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# Ecology and spatial patterns of large-scale vegetation units within the central Namib Desert

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ABSTRACT

This article offers a review of published knowledge and a new state-of-the-art analysis regarding the floristic composition, the functional composition and the plant communities found in the central Namib Desert. At the same time, this paper contributes to the understanding of the relationship between the plant species composition of the central Namib Desert and the prevailing environmental gradients, with an emphasis on diversity and ecology in space and time. This article builds on three thematic foci. The first focus (1) lies on the present knowledge of the composition and the characteristics of the flora. A comprehensive floristic database has been compiled based on all available sources. A second focus (2) lies on the characterization and spatial distribution of the vegetation units. Therefore, we created a new vegetation classification based on a unique vegetation-plot database (http://www.givd.info/ID/AF-00-007) and additional data summing up to 2000 relevés, resulting in 21 large-scale vegetation classes. Using a supervised classification approach based on the vegetation classification, remote sensing and environmental data, we were able to produce a new vegetation map of the Central Namib. This was updated using expert knowledge, field visits and through manual preprocessing. With the third focus (3) we explore the spatial patterns of the previous foci and discuss their relation to environmental parameters and gradients.



## 1. Introduction and study area

Vegetation is generally sparse in the Namib Desert, which forms a narrow strip along the west coast of southern Africa (Jürgens, 1991; Werger, 1978). However, in the Namib adaptation of plants to aridity commenced long before the formation of modern ocean currents (Ward et al., 1983). This long history of aridity led to the evolution of several very specific pools of endemic plant species, which are spatially distributed according to their environmental needs. However, until today, a spatially explicit approach to the different vegetation units of the Namib that would allow for a more in-depth analysis of this very old desert is still missing.

The present lack of a vegetation map is accompanied by the lack of a systematically sampled body of adequate data and a robust classification based on objective methods. Therefore, no environmental understanding of vegetation units could evolve, and hence no conceptual framework for conservation purposes and for more specific ecological research could be developed. The here presented study aims at filling these important gaps. We studied the combination of plant species within vegetation units in the study area and its spatial subunits. In this paper, special attention is given to the correlation between environmental gradients in space (and to a lesser extent in time) and the related pools of plant species defined by their structural and physiological adaptations. This format also allows for a review of published studies with regard to earlier vegetation mapping efforts.

The study area covers the Central Namib between and including the Ugab and Kuiseb catchments as its latitudinal boundaries, while it is bounded by the Atlantic Ocean in the west and the escarpment in the east. The Brandberg forms a very specific azonal element and is not part of this study.

Earlier definitions of the Central Namib follow a similar concept (e.g. Giess, 1971). A minor difference is that we do not use the Ugab or Huab rivers as the northern boundary but include those parts of the Ugab catchment located north of the study area.

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The same approach is applied to the Kuiseb, in spite of the fact that to the South of the Kuiseb, no really productive catchment can be identified within the dune field. We decided to take the southern boundary of the Erongo Region as the southern limit, with a line running from just south of Sandwich Harbour to the Koichab Pan.

Strictly speaking, lichens are not regarded as plants and lichen fields are not regarded as vegetation units. On the other hand, vast areas of the coastal Namib are nearly devoid of higher plants but show an extraordinary cover and a very high species richness of lichens (Loris and Schieferstein, 1992; Schieferstein, 1989; Walter, 1936). Because of their exceptional importance, the lichen fields are therefore included in this article.

## 2. Material and methods

This study is based on comprehensive databases of the flora, the vegetation and environmental parameters of the Central Namib. Lichen fields are also included because of their importance within the fog belt of the coastal Namib.

### 2.1. Floristic database

All available knowledge regarding the observation of plant taxa within the study area has been compiled and processed with a consistent nomenclature following the Windhoek Herbarium using BiotaBase (Muche et al., 2012) and BIOTACollections (Muche and Jürgens, 2011) as database software. This floristic database encompasses (a) all herbarium records of the study area recorded at the herbaria of Windhoek (WIND), Pretoria (PRE) and Hamburg (HBG), (b) published point occurrence data from relevant projects, e.g. the Namibian Tree Atlas Project (Curtis and Mannheimer, 2005) and numerous taxonomic and floristic articles, as well as (c) own field data. The resulting floristic database contains more than 65,000 records of plant point data from the study area.

