The vegetation of the Cusseque core site is very different from the other three core sites of the TFO study area. It forms part of the larger Miombo region extending over large parts of southern and central Africa. Compared to the middle and lower reaches of the Okavango Basin, the humid climate of the Angolan highlands supports a species-rich and dense vegetation. In this undulating landscape the topographic position is paramount in determining spatial patterns of the vegetation. While the elevated parts comprising plateaus and ridges are covered by Miombo forests and woodlands, the mid-slopes leading down to the valleys feature an open landscape dominated by geoxylid dwarf shrubs and grasses. At the valley bottom, where drainage lines converge, permanently wet peatlands have established.

Most woody species are brev-deciduous losing their leaves at the end of the rainy season, however, some evergreen species like Cryptosepalum exfoliatum ssp. pseudotaxus play a major role in the vegetation, too. A few weeks before the onset of the first rains, plants are resprouting and the fresh leaves flourish in colours ranging from deep red, orange to fresh green. In the following the vegetation units are described in reference to the mapping units of the land cover map (Schneibel et al. 2013).

Closed Miombo forests cover large areas of the core site and reach heights of up to 15 m. They are dominated by tree species of the Fabaceae family, mostly of the Caesalpinioideae subfamily. Three subunits can be distinguished:

a) Very dense woodlands with stands dominated by evergreen Cryptosepalum exfoliatum ssp. pseudotaxus trees covering large areas of the western section of the core site. Here, shifting cultivation is currently absent and hence woodlands are mostly unfragmented. As these woodlands are hardly affected by fire a thick moss layer covering the ground can establish. This subunit is further characterized by a high abundance of lianas such as Landolphia camptoloba forming a hardly penetrable thicket. Within this vegetation subunit stems do not reach large diameters resulting in a low standing woody biomass. It is not clear yet if this homogeneous vegetation structure and relatively low stand height (mostly < 12 m) resulted from cohort regeneration after major disturbance events or is due to low fertility of the predominantly ferralitic soils (Fig. 1).

b) The woodlands in the central parts of the core site exhibit mixed stands of Brachystegia spiciformis, Brachystegia bakeriana and Cryptosepalum exfoliatum ssp. pseudotaxus including various Combretum species. The canopy is less closed and trees are mostly semi-

### Table 1: Vegetation of the Cusseque core site in numbers: sampling size and biodiversity indices.

<table>
<thead>
<tr>
<th>Ecoregion</th>
<th>Sampling period</th>
<th>1,000 m² plots sampled</th>
<th>100 m² plots sampled</th>
<th>Vegetation unit (MODIS classification)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angolan Miombo woodlands</td>
<td>2011 - 2013</td>
<td>15</td>
<td>90</td>
<td>Miombo forests dominated by deciduous tree species</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Miombo forest dominated by Cryptosepalum maraviense</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>grasslands, Parinari capensis grassland (on humid</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>soils), wet grasslands and peatlands</td>
</tr>
</tbody>
</table>

**Dominant families (cover)**
- Fabaceae (s.l.), Ixonanthaceae, Chrysobalanaceae, Apocynaceae

**Dominant families (richness)**
- Fabaceae (s.l.), Combretaceae, Euphorbiaceae, Poaceae

**Species richness on 1,000 m²**
- 49 (34 - 61)

**Species richness on 100 m²**
- 36 (13 - 60)

**Evenness (J') on 1,000 m²**
- 0.512 (0.389 - 0.710)

**Evenness (J') on 100 m²**
- 0.607 (0.263 - 0.843)

**Simpson index (D_J) on 1,000 m²**
- 0.735 (0.621 - 0.906)

**Simpson index (D_J) on 100 m²**
- 0.816 (0.347 - 0.939)

Fig. 1: Closed Miombo forests dominated by Cryptosepalum exfoliatum ssp. pseudotaxus with thick moss layer on the ground and stems covered by lichens (photo: R. Revermann).
deciduous leading to a significant shrubby understorey formed by \textit{Copaifera baumiana}, \textit{Phyllocosmus lemaireanus} and \textit{Paropsis brazzaeana} as well as a herb layer composed of several tall-growing grasses, e.g. of the genera \textit{Hyparrhenia} and \textit{Stipagrostis}.

c) The woodlands east of the Cusseque River are covered by another subunit of the Miombo woodlands where the dominant tree species are \textit{Julbernardia paniculata} and \textit{Brachystegia spiciformis}. The canopy reaches heights of 15 m and hence is considerably higher than in the aforementioned vegetation subunits. Further important tree species occurring throughout the woodlands are \textit{Erythrophleum africanum}, \textit{Burkea africana} and \textit{Pterocarpus angolensis}.

\textbf{Miombo woodland (open/disturbed):} This vegetation unit comprises the rather open parts of the wooded areas that have been impacted by human activities and are exposed to a higher fire frequency. The dominant species do not belong to the Fabaceae and include for example \textit{Monotes caloneurus} of the family Dipteraceae and \textit{Uapaca kirkiana} and \textit{U. nitida} of the family Euphorbiaceae. Fallows and early regeneration stages are characterized by trees resprouting from root stocks and stem bases left standing during the time of cultivation. However, in some cases woodland regeneration is inhibited by extensive thickets of the fern \textit{Pteridium aquilinum}.

