32), with plots directed towards vegetation stands on the coastal cliffs. Plot locations were recorded using a Global Positioning System with the WGS84 reference system. For each relevé, we documented the sampled area (2–50 m²), total vegetation projected cover (10–100%), altitude (1–140 m a.s.l.), aspect, and the cover-abundance of all vascular plants using Braun-Blanquet’s original six-level scale (Braun-Blanquet 1932, p. 34).

To study species fidelity to higher-rank syntaxa, we constructed a second data set comprising all known relevés from Cabo Verde: 324 from Rivas-Martínez et al. (2017) and 160 from the present study, totalling 484 relevés. This is hereafter referred to as the *full data set*.

Intraspecific ranks (subspecies and varieties) were retained only when consistently determined for all occurrences of the respective species; otherwise, they were merged at the species level. Accordingly, the cliff data set comprises 60 species or infraspecific taxa, while the full data set includes 304.

Classification procedures

The data sets were imported into R 4.5.0 (R Core Team 2025), where all analyses were performed. To ensure full reproducibility of the classification procedure, we provide the complete data set of 484 relevés (Suppl. material 2), the corresponding header information (Suppl. material 3), a *shapefile* of Cabo Verde’s administrative areas (Suppl. material 4), and a set of auxiliary R functions (Suppl. material 5).

The analysis of the cliff data set is particularly challenging: although sampled in environmentally similar areas across Cabo Verde, the data set contains highly dissimilar relevés, characterized by low average species richness (mean $\alpha = 4.7$), low total diversity ($\gamma = 60$), and high turnover ($\beta = \gamma / \text{mean } \alpha = 12.7$). Notably, 41% of all 13,861 possible pairs among the 167 relevés share no species, resulting in a Jaccard distance of 1.

The floristic demarcation of the association concept is strictly based on the presence of *diagnostically important* species (Tüxen and Ellenberg 1936, p.174), i.e., on the presence of differential species. However, these authors recognize the systematic importance of species dominance, employed in the physiognomic characterization of the communities and in the establishment of facies.

In fact, dominance carries diagnostic value and can be a significant factor in establishing the comparative context within which differential species are identified (Landucci et al. 2020). We maintain that community physiognomy – determined by one or more dominant species – can be essential in defining that comparative context. In practice, if a researcher is unable to identify any differential species between two sets of relevés sharing the same physiognomy, it is likely that these sets correspond to the same association. Conversely, if two sets of relevés are clearly dominated by different species (or groups of species), this indicates an objective dissimilarity. We find no theoretical basis in vegetation science that would advise against analysing such sets separately, at least in an initial stage. When tabulated synoptically, the researcher may conclude that they lack differential species and decide to merge them under the same association (as different facies). Therefore, we integrated dominance into a multi-step classification approach, implemented in five steps:

(Step 1) Focusing on the dominant species, we conducted an initial analysis of the cliff data set to develop formal logic rules for splitting relevés into groups based on community physiognomy. This approach is analogous to that presented by Bruehlheide (1997) but strictly focuses on physiognomic characteristics. These formal logic rules can be translated into a dichotomous key.

(Step 2) Each established physiognomic group was then subjected to a second analysis, in which floristic groups were identified using TDV-optimization (Monteiro-Henriques 2025), supporting the establishment of preliminary associations. As a general guideline, we tested values of k (the number of groups) ranging from two up to the integer division of the number of relevés in the physiognomic group by 10, plus one. For each physiognomic group and k , we examined the graphical output of the “tabulation” function for the five solutions with the highest TDV scores.

(Step 3) The classification obtained in Step 2 was validated by: (i) inspecting the assignment of individual relevés to each preliminary association in light of the differential species identified for that unit; and (ii) examining, in a synoptic table, the existence of differential species among the species pools of the preliminary associations. This validation step is important because differential species in Step 2 were identified within physiognomic groups; consequently, communities belonging to different physiognomic groups may actually represent facies, i.e. they may differ in their dominant species while lacking differential species.

(Step 4) To identify higher-level groupings of associations, we experimentally applied TDV-optimization to a presence/absence version of the synoptic table, assessing the method’s ability to detect floristically differentiated groups that could represent higher-rank syntaxa, namely alliances.

(Step 5) To validate the preliminary higher-rank syntaxa obtained in Step 4, we analysed the sociological distribution of species using synoptic side-by-side tabulations of the full data set. Two fidelity measures were calculated for each rank: (i) the partial values used in the calculation of the differential value index (pDiffVals); and (ii) the

classical presence percentage. Characteristic species were then identified by comparing their pDiffVals across the synoptic side-by-side tabulations of the full data set and applying predefined rules (see below).

This multi-step approach additionally allowed the two analytical scales (association and higher-rank levels) to be disentangled, following procedures similar to those of Kalníková et al. (2021) and Strohbach and Strohbach (2023).

TDV-optimization yields a set of solutions with high TDV scores that can be further scrutinized, as this set may include different valid ways of classifying the same data set (see Monteiro-Henriques 2025). To assist in selecting among these solutions, we considered not only the TDV score, but also other characteristics of the partitions, namely: (i) the internal assignment precision (IAP); and (ii) the distribution of groups across the Cabo Verde islands (using a contingency table).

Given a vegetation table and a partition of its relevés into vegetation units, IAP represents the fraction of relevés (ranging from 0 to 1) that are unambiguously classified into a single vegetation unit, based on the species each relevé contains and the exclusive species of each vegetation unit or combinations thereof. IAP, used in Steps 2 and 3, was calculated using the function “internal_assignment” from the *diffval* package (Monteiro-Henriques and Cerdeira 2025).

The synoptic table mentioned in Step 3 (a side-by-side synoptic tabulation of the preliminary associations) was created as follows: Columns were arranged alphabetically by preliminary association. Species were then added sequentially according to the syntaxon in which they exhibited the highest presence percentage, following the same column order. Within each association, species were sorted in decreasing order of that percentage.

For the synoptic side-by-side tabulations mentioned in Step 5, column (syntaxon) and row (species) sorting followed the approach described for Step 3, but with prioritization by syntaxon rank: Columns were ordered alphabetically within each rank, from class to association. Species were then added sequentially according to the syntaxon in which they achieved the highest fidelity-related measure at each rank, starting at the class level, with orders, alliances and associations resolving ties successively. Finally, within each unique rank combination, species were sorted in descending order of the selected fidelity-related measure.

The pDiffVals are intermediate values in the calculation of the Differential Value (DiffVal), computed for each group under assessment, such as a syntaxon. The sum of the pDiffVals equals the DiffVal of that species for the given partition and table (Monteiro-Henriques 2025). The computation of pDiffVals, as well as the TDV-optimization mentioned in Steps 2 and 4, were implemented using the *diffval* package (Monteiro-Henriques and Cerdeira 2025; see also Monteiro-Henriques 2025).

We used pDiffVals to identify characteristic species of higher syntaxonomic ranks because: (i) pDiffVals are consistent with the clustering method employed; and (ii) the inherent penalization applied in the DiffVal calculation for species occurring in more than one vegetation unit

helps mitigate a common issue when comparing presence percentages among higher-rank syntaxa. Specifically, in non-monotypic syntaxa (i.e., those with more than one syntaxon at the next lower primary rank), presence percentages are typically highest at lower ranks, as these are floristically derived subdivisions of the higher ranks.

