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Plant functional composition and ecosystem properties: the case of peatlands in South Africa

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Abstract The assumption that ecosystems with similar emergent properties consist of similar functional groupings of plant species is tested by comparing three peatlands from different bioregions across South Africa. They are Mfabeni Swamp in the subtropical coastal region, Wakkerstroom on the inland plateau, and Goukou wetland in the Winter Rainfall region of the Western Cape. In each of the three peatlands, about 400 small vegetation plots have been made from which the abundance of each species per wetland can be assessed. The most dominant species in these plots have been investigated for 17 traits. The functional composition of the vegetation types has been compared across the three peatlands and Functional Diversity has been calculated, taking the dominance of each species into account. One peatland differed greatly from the other two, since the dominant species was of a functional type ("Palmiet/woody sedge") that was very divergent from any other peatland species found in the study. This functional type can be considered an ecosystem engineer and the effects that this functional type has on the ecosystem results in the occurrence of many other functional types that do not occur in the other peatlands. When we consider emergent traits of an ecosystem as a function of all the plant functional traits that occur in that ecosystem, then peatlands can be regarded as a heterogeneous group of ecosystems. Even if emergent properties such as peat formation are similar between ecosystems, those ecosystems may still consist of very different functional groups. Ecosystem engineers have an impact on the final functional composition of an ecosystem and the degree in which ecosystem engineering plays a role in peatlands differs between different peatlands.

Keywords Community assembly · Functional diversity · Dendrograms · Wetlands · Dominance · Ecosystem engineers

Nomenclature Germishuizen & Meyer (2003)

Abbreviations

PFT	Plant functional type
FD	Functional diversity

Introduction

Plant Functional Types (PFTs) are a collective term for the different typologies that researchers have made in recent decades to summarize species diversity in plant communities in ecologically similar groupings (Smith et al. 1997; Lavorel et al. 1997; Semenova and Van der Maarel 2000). They are relevant in ecological research as they provide an understanding for the

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evolutionary adaptations that plants have acquired to survive in a certain environment. Classifications of PFTs can be made a priori (tentatively) or a posteriori on the basis of measured traits (Smith et al. 1997; Díaz and Cabido 2001; Violle et al. 2007). The basis of plant functional classifications and the selection of traits is dependent on the aims and context of the study and this has led to functional classifications to predict responses to climatic changes (Woodward and Cramer 1996; Smith et al. 1997; Díaz and Cabido 1997; Box and Fujiwara 2005), small-scale disturbances (Lavorel et al. 1997; Grime 2001), or landscape-level disturbances (Noble and Gitay 1996). In some cases, large databases have been built screening large numbers of species in an area (Duarte et al. 1995; Knevel et al. 2003; Grime et al. 2007). Plant functional types in turn also have an impact on the ecosystem that they occupy and this led Lavorel and Garnier (2002) to differentiate between response traits (traits that explain the effects of the ecosystem on the plants) and effect traits (traits that explain the effects of the plants on the ecosystem).

Overall, plant traits give the community in which they occur, emergent attributes and various methods have been developed to describe plant communities by mainly looking at plant traits, skipping the intermediate step of species composition (Grime 2001; Shipley et al. 2006; Gaucherand and Lavorel 2007). Recently, the role of PFTs in community assembly has often been emphasized (Keddy 1992; Weiher and Keddy 1999; Shipley et al. 2006; Shipley 2010). This can be taken further by stating that ecosystem properties can be derived from species traits, taken the relative species abundance of each species into account (Shipley et al. 2006; Vile et al. 2006; Shipley 2010; Sonnier et al. 2010). This is also called the mass-ratio hypothesis (Grime 1998). This means that dominant species in an ecosystem have an overwhelming effect on ecosystem functioning, and this is also found by researchers interested in the correlation between species diversity and ecosystem functioning (Kinzig et al. 2002).

Because of the stated correlation between plant functional composition and ecosystem functioning (Tilman et al. 2005; Díaz and Cabido 2001; Lavorel and Garnier 2002), it can be assumed that ecosystems that show similar properties in functioning also have a similar functional composition as they exert similar stresses on the plants. Once functional groups are defined and recognized, it is cheaper and easier to determine functional composition than to measure ecosystem properties, so functional composition can be an important indicator for ecosystem health or underlying ecosystem properties.