\textbf{Shrubland ecotone:} Where environmental conditions slowly start being unfavourable for tall woodlands we find an ecotone comprising elements of both, the open dwarf shrub grasslands and the woodlands. In some areas, these ecotones stretch over several hundred metres reaching from the topslopes down to the mid slopes. Tree cover is low and individual trees are separated by large open areas. The most characteristic tree is \textit{Monotes glaber}; other typical trees include \textit{Terminalia brachystemma}, \textit{Protea gaguiedii}, \textit{Bobgunnia madagascariensis}, and \textit{Combretum apiculatum} (Fig. 2).

\textbf{Cryptosepalum maraviente grasslands:} This vegetation unit is very characteristic of the central plateau and referred to as “Anhares de ongote” or “Cassamba” in the local languages (Barbosa 1970). The dominant life form is the so called “geoxylic suffrutex”, referring to dwarf shrubs with enormous woody underground biomass and even the buds resting underneath the surface. Many species occurring here are very closely related to tree species of the Miombo woodlands and it is often still uncertain if they indeed correspond to different species or rather to ecotypes. \textit{Cryptosepalum maraviente} and \textit{Cryptosepalum exfoliatum} ssp. \textit{suffraticans} cover a large fraction of the ground of this vegetation unit. Further dwarf shrubs common in patches include \textit{Ochna manikensis} and \textit{Syzygium guineense} ssp. \textit{huillense}. White (1976) offers different hypotheses for the occurrence of this growth form, among others unfavourable edaphic conditions, frost, and fire. During the vegetation survey it was shown that these dwarf shrubs generally occur on mid- and footslopes with either shallow, ferralitic or sandy soils, both exhibiting seasonally changing soil-water conditions and some hydro-morphic features. Night frosts do occur in the dry months of the year, but only on the slopes and in the valleys, hardly on the plateau (Revermann & Finckh 2013; Fig. 3 and 4).

\textbf{Parinari capensis grasslands (on sandy soils):} This vegetation unit is spatially clearly delimitated and is found in the core site on the plains along the eastern side of the Cusseque River. It typically occurs on sandy deposits along larger river systems such as the Longa River. The main aspect in the late rainy season is shaped by several tall grass species such as \textit{Monocymbium ceresiiforme}, \textit{Stipa- grostis} spp., and \textit{Hyparrhenia} ssp. amongst others. However, geoxylic suffrutices such as \textit{Parinari capensis}, \textit{Ochna arenaria}, \textit{Ochna cinnabarina}, \textit{Syzygium guineense} ssp. \textit{huillense}, and

Fig. 2: Shrubland ecotone (photo: R. Revermann).
Fig. 3: *Cryptosepalum maraviense* grassland (Anhares de Ongote / Cassamba) in October just before the onset of the first rains showing colourful resprouts of *Cryptosepalum maraviense*; grasses are not present yet (photo: R. Revermann).

Fig. 4: *Cryptosepalum maraviense* grassland on ferralitic soils along the slopes at the end of the rainy season in May. At this time, grasses dominate the aspect of this vegetation unit. Peat bogs are located at the valley bottom in the centre of the photo (photo: R. Revermann).

Fig. 5: *Parinari capensis* grassland (on sandy soils) at the beginning of the rainy season (photo: R. Revermann).

Fig. 6: *Parinari capensis* grassland on sandy soils at the start of the dry season; tall Poaceae and solitary *Burkea africana* trees dominate the appearance at this time of the year (photo: R. Revermann).
Protea welwitschii form an integral part of community composition and dominate the vegetation at the end of the dry season and the beginning of the rainy season, although with a much smaller underground biomass than in the Cryptosepalum maraviense grasslands (Fig. 5 and 6).

Wet grasslands: Grasslands on wet mineral soils occur adjacent to the peatlands or in the heads of the valleys, dominated by tufted, perennial grasses and some sedges.

Peatlands: The valley bottoms covered by thick peat layers are characterized by typical wetland vegetation dominated by sedges of the genera Kyllinga, Cyperus, and Eleocharis. Furthermore, several Drosera species can be found as well as the dwarf shrub Protea paludosa and many orchids (Fig. 7 and 8).

Reed beds and open water: Species of the stream communities include the distinctive Limnophyton angolense whereas high reeds of Phragmites mauritianus are present in deeper water (Fig. 9).
Fig. 12: Species richness on the Cusseque core site according to vegetation units and on two different spatial scales. Values are shown for vegetation plots sized 100 m² and 1,000 m², indicated by the same colour. Note that sample sizes may be different for the two plot sizes; wetlands were only sampled on 100 m² plots.

The range of habitats and vegetation communities appearing within the Cusseque core site is striking. The vascular plant diversity is highest among the four studied core sites with regards to alpha diversity if species richness is considered. In the Miombo woodlands it reaches values of 60 species per 100 m² with a median of 36. However, some vegetation units are dominated by tree species reaching high cover values resulting in a rather low evenness if compared to the woodlands on Kalahari sands (Fig. 12).

For details on the applied methods and study design please refer to the Electronic Appendix.

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References


Responsible authors: R. Revermann, F. Maiato, A. Gomes, F. Lages, M. Finckh