To identify *strict* characteristic species, only consistently centred species (i.e., those for which the highest pDiffVals at the alliance, order and class levels occur within the same class) were considered. These were evaluated by contrasting the pDiffVals of the preliminary higher-rank syntaxa across the full data set, following the combinatorial rules outlined below:

I. Class level. A species was considered characteristic of a class if: (i) the highest pDiffVal (across all higher ranks) occurred in that class; or (ii) in the case of non-monotypic classes, the maximum pDiffVal was achieved in a subordinate order, and the species was present in all subordinate orders.

II. Order level. A species was considered characteristic of an order if: (i) the highest pDiffVal (across all higher ranks) occurred in that order and, if applicable, the species did not occur in all sister orders (i.e., orders within the same class); or (ii) the following cumulative conditions were met: (1) the order is a singleton in its class and is non-monotypic; (2) the maximum pDiffVal is achieved in a subordinate alliance; and (3) the species is present in all subordinate alliances.

III. Alliance level. A species was considered characteristic of an alliance if: (i) the highest pDiffVal (across all higher ranks) occurred in that alliance and, if applicable, the species did not occur in all sister alliances (i.e., alliances within the same order). To filter out less faithful species at the alliance level, we required a pDiffVal ≥ 0.07 .

Species falling outside the predefined rules were not considered characteristic, although some phytosociologists might classify them as characteristic, differential, transgressive (sensu Westhoff and van der Maarel 1978; Mucina 1993) or transgressive/ingressive (sensu Poldini and Sburlino 2005). However, their formal definition and implementation are complex, often involving subjectivity when multiple criteria compete.

For monotypic syntaxa (those with a single syntaxon at the next lower primary rank), we extended characteristic species from the respective lower rank to the parent syntaxa, a procedure that Braun-Blanquet (1932, p. 60) appeared to favour – even for non-monotypic syntaxa – when noting that “The higher the systematic rank of the unit of vegetation, the richer it is in characteristic species”.

A final rearranged synoptic table of the coastal cliff vegetation of the Cabo Verde archipelago was produced, reflecting all implemented steps. Syntaxa were formally described whenever appropriate, following the fourth edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021).

The parameterization of the TDV-optimization for Step 2 is provided in Suppl. material 6: table S6.1, and for Step 4 in Suppl. material 6: table S6.2.

Results and discussion

Outputs of the classification procedures

Step 1 – Community physiognomy

Focusing on the dominant species, we developed formal logic rules to classify relevés into physiognomic groups and translated these rules into a dichotomous key (see Suppl. material 7). Applying this key to the 167 relevés resulted in an initial division of the data set into nine physiognomic groups, each comprising between ten to 42 relevés (see the first and second columns of Table 1).

Step 2 – Numerical analysis (associations)

Inspection of the graphical output for the five highest-scoring TDV solutions (Suppl. material 8) indicated that further increasing k was unnecessary, as companion/common species were generally scarce and no clear checkerboard patterns emerged among the highest tested k values. Suppl. material 8 also shows the selected solution for each physiognomic group and provides the rationale for its choice. In total, 17 preliminary associations were identified (see the last three columns of Table 1).

Step 3 – Validation of associations

Across the cliff data set as a whole, IAP was 0.701, indicating the precision of assigning relevés to the preliminary associations. This relatively low value is expected for this data set, as several relevés contain very few species. When the physiognomic analysis defined in Step 1 is incorporated

into the classification, the IAP rises to 0.958 (i.e., only seven species-poor relevés showed ambiguous placement among the selected solutions in Suppl. material 8). The increase in IAP illustrates the advantage of integrating physiognomy into the classification procedure.

Additionally, the IAP for the synoptic table was 1.00, demonstrating the existence of differential species – or combinations of differential species – between the species pools associated with each preliminary association, thereby further supporting their formal treatment as associations. This was confirmed by examining a first synoptic table (a side-by-side synoptic tabulation of the preliminary associations). The R code used to calculate the IAP values mentioned above and to generate the synoptic table directly as an Excel spreadsheet is given in Suppl. material 9, while the synoptic table itself is provided in Suppl. material 10.

Step 4 – Numerical analysis (higher-rank syntaxa)

The presence-absence version of the synoptic table allowed the identification of two groups with clear ecological, geomorphological and biogeographic interpretations (Suppl. material 11): one group comprising five plant communities and nine exclusive species (from São Vicente and Santa Luzia), and a second group comprising the remaining twelve communities and 43 exclusive species (from Santo Antão, São Nicolau, Brava, Fogo, and Santiago). The communities of the first group occur within hyperarid to ultrahyperarid ombrotypes on coralline sands deposited over lava coastal platforms or crevices, whereas the second group predominantly thrives within arid ombrotypes on weathered basaltic substrates, including colluvial deposits and crevices in coastal cliffs.

We preliminarily designated the first group as *Limonium brunneri* and the second as *Polycarpaeo lycioidis-Limonium braunii*, noting that some exclusive species may serve as

Table 1. The nine physiognomic groups obtained in Step 1 and the 17 preliminary associations identified in Step 2.

Physiognomic group (dominant species)	No. of relevés	Tested k	Preliminary associations	No. of relevés
1. <i>Limonium brunneri</i>	13	2	a. Community of <i>Limonium brunneri</i> and <i>Frankenia caboverdeana</i>	3
			b. <i>Suaedo caboverdeanae-Limonietum brunneri</i>	10
2. <i>Limonium jovibarba</i>	10	2	c. <i>Frankenia caboverdeanae-Limonietum jovibarbae</i>	10
3. <i>Gomphrena vermicularis</i>	15	2	d. <i>Gomphrenetum vermicularis</i> (= <i>Blutaparonetum vermicularis</i>)	12
			e. Community of <i>Gomphrena vermicularis</i> and <i>Limonium braunii</i>	3
			f. Community of <i>Frankenia caboverdeana</i> and <i>Limonium braunii</i>	3
4. <i>Limonium braunii</i>	42	2 to 5	g. <i>Polycarpaeo lycioidis-Limonietum braunii</i>	10
			h. <i>Zygophyllo waterlotii-Limonietum braunii</i>	11
			i. <i>Campylantho spathulati-Limonietum braunii</i>	18
			j. <i>Frankenia caboverdeanae-Polycarpaeetum lycioidis</i>	10
5. <i>Polycarpaea gayi</i> var. <i>lycioides</i>	20	2 and 3	k. <i>Dauco humilis-Polycarpaeetum lycioidis</i>	10
6. <i>Zygophyllum waterlotii</i>	10	2	l. <i>Frankenia pseudoericifoliae-Zygophylletum waterlotii</i>	10
			m. <i>Nanorrhina elegantis-Paronychietum illecebroideis</i>	10
7. <i>Paronychia illecebroideis</i> , <i>Frankenia caboverdeana</i> , and <i>Lotus purpureus</i>	22	2 and 3	n. <i>Patellifolio procumbentis-Paronychietum illecebroideis</i>	10
			o. Community of <i>Lotus bollei</i> and <i>Frankenia caboverdeana</i>	2
8. <i>Suaeda caboverdeana</i>	19	2	p. <i>Loto bollei-Suaedetum caboverdeanae</i>	19
9. <i>Frankenia pseudoericifolia</i> , <i>Zygophyllum simplex</i> , and <i>Lotus bollei</i>	16	2	q. <i>Zygophyllo simplicis-Frankenietum pseudoericifoliae</i>	16

characteristic species of alliances (to be validated in Step 5). Similarly, some species common to both groups, could function as characteristic species of an order (preliminarily called *Polycarpaeo lycioidis-Limonietalia braunii*) or class (preliminarily called *Polycarpaeo lycioidis-Limonietea braunii*), a proposition that will also be evaluated in Step 5.