Weiher and Keddy (1999) distinguished between two different kinds of plant traits: those traits that are an adaptation of the plant to deal with the stresses associated with a certain environment, and those traits that help the plant to remain competitive within the community in its interactions with other species. Wetlands are a good showcase for plant functional traits of both kinds: there is a specific stress that constrains plants growing in wetlands, particularly anoxia in the root zone (Wheeler 1999), but it is also regarded as a highly productive environment (Keddy 2000; Cronk and Fennessy 2002) so for those species that can adapt there is a lot to gain and this results in strong competition. Most core wetland plants are clonal species that are very efficient competitors for habitat space (Wisheu and Keddy 1992; Boutin and Keddy 1993; Cronk and Fennessy 2002). Both stresses result in strong convergence in evolutionary traits of wetland plants and functional types can be recognized on the basis of trait complexes. The study by Boutin and Keddy (1993) on wetland plants in the United States revealed three basic functional types in wetland plants: dominant matrix species, interstitial species, and annuals. However, comparison between wetlands of different regions and continents, will likely reveal that there is still far more variation in functional characteristics in wetland species.

One of the processes in which plant functional types have their impact on ecosystem functioning in turn is peat formation in wetlands (Rydin and Jeglum 2006). The type, chemical composition, and decomposition rate of peat all depends on the botanical identity of the dead organic matter. The clonal matrix dominant species in any peatland has thus a major impact on the substrate in which itself and all the other species are growing.

South Africa is a country that, although it is generally regarded as an arid region, has a wide variety of wetland types (Tooth and McCarthy 2007; Ewart-Smith et al. 2006). Peatlands are particularly rare, but they do occur in small pockets along the southern and eastern coast and along the inland mountain escarpment. South African peatlands are generally of a topogeneous origin: groundwater flows through a mineral substrate before it enters the peat (Rydin and Jeglum 2006). Because of the scarcity of peatlands in

South Africa, only few vegetation studies have been made on South African peatlands (Bloem et al. 1993; Venter 2002).

The aim of the present study is to highlight the differences in functional composition of South African peatlands in different climatic and biogeographic zones. The intention is not to “predict” what the functional composition will be as a function of climate or biophysical factors, but rather to find whether, in areas with a different species pool, similar functional types can be found in similar ecosystems. So, it is rather about whether, in regions with completely different species pools, the species that are “filtered” from this species pool (Hubbell 2001) are similar in their functioning irrespective of their taxonomic position. This comparison will enable us to infer differences in ecological functioning of the different peatland ecosystems of the subcontinent and thereby to make assumptions about commonalities and differences among peatland ecosystems in general.

Methods

Three peatlands in South Africa were selected for the analysis of their functional composition (Fig. 1). The first one is Mfabeni Swamp on the coastal plain in Northern KwaZulu-Natal which receives mostly summer rainfall and has a subtropical, humid climate. The second one is Wakkerstroom wetland, on the edge of the Highveld plateau in Mpumalanga, which receives mostly summer rainfall and has a temperate climate with regular frost in winter. The third peatland that was included in the study is Goukou wetland in the Overberg region of the Western Cape. This area has a mediterranean climate with rainfall mostly in winter, spring, and autumn.

Both Wakkerstroom and Goukou wetlands represent valley bottom wetlands that are fed by an upstream river that loses confinement and spreads its flow over a large surface area. Mfabeni wetland is hydrologically different in that it is fed by