The compilation of all species records from the herbaria (WIND, PRE, HBG), the literature and the vegetation-plot database (see below) first resulted in a total of 1085 species. Each of these species was checked for (a) correct taxonomic status (excluding 59 names), (b) superfluous names following the hierarchy of species, subspecies and varieties (excluding another 68 names) and (c) a robust confirmation of occurrence in the study area (excluding 107 names). It was not possible to verify all specimens in the respective herbaria so that the entire species pool could not be identified to our complete satisfaction. Another 44 species are therefore still regarded as uncertain since it was impossible to see all specimens in the herbaria because of insufficient evidence (e.g. one single record in a list within one publication only or because no reference to specimen has been made).

### 2.2. Vegetation-plot database

A vegetation-plot database using the same consistent taxonomic nomenclature has been generated using BiotaBase (registered at www.GIVD.info under ID: AF-00-007; Dengler et al., 2011). Data compiled since the early 1990s formed the basis for classifying species assemblage data into major vegetation types. For the classification, 2000 relevé data sets (B. Hachfeld: 949, N. Juergens: 897, B. Strohbach: 154), using a standard size of 1000 $m^2$, including geographic coordinates, habitat information and all observed species occurrences with percentage cover estimates and (partly) abundance data were used. We evenly sampled the spatial diversity of the Central Namib by taking records at regular intervals and in all distinguishable vegetation and habitat types. The geographical spread of samples was homogeneous with two exceptions: First, the dune field south of the Kuiseb River could not be sampled but in a few places. Second, the density of relevés is slightly lower at the eastern margin of the study area.

It is worth mentioning that both plant databases have been extended over many years, thereby including different seasons as well as dry and wet years. Many relevés do not show the entire local species pool at the time of documentation. This must be taken into consideration when interpreting occurrences of therophytes, geophytes and hemicryptophytes. Conditions of strongly grazed plant individuals in particular during dry seasons may have resulted in some inconsistencies in plant identifications, e.g. *Stipagrostis hirtigluma* ssp. *hirtigluma* versus *Stipagrostis uniplumis* var. *intermedia*.

### 2.3. Lichen database

As strong relationships exist between the form (morphology) of crust organisms and their ecological function (Rogers, 1977), the concept of morphological groups was used to locate 874 homogenous reference sites (Eldridge and Rosentreter, 1999). At these sites, spectral properties of lichens were collected *in situ* using an ASD FieldSpec FR spectroradiometer covering the 350–2500 nm spectral range at a spectral resolution of 1 nm. Using this reference data set, a hierarchical classification scheme for mapping the distribution of lichen fields in the central Namib Desert based on remote sensing data was created (Schultz, 2006).

### 2.4. Environmental parameters

Environmental gradients were integrated into the vegetation mapping strategy. The data set consists of the following data: (1) climatic data were extracted from the 30 arc-seconds resolution WorldClim data set (Hijmans et al., 2005), which represents globally averaged climate data for the period 1950–2000; (2) a digital elevation model (DEM) was genereated on basis of the 1 arc-second resolution ASTER-GDEM version 1.0 elevation data set (METI/NASA, 2009). Based on the DEM covering the whole Central Namib with a 30 m grid resolution, several ecologically relevant topographical parameters were derived, among others (3) inclination in degree, (4) exposition, (5) diurnal anisotropic heating, which represents a continuous measure of exposition dependent energy (Hengl and Reuter, 2011), and (6) the vector ruggedness measure (VRM, Sappington et al., 2007), which measures landscape roughness. A digital geological map (7) at a scale of 1:250,000 was provided by the Geological Survey of the Ministry of Mines and Energy (MME) of Namibia. Furthermore, median, minimum, maximum and range of satellite derived measures of biomass were calculated from a monthly data set of 2010 global MOD13Q1 EVI (EVI = Enhanced Vegetation Index) images with a ground resolution of 250 m (NASA LP-DAAC, 2010). Furthermore, two fully pre-processed Landsat 7 ETM + scenes (Path/Row/Date: 180/75/2003-04-22; 179/76/2003-05-01) were utilized for the mapping and supervised classification of the distribution of the lichen-dominated biological soil crust communities. Based on Landsat 7 ETM + acquisitions, satellite mosaic data (RGB channels = 7–4–2) were used for the vegetation mapping task for the entire study area (MDA, 2004). See Table 1 for a list of all assembled data sets.

### 2.5. Vegetation classification

For vegetation classification, an initial set of 1574 relevés with 440 species and their cover values were extracted from AF-00-007 and imported into the phytosociological classification software JUICE 7.0 (Tichý, 2002). Within JUICE, a numerical pre-classification was carried out using hierarchical clustering of relevés by square