Step 5 – Validation of higher-rank syntaxa

Characteristic species were determined for all preliminary syntaxa, supporting their formal treatment. Refer to Suppl. material 12 for the R code to generate the synoptic side-by-side tabulations as an Excel spreadsheet, and to Suppl. material 13 for the tabulations themselves. The final, rearranged synoptic table is presented in Table 2.

Comparison with Macaronesian and continental syntaxa

Rivas-Martínez et al. (2017) place the Cabo Verde archipelago biogeographically within the Paleotropical Kingdom, Afrotropical Subkingdom, Tropical Saharan Region, and Cabo Verde Province. *Poaceae* are predominantly of tropical origin (Duarte et al. 2024), and the native savanna-forming trees belong to tropical genera such as *Dichrostachys*, *Faidherbia*, *Ficus*, and *Sideroxylon* (Rivas-Martínez et al. 2017; Costa et al. 2017a, 2017b; Neto et al. 2020). These floristic differences, together with its bioclimatic characteristics (rainfall concentrated in the hot season), place the Cabo Verdean coastlines well outside the Mediterranean–Atlantic coastal cliffs of the class *Crithmo-Staticetea*.

Initially, only one order was recognized within *Crithmo-Staticetea*, the *Crithmo-Staticetalia*, described from the Mediterranean coast of France and progressively extended to encompass strongly halophilous, species-poor vegetation of rocky cliffs along the Atlantic and Mediterranean coasts of Europe, North Africa, and the Middle East. Subsequently, two additional orders were included, namely the grasslands of *Crithmo-Armerietalia maritimae* and the dwarf scrubs of *Helichrysetalia italici*, both subaerohaline and not extending to the Macaronesian archipelagos (the Azores, Madeira and the Canary Islands). In contrast, *Crithmo-Staticetea* communities occurring in the Macaronesian archipelagos are currently included in the endemic order *Frankenio-Astydamietalia* (Mucina et al. 2016).

The placement of *Frankenio-Astydamietalia* within *Crithmo-Staticetea* is supported by the presence of several taxa shared between Macaronesia and the European or African mainland, including *Asplenium marinum*, *Carex extensa*, *Crithmum maritimum*, *Daucus carota* subsp. *azoricus* (cf.), *Dactylis glomerata* subsp. *hackelii* (cf.), *Frankenia laevis*, *Pallenis maritima* (cf.), and *Senecio leucanthemifolius* (cf.) (Mucina et al. 2016).

Our results demonstrate that the coastal cliff vegetation of the Cabo Verde archipelago does not share any species

with the *Crithmo-Staticetea*. This complete floristic disjunction supports the recognition of an independent taxonomic unit at the class level. Nevertheless, given the environmental and geomorphological setting of these cliffs, and the presence of genera such as *Limonium*, *Lotus*, *Daucus*, *Frankenia*, *Launaea*, and *Tetraena*, we consider this class to be geovicarious to the Atlantic–Mediterranean class *Crithmo-Staticetea*, while enriched with several Saharan, Sahelian, and Afrotropical elements.

Rivas-Martínez et al. (2017) interpreted some species characteristic of the Cabo Verde coastal cliffs as characteristic of other syntaxa (e.g., *Frankenia caboverdeana*, *F. pseudoericifolia*); however, at that time, only a limited number of relevés had been sampled from these environments. By systematically targeting coastal cliffs across the entire archipelago, our study provides evidence for the recognition of a novel vegetation class, with own characteristic species.

Formal diagnoses of the new syntaxa

At the association level, communities represented by fewer than ten relevés were left without a formal taxonomic assignment and are referred to as “Community of...”. An overview of Cabo Verdean coastal cliff syntaxa is presented in Table 3.

Diagnostic species are listed alphabetically. The following abbreviations denote diagnostic status, informed by the synoptic table (Table 2): **char.** – characteristic species within higher-rank syntaxa; **cond. char.** – conditional characteristic species within higher-rank syntaxa; **const.** – constant species within associations/communities (presence $\geq 60\%$; not indicated when a species is classified as differential or dominant); **diff.** – differential species within associations/communities (presence $\geq 10\%$); **diff. all.** – differential species between sister alliances (i.e., alliances within the same order); **dom.** – dominant (structural/constant) species.

Bioclimatic descriptions and detailed maps are available in Rivas-Martínez et al. (2017). A complete species list and photographs of selected syntaxa and taxa are provided in Suppl. material 14.

Class: *Polycarpaeo lycioidis-Limonietea braunii* J.C. Costa, Bioret, I. Gomes et C. Neto cl. nov. hoc loco

Holotypus: *Polycarpaeo lycioidis-Limonietalia braunii* J.C. Costa, Bioret, I. Gomes et C. Neto 2026 (this article)

Diagnostic species: *Aizoon canariensis* (cond. char.), *Frankenia caboverdeana* (char.), *Frankenia pseudoericifolia* (char.), *Heliotropium ramosissimum* (cond. char.).

Description: Chasmophytic and chomophytic vegetation of Cabo Verdean sea cliffs, predominantly dominated by chamaephytes; subject to saline spray, strong winds, and severe edaphic drought; occurring within a hyperdesertic to desertic, euhypercceanic tropical bioclimate.

Table 2. Synoptic table (presence percentage) of coastal cliff vegetation of the Cabo Verde archipelago. Key for the alliances: **Pl:** *Polycarpaeo lycioidis-Limonium braunii*; **Lb:** *Limonium brunneri*. Key for associations: **a:** Community of *Limonium brunneri* and *Frankenia caboverdeana*; **b:** *Suaedo caboverdeanae-Limonietum brunneri*; **c:** *Frankenia caboverdeanae-Limonietum jovibarbae*; **d:** *Gomphrenetum vermicularis*; **e:** Community of *Gomphrena vermicularis* and *Limonium braunii*; **f:** Community of *Frankenia caboverdeana* and *Limonium braunii*; **g:** *Polycarpaeo lycioidis-Limonietum braunii*; **h:** *Zygophyllo waterlotii-Limonietum braunii*; **i:** *Campylantho spathulati-Limonietum braunii*; **j:** *Frankenia caboverdeanae-Polycarpaeetum lycioidis*; **k:** *Dauco humilis-Polycarpaeetum lycioidis*; **l:** *Frankenia pseudoericifoliae-Zygophylletum waterlotii*; **m:** *Nanorrhino elegantis-Paronychietum illecebroidis*; **n:** *Patellifolio procumbentis-Paronychietum illecebroidis*; **o:** Community of *Lotus bollei* and *Frankenia caboverdeana*; **p:** *Loto bollei-Suaedetum caboverdeanae*; **q:** *Zygophyllo simplicis-Frankenietum pseudoericifoliae*. The key for the physiognomic groups' numbers is given in Table 1. Note that physiognomic group seven spans through the two alliances. Species are ordered by their faithfulness to syntaxa – from the class level to the association level. Characteristic species of the class, order and alliances (Step 5) are enclosed in light-grey boxes. Differential species identified within the physiognomic groups (Step 2) are indicated with a frame and in bold. Additional differential species that distinguish each association from any other association (Step 3) are shaded in dark grey. Other species (companion, accidental, and others) are listed at the end of the table. Columns in italics indicate lower diagnostic reliability, as they are based on only two or three relevés.