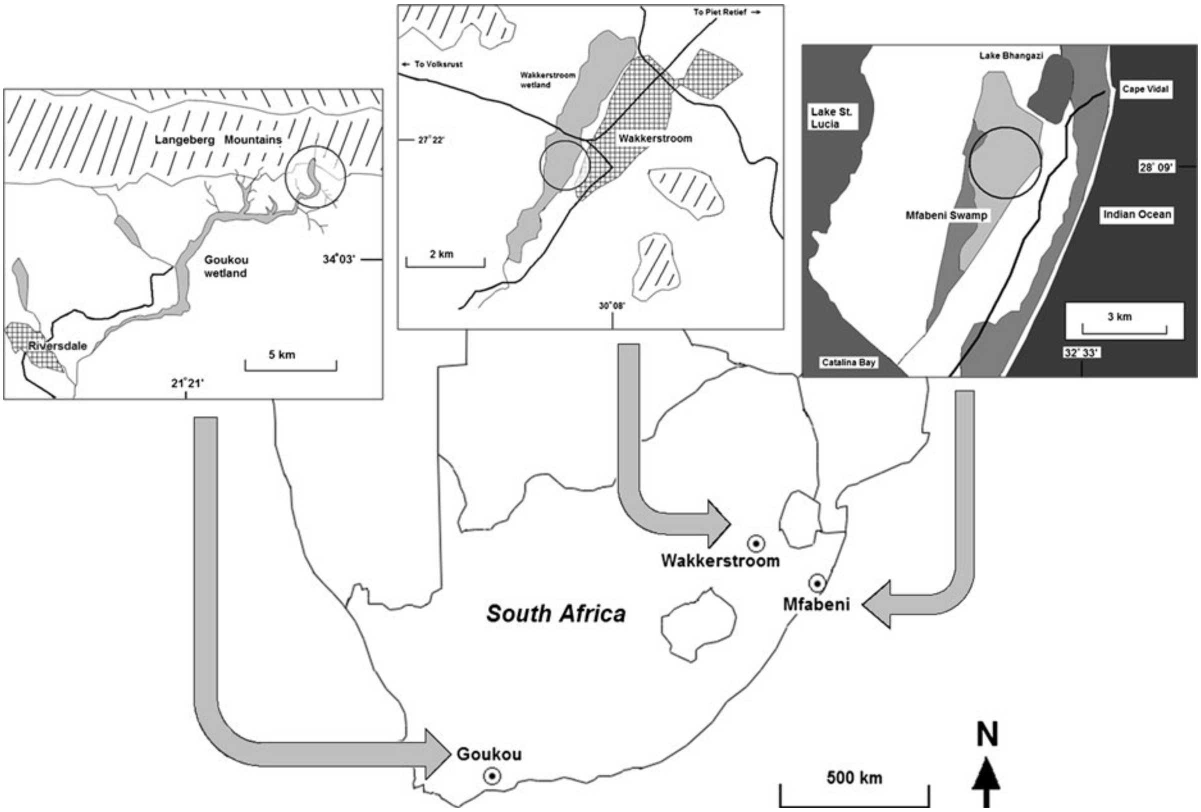


Fig. 1 Map indicating the locality of Mfabeni Swamp, Wakkerstroom Wetland and Goukou Wetland and the approximate area within the wetlands where functional composition was determined (indicated by a circle on the map)

groundwater seeping through sandy substrates onto a large flat, although its outlet is a small stream. In all three situations peat is formed however, most extensively in Mfabeni, where the peat also has the highest Von Post humification index (Rydin and Jeglum 2006). Goukou has extensive peat layers (>10 m thick) although there are still some inputs of clastic sediments toward the edges and the peat has a coarser structure and a low humification index. In Wakkerstroom wetland, the peat layer is only shallow (1–2 m thick) and localized but has a high humification index (Table 3). Peat samples have been taken from the sampling sites and have been analyzed for chemical composition.

The vegetation types that are represented by these three peatlands are not the only ones that occur on peat within South Africa, but they are certainly representative of many peatlands, as a recent survey of wetland vegetation types in South Africa indicates (Sieben et al. unpublished). The vegetation types that are missing from the present survey are mainly those that are difficult to access (Papyrus swamps in Northern Zululand), those that only occur in small patches (*Abildgaardia hygrophylla* peatlands in coastal Pondoland, Mountain Fynbos wetlands in the Western Cape), those that produce monocultures (*Merxmuellera cincta* peatlands in the Southern Cape, Common reed peatlands on the Highveld), and those where there are practical constraints on the sampling of mature specimens in their entirety (Swamp Forests in northern Zululand).

In each of the peatlands, a site was selected that had a permanently wet peat substrate, was easily accessible but that still showed a mixture of various species (i.e., it was not dominated by monospecific stands of the climax species). On this site, five transects of eighty plots each were laid out along a straight line where the abundance of each species was assessed in small subsequent quadrants (see also Bartha et al. 2004). These small quadrants are 25 × 25 cm in size (50 × 50 cm in the case of Goukou) and species within the plots were recorded on a three point scale: 1