Alliance	Pl	Pl	Pl	Pl	Pl	Pl	Pl	Pl	Pl	Pl	Pl	Pl	Pl	Lb	Lb	Lb	Lb	Lb
Physiognomic group	2	3	3	4	4	4	4	5	5	6	7	7	7	1	1	8	9	7
Associations/communities	c	d	e	f	g	h	i	j	k	l	m	n	a	b	p	q	o	
Number of relevés	10	12	3	3	10	11	18	10	10	10	10	10	10	3	10	19	16	2
Characteristic taxa of the class and order																		
<i>Frankenia pseudoericifolia</i> ●	.	58	.	.	50	100	33	.	.	50	.	50	100	100	63	100	100	
<i>Aizoon canariense</i> ¹	.	67	.	67	.	73	56	10	.	60	50	70	.	.	16	19		
<i>Frankenia caboverdeana</i> ●	100	.	33	100	.	.	89	100	.	.	.	60	100	.	.	.		100
<i>Heliotropium ramosissimum</i> ¹	.	.	.	.	.	.	6	10	.	.	20	.	.	.	.	19	.	
Characteristic taxa of alliance <i>Polycarpaeo lycioidis-Limonium braunii</i>																		
<i>Paronychia illecebroides</i> ●	70	25	.	67	.	.	56	90	.	.	100	60	.	.	.	.	.	
<i>Limonium braunii</i> ●	.	.	100	100	100	100	100	100	.	.	.	.	.	.	.	.	.	
<i>Polycarpaea gayi</i> var. <i>lycioides</i> ●	.	.	.	.	80	.	39	100	100	.	.	.	.	.	.	.	.	
Characteristic taxa of alliance <i>Limonium brunneri</i>																		
<i>Lotus bollei</i> ●	.	.	.	.	.	.	.	.	.	.	.	.	.	33	70	37	75	50
<i>Limonium brunneri</i> ●	.	.	.	.	.	.	.	.	.	.	.	.	.	100	100	.	.	
Differential taxa of associations and communities																		
<i>Limonium jovibarba</i> ●	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Launaea picridioides</i> ●	80	.	.	33	.	.	.	70	.	.	.	.	.	.	.	.	.	
<i>Diploaxis gracilis</i> ●	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Gomphrena vermicularis</i>	.	100	100	.	.	.	.	10	.	.	.	.	.	.	.	.	.	
<i>Cressa salina</i>	.	42	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Ipomoea pes-caprae</i>	.	.	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Dactyloctenium aegyptium</i> ²	.	8	.	100	.	.	.	.	60	.	70	50	.	.	.	.	.	
<i>Launaea gorgadensis</i> ●	.	.	.	100	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Cynanchum daltonii</i> ●	.	.	.	33	.	.	6	.	.	.	.	.	.	.	.	.	.	
<i>Sonchus oleraceus</i>	.	.	.	33	.	.	.	.	10	.	.	.	.	.	.	.	.	
<i>Campanula bravenensis</i> ●	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Zygophyllum gaetulum</i> subsp. <i>waterlotii</i>	.	.	.	.	.	100	.	.	.	100	.	.	.	.	.	.	.	
<i>Asparagus squarrosus</i> ●	.	.	.	.	.	.	33	.	.	.	.	.	.	.	.	.	.	
<i>Helianthemum gorgoneum</i> ●	.	.	.	.	.	.	11	.	.	.	.	.	.	.	.	.	.	
<i>Campylanthus glaber</i> subsp. <i>spathulatus</i> ●	.	.	.	.	.	.	50	70	.	.	.	.	.	.	.	.	.	
<i>Diploaxis gorgadensis</i> ●	.	.	.	.	.	.	17	50	.	.	.	.	.	.	.	.	.	
<i>Lavandula rotundifolia</i> ●	.	.	.	.	.	.	.	30	.	.	.	.	.	.	.	.	.	
<i>Daucus humilis</i> ●	.	.	.	.	.	.	.	.	90	.	.	.	.	.	.	.	.	
<i>Asteriscus daltonii</i> subsp. <i>vogelii</i> ●	.	.	.	.	10	.	17	30	80	.	.	.	.	.	.	.	.	
<i>Commicarpus helenae</i>	.	.	.	.	.	.	.	.	80	.	30	.	.	.	.	.	.	
<i>Launaea intybacea</i>	.	.	.	.	10	.	11	.	80	30	.	.	.	.	.	.	.	
<i>Tridax procumbens</i> ²	.	.	.	.	20	.	6	.	60	.	.	.	.	.	.	.	.	
<i>Forsskaolea procrdifolia</i> ●	.	.	.	.	.	.	.	.	50	.	.	.	.	.	.	5	.	
<i>Aerva javanica</i>	.	.	.	.	.	.	.	.	40	.	.	.	.	.	.	.	.	
<i>Ipomoea quamoclit</i> ²	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	
<i>Sida salviifolia</i> ²	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	
<i>Cenchrus ciliaris</i>	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	

Alliance	PI	PI	PI	PI	PI	PI	PI	PI	PI	PI	PI	PI	PI	Lb	Lb	Lb	Lb	Lb
Physiognomic group	2	3	3	4	4	4	4	5	5	6	7	7	7	1	1	8	9	7
Associations/communities	c	d	e	f	g	h	i	j	k	l	m	n	n	a	b	p	q	o
Number of relevés	10	12	3	3	10	11	18	10	10	10	10	10	10	3	10	19	16	2
<i>Cucumis anguria</i> ²	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.
<i>Nicotiana glauca</i> ²	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.
<i>Portulaca oleracea</i>	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.
<i>Cynodon dactylon</i>	.	8	.	.	.	.	.	.	.	60	.	.	.	.	.	.	.	.
<i>Atriplex halimus</i> ²	.	.	.	.	27	.	.	.	.	30	.	.	.	.	.	.	.	.
<i>Corchorus depressus</i>	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	5	.	.
<i>Heliotropium pterocarpum</i>	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	11	.	.
<i>Launaea arborescens</i> subsp. <i>melanostigma</i> ●	.	8	.	.	.	18	.	.	.	20	.	.	.	.	.	.	.	.
<i>Campylanthus glaber</i> subsp. <i>glaber</i> ●	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.
<i>Nanorrhinum elegans</i> ³ ●	50	.	.	.	70	.	.	.	70	60	80	.	.	.	.	.	.	.
<i>Lotus purpureus</i> ³ ●	.	.	.	33	.	.	.	.	50	60	80	30	.	.	.	.	.	.
<i>Gymnocarpus sclerocephalus</i>	.	17	.	.	.	.	.	.	.	30	.	.	.	.	.	.	.	.
<i>Patellifolia procumbens</i> ³	50	8	33	67	.	.	.	.	.	20	.	80	.	.	.	.	.	.
<i>Polycarpha caboverdeana</i> ●	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.
<i>Suaeda caboverdeana</i> ³ ●	.	.	.	.	.	.	.	.	.	.	.	.	.	.	90	100	6	.
<i>Tetraena vicentina</i> ³ ●	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26	12	.
<i>Aristida funiculata</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12	.
<i>Fagonia latifolia</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	50
Other taxa																		
<i>Zygophyllum simplex</i>	.	17	.	.	.	.	.	.	40	10	.	80	67	70	47	94	100	.
<i>Sporobolus spicatus</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	6	.
<i>Abutilon pannosum</i>	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Sesuvium portulacastrum</i> subsp. <i>persoonii</i>	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Sporobolus robustus</i>	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Enneapogon desvauxii</i>	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.

Legend: ¹ Conditional characteristic species of a higher-rank syntaxon, as the species has a wide distribution outside Cabo Verde; ² Introduced to Cabo Verde; ³ Differential species between the alliances; ● Endemic to Cabo Verde.

Order: *Polycarpaeo lycioidis-Limonietalia braunii* J.C. Costa, Bioret, I. Gomes et C. Neto ord. nov. hoc loco

Holotypus: *Polycarpaeo lycioidis-Limonion braunii* J.C. Costa, Bioret, Monteiro-Henriques, I. Gomes et C. Neto 2026 (this article)

Diagnostic species (same as class): *Aizoon canariensis* (cond. char.), *Frankenia caboverdeana* (char.), *Frankenia pseudoericifolia* (char.), *Heliotropium ramosissimum* (cond. char.).

Description: Vegetation of sea cliffs in the Cabo Verde Islands, permanently exposed to saline sea winds and severe edaphic drought, occurring within infratropical to thermotropical, arid to hyperarid bioclimates.

1. Alliance: *Polycarpaeo lycioidis-Limonion braunii* J.C. Costa, Bioret, Monteiro-Henriques, I. Gomes et C. Neto all. nov. hoc loco

Holotypus: *Campylantho spathulati-Limonietum braunii* J.C. Costa, Bioret, I. Gomes et C. Neto 2026 (this article)

Diagnostic species: *Limonium braunii* (char.), *Lotus purpureus* (diff. all.), *Nanorrhinum elegans* (diff. all.), *Paronychia illecebroides* (char.), *Patellifolia procumbens* (diff. all.), *Polycarpha gayi* var. *lycioides* (char.).

Description: Permanent communities on basaltic sea cliffs, occupying colluvial deposits from cliff collapses,

dejection cones, and coastal platforms; permanently exposed to salt-laden sea winds and intense edaphic drought; occurring within an infratropical to thermotropical arid (rarely hyperarid) bioclimate. These communities are found on the islands of Brava, Fogo, Santiago, Santo Antão, and São Nicolau.

1.1 Frankenio caboverdeanae-Limonietum jovibarbae Bioret, J.C. Costa et C. Neto ass. nov. hoc loco

Holotypus: relevé 101 (Suppl. materials 2, 3), between Estância Brás and Ribeira Funda (São Nicolau Island), at 16°40'17.56"N, 24°19'51.45"W; plot area: 10 m²; total projected cover: 60%; altitude: 130 m a.s.l.; aspect: N; vascular plant composition: *Limonium jovibarba* 3, *Frankenia caboverdeana* 2, *Diplotaxis gracilis* +, *Launaea picridioides* +, *Paronychia illecebroides* +.

Diagnostic species: *Diplotaxis gracilis* (diff.), *Frankenia caboverdeana* (dom.), *Launaea picridioides* (diff.), *Limonium jovibarba* (diff., dom.), *Nanorrhinum elegans* (diff.), *Paronychia illecebroides* (const.).

Description: A chamaephytic and chasmophytic association on basaltic walls exposed to salt-laden sea winds. It occurs on the western faces of the northern cliffs of São Nicolau Island, within a thermotropical arid bioclimate. The hosting rock walls are very high, creating humid microconditions with numerous springs emerging from

Table 3. Overview of Cabo Verdean coastal cliff vegetation.

<i>Polycarpaeo lycioidis-Limonietea braunii</i>
<i>Polycarpaeo lycioidis-Limonietalia braunii</i>
1. <i>Polycarpaeo lycioidis-Limonion braunii</i>
1.1 <i>Frankenia caboverdeanae-Limonietum jovibarbae</i>
1.2 <i>Gomphrenetum vermicularis</i>
1.3 Community of <i>Gomphrena vermicularis</i> and <i>Limonium braunii</i>
1.4. Community of <i>Frankenia caboverdeana</i> and <i>Limonium braunii</i>
1.5 <i>Polycarpaeo lycioidis-Limonietum braunii</i>
1.6 <i>Zygophyllo waterlotii-Limonietum braunii</i>
1.7 <i>Campylantho spathulati-Limonietum braunii</i>
1.8 <i>Frankenia caboverdeanae-Polycarpaeetum lycioidis</i>
1.9 <i>Dauco humilis-Polycarpaeetum lycioidis</i>
1.10 <i>Frankenia pseudoericifoliae-Zygophylletum waterlotii</i>
1.11 <i>Nanorrhino elegantis-Paronychietum illecebroidis</i>
1.12 <i>Patellifolia procumbentis-Paronychietum illecebroidis</i>
2. <i>Limonion brunneri</i>
2.1 Community of <i>Limonium brunneri</i> and <i>Frankenia caboverdeana</i>
2.2 <i>Suaedo caboverdeanae-Limonietum brunneri</i>
2.3 <i>Loto bollei-Suaedetum caboverdeanae</i>
2.4 <i>Zygophyllo simplicis-Frankenietum pseudoericifoliae</i>
2.5 Community of <i>Lotus bollei</i> and <i>Frankenia caboverdeana</i>

cracks and structural discontinuities. This water originates from infiltration through volcanic soils at higher elevations, fed by rainfall and fog interception. Additionally, shading of the rock walls contributes to maintaining a humid environment (Figure 2a).

1.2 *Gomphrenetum vermicularis* Rivas-Martínez, Lousã, J.C. Costa et M.C. Duarte 2017 nom. mut. nov. hoc loco

(≡) *Blutaparonetum vermicularis* Rivas-Martínez, Lousã, J.C. Costa et M.C. Duarte 2017 (Rivas-Martínez et al. 2017, p. 63).

Original diagnosis: Rivas-Martínez et al. (2017).

Taxonomic sources: Plants of the World Online (POWO 2025), Ortuño Limarino and Borsch (2020).

Diagnostic species: *Aizoon canariense* (diff., dom.), *Cressa salina* (diff.), *Frankenia pseudoericifolia* (diff., dom.), *Gomphrena vermicularis* (= *Blutaparon vermiculare*; diff., dom.), *Gymnocarpus sclerocephalus* (diff.), *Paronychia illecebroides* (diff.), *Zygophyllum simplex* (diff.).

Description: On the island of Santiago, a permanent community occurs on coastal platforms of sandy-loamy sediments of coral origin and on basaltic sea cliffs, exposed to strong salt-laden winds and occasionally inundated by seawater during major storms. It develops within a thermo-infratropical arid bioclimate. Because it occupies sea cliffs, we assign this association to *Polycarpaeo lycioidis-Limonietea braunii* rather than to *Arthrocnemetea franzi*. We reproduce the type relevé from Rivas-Martínez et al. (2017), taken on a sea cliff in Biscainhos, Santiago Island, with an area of 4 m²: *Gomphrena vermicularis* 4, *Paronychia illecebroides* +, *Launaea arborescens* subsp. *melanostigma* +.

1.3 Community of *Gomphrena vermicularis* and *Limonium braunii*

Diagnostic species: *Frankenia caboverdeana* (diff.), *Gomphrena vermicularis* (diff., dom.), *Ipomoea pes-caprae* (diff.), *Limonium braunii* (diff.), *Patellifolia procumbens* (diff.).

Description: This community occurs on sea cliffs that are episodically washed by seawater on Santo Antão Island, within a thermotropical arid bioclimate.

1.4. Community of *Frankenia caboverdeana* and *Limonium braunii*

Diagnostic species: *Aizoon canariense* (const.), *Cynanchum daltonii* (diff.), *Dactyloctenium aegyptium* (diff.), *Frankenia caboverdeana* (dom.), *Launaea gorgadensis* (diff.), *Launaea picridioides* (diff.), *Limonium braunii* (diff.), *Lotus purpureus* (diff.), *Paronychia illecebroides* (const.), *Patellifolia procumbens* (diff.), *Sonchus oleraceus* (diff.).