Table 1 Investigated plant traits

Plant trait	Method of measurement	Unit	Scale
Shoot length	Average shoot length of 10 mature plants	mm	Ratio
Rooting depth	Average maximum rooting depth of mature 10 plants	mm	Ratio
Rhizome internode length	Average length between 10 internodes on rhizome or stolon	mm	Ratio
Stem diameter	Average diameter of 10 stems at base level (in mm)	mm	Ratio
Total Biomass	Average value of total biomass divided by number of mature shoots (in case of a tuft or rhizome)	mm	Ratio
Shoot/root biomass ratio	Ratio of biomass of shoots and roots based on an average between 10 plants (or groups of plants in case of a tuft or rhizome)	g/g	Ratio
Leaf length/width ratio	Ratio between the length and the width of a leaf based on an average of 10 leaves	mm/mm	Ratio
Specific leaf area	Dry weight divided the total surface area, based on an average of 10 leaves	g/mm^2	Ratio
C/N ratio	Mass ratio of Carbon versus Nitrogen	g/g	Ratio
Aerenchym stem	Scale of 1 to 3 (1 = no aerenchym, 2 = less than 50% aerenchym, 3 = predominantly aerenchym)	Class	Ordinal
Woodyness stem	Scale of 1 to 3 (1 = no woody tissues, 2 = less than 50% woody tissues, 3 = predominantly woody tissues)	Class	Ordinal
Hollowness of stem	Scale of 1 to 3 (1 = stem not hollow, 2 = hollow space less than 50%, 3 = hollow space more than 50%)	Class	Ordinal
Rooting type	Adventitious, Taproot, Fine mesh, Annual, Tuft, Rhizome, Stolon	Class	Nominal
Leaf orientation	Leaves all at base, leaves on top of a stem, leaves on stem, leaves in one plane (as in a fern)	Class	Nominal
Growth form	Shrub, Graminoid, Annual, Forb, Geophyte, Moss	Class	Nominal
Clonal strategy	Tuft, Guerilla, Phalanx, Not clonal	Class	Nominal
Metabolism	C3, C4, parasitism, carnivorous	Class	Nominal

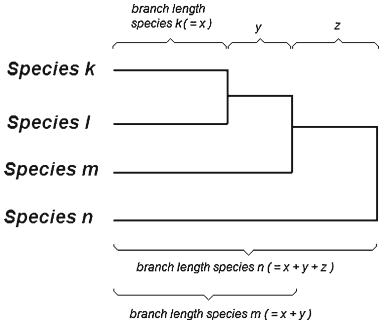
indicates that a species occurs only with a single or a few small individuals, 2 indicates that the species covers but less than 50% in the plot and 3 indicates that the species was dominant within the plot as it covered more than 50%. The most common species in these plots were collected and several functional traits were measured on them. Table 1 indicates the plant traits that were measured for each species and the methods by which they were calculated. These measurements were taken on ten mature specimens with complete roots that were collected in the field (when it contained a clonal species the weight measurements were later divided by the number of mature shoots on the rhizome) and on fresh leaves and stems that were stored in bottles with an alcohol solution.

Functional traits that are regarded as having general importance have been derived from the list suggested by Weiher et al. (1999), but seed characters have been ignored since most wetland plants are clonal species and the vegetative characters are regarded as having most importance. Some more specific traits that relate to the hydraulic architecture of the plants and the adaptation to the wetland habitat have been included, but mostly as qualitative characters (Wheeler 1999; Cronk and Fennessy 2002).

A few species were collected in more than a single wetland. In most cases, the functional characters have been measured separately for those species that were collected twice, but in one case (*Pycreus nitidus*), missing data was inferred from the same species in a different wetland.

The data on functional traits were entered into a trait matrix, and from this matrix similarity indices based on Euclidian distance between species were calculated using the program Primer 5 for Windows. A dendrogram was derived from this similarity matrix and this helped to delineate the functional groups. Those species that were not collected for analysis because of their scarcity in the plots were allocated to a functional group a posteriori, so that they can be included in the calculation of functional composition of the wetland. The calculation of the dominance values of the wetland as a whole was based on the sum of all occurrences in the individual plots in the transects. In this, a value of 1 was counted as a 10%, a value of 2 was taken as a 40% cover, and a value 3 was taken as an 80% cover. By adding all covers for the individual plots, an indication of relative abundance for each species could be derived for the wetland as a whole. This will play a role in determining the importance of each species in emergent ecosystem properties dependent on plant functional traits (Grime 1998; Vile et al. 2006). The fraction of the total cover that is occupied by species i is referred to as p_i, and this value is an indication of the relative abundance of species i.