Description: This community occurs among basaltic pebbles on clayey colluvial soils, on gently sloping cliffs exposed to salt-laden winds. It is found on the northern façade of São Nicolau Island, within a thermotropical arid bioclimate (Figure 2b).

1.5 *Polycarpaeo lycioidis-Limonietum braunii* J.C. Costa, Bioret, I. Gomes, Capelo, Arsénio, A. Figueiredo et C. Neto ass. nov. hoc loco

Holotypus: relevé 21 (see Suppl. materials 2, 3), Fajãzinha, Mosteiros (Fogo Island), at 15°02'54.35"N, 24°21'23.83"W; plot area: 4 m²; total projected cover: 60%; altitude: 5 m a.s.l.; aspect: N; vascular plant composition: *Limonium braunii* 4, *Nanorrhinum elegans* +, *Polycarpaea gayi* var. *lycioides* +, *Tridax procumbens* +.

Diagnostic species: *Campanula bravensis* (diff.), *Frankenia pseudoericifolia* (diff.), *Limonium braunii* (diff., dom.), *Nanorrhinum elegans* (diff.), *Polycarpaea gayi* var. *lycioides* (diff.).

Description: This chasmophytic association occurs within an infra- to thermotropical arid bioclimate, on cliffs exposed to strong salt-laden sea winds and periodically sprayed by seawater on Fogo Island (Figure 2c).

1.6 *Zygophyllo waterlotii-Limonietum braunii* J.C. Costa, I. Gomes et C. Neto ass. nov. hoc loco

Holotypus: relevé 32 (see Suppl. materials 2, 3), Ponta Jalunga (Brava Island), at 14°53'31.02"N, 24°40'31.31"W; plot area: 4 m²; total projected cover: 35%; altitude: 18 m a.s.l.; aspect: N; vascular plant composition: *Limonium braunii* 3, *Frankenia pseudoericifolia* 2, *Zygophyllum waterlotii* 1, *Aizoon canariensis* +.

Diagnostic species: *Aizoon canariense* (const.), *Atriplex halimus* (diff.), *Frankenia pseudoericifolia* (dom.), *Launaea arborescens* subsp. *melanostigma* (diff.), *Limonium braunii* (diff., dom.), *Zygophyllum waterlotii* (diff., dom.).

Description: This community was observed on gently inclined rocky sea cliffs along the northern coast of Brava



Figure 2. Typical views of the vegetation communities of the Cabo Verde coastal cliffs: **(a)** *Frankenio caboverdeanae*-*Limonietum jovibarbae* (São Nicolau); **(b)** Community of *Frankenia caboverdeana* and *Limonium braunii* (São Nicolau); **(c)** *Polycarpaeo lycioidis*-*Limonietum braunii* (Fogo); **(d)** Community of *Limonium brunneri* and *Frankenia caboverdeana* (Santa Luzia); **(e)** *Suaedo caboverdeanae*-*Limonietum brunneri* (São Vicente); **(f)** *Loto bollei*-*Suaedetum caboverdeanae* (São Vicente). Photographs by Carlos Neto.

Island, strongly exposed to salt-laden winds. It occurs within an infratropical arid bioclimate.

1.7 *Campylantho spathulati-Limonietum braunii* J.C. Costa, Bioret, I. Gomes et C. Neto ass. nov. hoc loco

Holotypus: relevé 1 (see Suppl. materials 2, 3), Ribeira de Ponta do Sol (Santo Antão Island), at 17°11'38.92"N, 25°04'58.05"W; plot area: 20 m²; total projected cover: 30%; altitude: 50 m a.s.l.; aspect: NE; vascular plant composition: *Campylanthus spathulatus* 2, *Frankenia cabover-*

deana 2, *Limonium braunii* 2, *Diplotaxis gorgadensis* +, *Paronychia illecebroides* +.

Diagnostic species: *Asparagus squarrosus* (diff.), *Campylanthus glaber* subsp. *spathulatus* (diff., dom.), *Diplotaxis gorgadensis* (diff.), *Frankenia caboverdeana* (dom.), *Frankenia pseudoericifolia* (diff., dom.), *Helianthemum gorgoneum* (diff.), *Launaea intybacea* (diff.), *Limonium braunii* (dom.).

Description: This chasmophytic community occurs on sea cliffs exposed to saline sea winds and occasionally splashed by sea spray. It develops within an infra- to thermotropical arid bioclimate on Santo Antão Island.

1.8 *Frankenio caboverdeanae*-*Polycarpaeetum lycioidis* J.C. Costa, Bioret, I. Gomes et C. Neto ass. nov. hoc loco

Holotypus: relevé 121 (see Suppl. materials 2, 3), between Cruzinha da Garça and Fontainhas (Santo Antão Island), at 17°10'26.63"N, 25°08'57.25"W; plot area: 10 m²; total projected cover: 80%; altitude: 8 m a.s.l.; aspect: NE; vascular plant composition: *Polycarpaea gayi* var. *lycioides* 4, *Frankenia caboverdeana* 3, *Limonium braunii* 1, *Paronychia illecebroides* +.

Diagnostic species: *Aizoon canariense* (diff.), *Campylanthus glaber* subsp. *spatulatus* (diff.), *Diploaxis gorgadensis* (diff.), *Frankenia caboverdeana* (diff.), *Gomphrena vermicularis* (diff.), *Heliotropium ramosissimum* (diff.), *Launaea picridioides* (diff.), *Lavandula rotundifolia* (diff.), *Limonium braunii* (diff.), *Paronychia illecebroides* (diff.), *Polycarpaea gayi* var. *lycioides* (dom.).

Description: On Santo Antão Island, we observed a community on colluvial deposits from sea-cliff collapses and dejection cones with sea exposure, subjected to saline winds. It occurs within an infra- to thermotropical arid bioclimate.

1.9 *Dauco humilis*-*Polycarpaeetum lycioidis* J.C. Costa, Bioret, I. Gomes, Capelo, Arsénio, A. Figueiredo et C. Neto ass. nov. hoc loco

Holotypus: relevé 128 (see Suppl. materials 2, 3), Fajãzinha, Mosteiros (Fogo Island), at 15°02'53.99"N, 24°21'24.11"W; plot area: 20 m²; total projected cover: 40%; altitude: 10 m a.s.l.; aspect: NW; vascular plant composition: *Polycarpaea gayi* var. *lycioides* 3, *Asteriscus daltonii* subsp. *vogelii* 2, *Daucus humilis* 1, *Lotus purpureus* 1, *Nanorrhinum elegans* +, *Tridax procumbens* +.

Diagnostic species: *Aerva javanica* (diff.), *Asteriscus daltonii* subsp. *vogelii* (diff.), *Cenchrus ciliaris* (diff.), *Commicarpus helenae* (diff.), *Cucumis anguria* (diff.), *Dactyloctenium aegyptium* (diff.), *Daucus humilis* (diff.), *Forsskaolea procrisifolia* (diff.), *Ipomoea quamoclit* (diff.), *Launaea intybacea* (diff.), *Lotus purpureus* (diff.), *Nanorrhinum elegans* (diff.), *Nicotiana glauca* (diff.), *Polycarpaea gayi* var. *lycioides* (dom.), *Portulaca oleracea* (diff.), *Sida salviifolia* (diff.), *Sonchus oleraceus* (diff.), *Tridax procumbens* (diff.), *Zygophyllum simplex* (diff.).

Description: On colluvial deposits from sea-cliff collapses, exposed to saline winds, we observed a permanent community composed of several endemic chamaephytes and hemicryptophytes, enriched with nitrophilous species and including several taxa introduced to Cabo Verde (*Cucumis anguria*, *Dactyloctenium aegyptium*, *Ipomoea quamoclit*, *Nicotiana glauca*, *Sida salviifolia*, *Tridax procumbens*). It occurs within an infra- to thermotropical arid bioclimate on Fogo Island.

1.10 *Frankenia pseudoericifoliae*-*Zygophylletum waterlotii* J.C. Costa, I. Gomes et C. Neto ass. nov. hoc loco

Holotypus: relevé 142 (see Suppl. materials 2, 3), Ponta Jaluga (Brava Island), at 14°53'28.37"N, 24°40'32.67"W; plot

area: 20 m²; total projected cover: 50%; altitude: 22 m a.s.l.; aspect: NE; vascular plant composition: *Zygophyllum waterlotii* 3, *Frankenia pseudoericifolia* 2, *Nanorrhinum elegans* 1, *Aizoon canariense* +, *Campylanthus glaber* subsp. *glaber* +, *Cynodon dactylon* +, *Lotus purpureus* +.

Diagnostic species: *Aizoon canariense* (const.), *Atriplex halimus* (diff.), *Campylanthus glaber* subsp. *glaber* (diff.), *Corchorus depressus* (diff.), *Cynodon dactylon* (diff.), *Frankenia pseudoericifolia* (dom.), *Heliotropium pterocarpum* (diff.), *Launaea arborescens* subsp. *melanostigma* (diff.), *Lotus purpureus* (const.), *Nanorrhinum elegans* (dom.), *Zygophyllum waterlotii* (diff., dom.).

Description: We observed this community on the north-facing cliffs of Brava Island, on gravelly flat platforms (leptosols) exposed to salt-laden sea winds. It occurs within an infratropical arid bioclimate.

1.11 *Nanorrhino elegantis*-*Paronychietum illecebroidis* J.C. Costa, Bioret, I. Gomes, Capelo, M.C. Duarte, M. Romeiras et C. Neto ass. nov. hoc loco

Holotypus: relevé 89 (see Suppl. materials 2, 3), Ponta Salina (Fogo Island), at 15°01'10.79"N, 24°26'5.60"W; plot area: 5 m²; total projected cover: 80%; altitude: 5 m a.s.l.; aspect: NE; vascular plant composition: *Paronychia illecebroides* 4, *Dactyloctenium aegyptium* 3, *Nanorrhinum elegans* 3, *Lotus purpureus* 2.

Diagnostic species: *Commicarpus helenae* (diff.), *Dactyloctenium aegyptium* (const.), *Gymnocarpus sclerocephalus* (diff.), *Heliotropium ramosissimum* (diff.), *Lotus purpureus* (diff., dom.), *Nanorrhinum elegans* (diff., dom.), *Paronychia illecebroides* (dom.).

Description: This community occurs on basaltic flat or gently sloping areas near the sea, exposed to strong salt-laden winds, on the islands of Fogo and Santiago. It develops within an infratropical arid bioclimate.

1.12 *Patellifolio procumbentis*-*Paronychietum illecebroidis* Bioret, J.C. Costa et C. Neto ass. nov. hoc loco

Holotypus: relevé 110 (see Suppl. materials 2, 3), Belém (São Nicolau Island), at 16°38'39.87"N, 24°13'42.82"W; plot area: 10 m²; total projected cover: 25%; altitude: 2 m a.s.l.; aspect: NE; vascular plant composition: *Frankenia pseudoericifolia* 3, *Paronychia illecebroides* 1, *Dactyloctenium aegyptium* +, *Patellifolia procumbens* +, *Zygophyllum simplex* +.

Diagnostic species: *Aizoon canariense* (diff., dom.), *Frankenia caboverdeana* (diff., dom.), *Frankenia pseudoericifolia* (diff., dom.), *Lotus purpureus* (dom.), *Paronychia illecebroides* (diff., dom.), *Patellifolia procumbens* (diff.), *Zygophyllum simplex* (const.).

Description: This chamaephytic community occurs on the north coast of São Nicolau Island, in basaltic leptosols with stones shaped by the sea and exposed to salt-laden winds. It exhibits two facies: the typical one (relevés 107–111), and a facies with high cover values of *Frankenia caboverdeana* (relevés 112–116), the latter occurs in stony

sites with a thin layer of sand. The community is found within a thermotropical arid to hyperarid bioclimate.

2. Alliance: *Limonium brunneri* J.C. Costa, Bioret, Monteiro-Henriques, I. Gomes et C. Neto all. nov. hoc loco

Holotypus: *Suaeda caboverdeanae-Limonietum brunneri* J.C. Costa, Bioret, I. Gomes et C. Neto 2026 (this article)

Diagnostic species: *Limonium brunneri* (char.), *Lotus bollei* (char.), *Suaeda caboverdeana* (diff. all.), *Tetraena vicentina* (diff. all.).

Description: Permanent communities on sandstone formations consisting of coralline sands with limestone cement, occurring on cliffs and coastal platforms within an infratropical to thermotropical hyperarid to ultrahyperarid bioclimate. They are found on the islands of São Vicente and Santa Luzia.

2.1 Community of *Limonium brunneri* and *Frankenia caboverdeana*

Diagnostic species: *Frankenia caboverdeana* (diff., dom.), *Frankenia pseudoericifolia* (const.), *Limonium brunneri* (diff., dom.), *Lotus bollei* (diff.), *Zygophyllum simplex* (const.).

Description: This community occurs on basaltic sea cliffs along the north-facing slopes of Santa Luzia Island, exposed to salt-laden winds. It develops within a thermotropical hyperarid bioclimate (Figure 2d).

2.2 *Suaeda caboverdeanae-Limonietum brunneri* J.C. Costa, Bioret, I. Gomes et C. Neto ass. nov. hoc loco

Holotypus: relevé 46 (see Suppl. materials 2, 3), west of Vila Miséria (São Vicente Island), at 16°49'23.25"N, 24°51'46.26"W; plot area: 10 m²; total projected cover: 40%; altitude: 30 m a.s.l.; aspect: N; vascular plant composition: *Limonium brunneri* 3, *Frankenia pseudoericifolia* 1, *Suaeda caboverdeana* 1, *Lotus bollei* +, *Zygophyllum simplex* +.

Diagnostic species: *Frankenia pseudoericifolia* (dom.), *Limonium brunneri* (diff., dom.), *Lotus bollei* (const.), *Polycarpaea caboverdeana* (diff.), *Suaeda caboverdeana* (diff.), *Zygophyllum simplex* (const.).

Description: A chasmophytic association on recent lava coastal platforms covered by a very thin layer of coralline sand (mainly derived from erosion of nearby calcareous sandstones), exposed to sea spray. It occurs on the eastern coast of São Vicente Island, at the base of the Viana volcano, within a thermotropical ultrahyperarid bioclimate (Figure 2e).

2.3 *Loto bollei-Suaedetum caboverdeanae* J.C. Costa, Bioret, I. Gomes et C. Neto ass. nov. hoc loco

Holotypus: relevé 66 (see Suppl. materials 2, 3), Praia Grande (São Vicente Island) 16°49'45.93"N, 24°52'34.96"W; plot area: 50 m²; total projected cover: 90%; altitude:

10 m a.s.l.; aspect: NE; vascular plant composition: *Suaeda caboverdeana* 5, *Frankenia pseudoericifolia* +, *Lotus bollei* +, *Zygophyllum simplex* +.

Diagnostic species: *Frankenia pseudoericifolia* (const.), *Heliotropium pterocarpum* (diff.), *Lotus bollei* (diff.), *Suaeda caboverdeana* (diff., dom.), *Tetraena vicentina* (diff., dom.).

Description: On recent lava flows near the sea on the north coast of São Vicente Island, and on rocky sites splashed by sea spray on Santa Luzia Island, we observed a community dominated by nanophanerophytes (*Suaeda caboverdeana* and *Tetraena vicentina*). It occurs within an infra- to thermotropical hyperarid to ultrahyperarid bioclimate (Figure 2f).

2.4 *Zygophyllo simplicis-Frankenietum pseudoericifoliae* J.C. Costa, Bioret, I. Gomes et C. Neto ass. nov. hoc loco

Holotypus: relevé 153 (see Suppl. materials 2, 3), Santa Luzia Island 16°47'49.95"N, 24°45'39.93"W; plot area: 10 m²; total projected cover: 30%; altitude: 5 m a.s.l.; aspect: N; vascular plant composition: *Frankenia pseudoericifolia* 3, *Lotus bollei* 1, *Zygophyllum simplex* 1.

Diagnostic species: *Aristida funiculata* (diff.), *Frankenia pseudoericifolia* (dom.), *Heliotropium ramosissimum* (diff.), *Lotus bollei* (diff., dom.), *Tetraena vicentina* (diff.), *Zygophyllum simplex* (dom.).

Description: On the north and west coasts of Santa Luzia Island, on skeletal leptosols of pebbles with a thin layer of coralline sand near the sea and exposed to saline winds, we observed a sparse community dominated by chamaephytes and therophytes (< 15 cm tall). It occurs within an infra- to thermotropical hyperarid bioclimate.

2.5 Community of *Lotus bollei* and *Frankenia caboverdeana*

Diagnostic species: *Fagonia latifolia* (diff.), *Frankenia caboverdeana* (diff., dom.), *Frankenia pseudoericifolia* (diff.), *Lotus bollei* (diff.), *Zygophyllum simplex* (const.).

Description: On the northern façade of Santa Luzia Island, among stones and exposed to sea spray, we observed a community of small chamaephytes and therophytes, within an infratropical hyperarid bioclimate.

Limitations

We acknowledge that the syntaxonomy published in Rivas-Martínez et al. (2017) was not subjected to numerical validation, as it was derived from manual tabulations. While we regard such validation as necessary, it lies beyond the scope of the present work. Nevertheless, the synoptic side-by-side tabulations in Suppl. material 13 show several species centred in each class and numerous characteristic species across the different syntaxa, suggesting that future numerical analyses may have only a modest impact on the current syntaxonomy.

Conclusions

A five-step classification approach was applied to the coastal cliff vegetation of Cabo Verde, spanning from the association to the class levels. A syntaxonomic synthesis was achieved, with 13 associations, two alliances, one order, and one class. These syntaxa reinforce Cabo Verde's affinity with the *Warm deserts and semi-deserts* subbiome (Loidi et al. 2022) and the biogeographical placement of Cabo Verde within the *Tropical Sahara* region (*Paleotropical Kingdom*) as per Rivas-Martínez et al. (2017), highlighting its distinctness from communities in the *Mediterranean* and *Eurosiberian* regions (Holarctic Kingdom; but see Fernández-Palacios et al. 2024).

TDV-optimization, including its innovative application to the synoptic table, proved to be a useful tool for vegetation classification. The method was effective despite relying solely on presence-absence information, unveiling relevant co-occurrence/co-absence patterns with clear biogeographic and ecological interpretation. The DiffVal index, especially its partial values (pDiffVals), which inherently down-weight a species' presence according to its distribution across other groups/syntaxa, successfully distinguished characteristic species at higher syntaxonomic ranks.

Future studies are needed to expand knowledge of Cabo Verdean and other African vegetation and to numerically validate its syntaxonomy, thereby paving the way for effective, evidence-based nature conservation policies.

Data availability

The supplementary materials provide the full data set used in this article (species composition and header data of the relevés), as well as the complete, annotated R code to ensure reproducibility.

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Author contributions

JCC, CN, FB and IG planned the research; JCC, CN, FB, IG, JC, MCD, and PA conducted the field sampling; JCC and CN prepared the data set; TMH performed the numerical analyses; TMH drafted the manuscript with contributions from CN and JCC, and all authors critically revised the manuscript.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI. Regarding the use of AI in the preparation of this manuscript, the authors declare the following: GPT, Microsoft Copilot.

Used for: Language, style and writing. Large language models were employed solely for the linguistic revision of the manuscript (grammar and clarity). They were not used to generate scientific content or at any stage of the data analysis.

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Supplementary material

Supplementary material 1

Terminology adopted in this study (*.pdf)

Link: <https://doi.org/10.3897/VCS.173501.suppl1>

Supplementary material 2

Full data set (484 relevés): species cover-abundance (*.csv in zip-archive)

Link: <https://doi.org/10.3897/VCS.173501.suppl2>

Supplementary material 3

Full data set (484 relevés): header information (*.csv in zip-archive)

Link: <https://doi.org/10.3897/VCS.173501.suppl3>

Supplementary material 4

Shapefile with Cabo Verde's administrative areas (Database of Global Administrative Areas – GADM) (*.zip)

Link: <https://doi.org/10.3897/VCS.173501.suppl4>

Supplementary material 5

Auxiliary R functions for reproducibility (*.R in zip-archive)

Link: <https://doi.org/10.3897/VCS.173501.suppl5>

Supplementary material 6

Parameterization of TDV-optimization in Steps 2 and 4 (*.pdf)

Link: <https://doi.org/10.3897/VCS.173501.suppl6>

Supplementary material 7

Step 1: Dichotomous key for the physiognomic groups and associated formal logic rules (*.pdf)

Link: <https://doi.org/10.3897/VCS.173501.suppl7>

Supplementary material 8

Step 2: Annotated R code with the graphical output of TDV-optimization for each physiognomic group and justification of selected solutions (*.pdf)

Link: <https://doi.org/10.3897/VCS.173501.suppl8>

Supplementary material 9

Step 3: Annotated R code for computing IAP and generating the first synoptic table of the cliff data set (*.pdf)

Link: <https://doi.org/10.3897/VCS.173501.suppl9>

Supplementary material 10

Step 3: Synoptic table of the cliff data set (*.xlsx in zip-archive)

Link: <https://doi.org/10.3897/VCS.173501.suppl10>

Supplementary material 11

Step 4: Annotated R code with the graphical output of TDV-optimization applied to the synoptic table and justification of selected solution (*.pdf)

Link: <https://doi.org/10.3897/VCS.173501.suppl11>

Supplementary material 12

Step 5: Annotated R code for generating the synoptic side-by-side tabulations of the full data set (*.pdf)

Link: <https://doi.org/10.3897/VCS.173501.suppl12>

Supplementary material 13

Step 5: Synoptic side-by-side tabulations of the full data set (*.xlsx in zip-archive)

Link: <https://doi.org/10.3897/VCS.173501.suppl13>

Supplementary material 14

List of sampled taxa and photographs of flora and vegetation (*.pdf)

Link: <https://doi.org/10.3897/VCS.173501.suppl14>