Various indices of functional diversity and functional traits have been developed to compare the ecosystems with each other (Petchey and Gaston 2002, 2006, 2007; Petchey et al. 2004). In the current study, functional diversity has been calculated in two different ways. A dendrogram was constructed for each of the three peatlands and the Functional Diversity has been derived from the total branch length of each of these dendrograms, following Petchey and Gaston (2006). Because this way of calculating functional diversity does not take relative abundance into account and thereby overemphasizes the functional characters of rare species, a weighting method was devised so that the branch length of each species i is multiplied by the factor p_i. A branch at the base of the dendrogram that splits up in three branches k, l, and m is multiplied by the factor $(p_k + p_l + p_m)$. This calculating process is illustrated in Fig. 2. Adding all the branch lengths together in this way will obtain a weighted value for the FD that will account for the dominance of each species. In this way, a functionally divergent species



Weighted branch length species k: $x \times p_k$
Weighted branch length species n: $(x + y + z) \times p_n$
Weighted FD total diagram: $(x \times p_k) + (x \times p_l) + \{y \times (p_k + p_l)\} + \{(x + y) \times p_m\} + \{z \times (p_k + p_l + p_m)\} + \{(x + y + z) \times p_n\}$

Fig. 2 Incorporating a weighting process in the calculation in the Functional Diversity Index based on the relative abundance of each species in the peatland. The index p_k refers to the prevalence of plant species k as a fraction of the cover of all species in the sampling site will add more to functional diversity when it is dominant, than when it is only very rare.

The position of dominant and co-dominant species in the functional dendrogram needs to be considered to get a good understanding of species interactions in the three peatlands. It makes quite a difference whether the dominant species is a species that is functionally divergent from the co-dominants and other species in the wetland or whether the dominant species is functionally similar to the co-dominants and other species.

Results

The total number of species collected in each of the three peatlands that were included in the functional analysis was not equal to the total number of species recorded in the transects (16 out of 31 species in Goukou, 16 out of 20 species in Mfabeni, and 9 out of 16 species in Wakkerstroom, see Table 2). A number of species were considered so infrequent that they were not worth collecting. The total cover of all species included in the functional analysis ranged between 98.3% and 99.7%, and the small percentage that was left out in the analysis represented between 4 species in Mfabeni and 15 species in Goukou, where a large number of rare and infrequent species were found. In most cases, however, it was obvious to which functional group these scarce species should be allocated.

The dendrogram of all species in the three peatlands combined indicates the presence of 13 functional groups (Fig. 3). The abundance of these functional groups and the resulting functional composition is different for each of the three peatlands (Fig. 4). Species that were not collected for functional analysis and that were not allocated to any functional group a posteriori were put in a separate category "Other" in Fig. 4, but the total cover of these species is negligible in all three peatlands.

When a single species was collected in more than one wetland, it obviously ended up in the same functional group, even though there may be some slight functional differences. It is clear that there are quite a number of functional groups that occur in only a single peatland and especially Goukou wetland has many "unique" functional groups. In total, nine different functional groups were found in Goukou wetland, five of which were found exclusively there. Eight different functional groups were found in Mfabeni Swamp, two of which were found exclusively there. Only four different functional types were found in Wakkerstroom wetland and none of these functional types were found exclusively there.

The species were most evenly distributed over all functional groups in Mfabeni wetland, and in that respect, Mfabeni can be regarded as the most functionally "even" wetland; however all three dominant functional groups are quite closely related to each other.

Table 2 Characteristics relating to functional diversity for the three peatlands

	Goukou	Mfabeni	Wakkerstroom
Number of species recorded	31	20	16
Number of species in functional database	17	16	9
Total number of plots	420	397	402
Number of functional types	9	8	4
Total cover of all species with functional data	98.7%	99.6%	98.3%
Total cover by dominant	61.9%	27.2%	37.3%
Functional evenness	0.59	0.72	0.42
Functional Diversity (FD)	149.7	119.7	66.5
Weighted Functional Diversity	16.7	13.0	12.2
Dominant	*Prionium serratum*	*Rhynchospora holoschoenoides*	*Carex acutiformis*
Functional group dominant	Palmiet—Unique functional type	Rhizomatous graminoid	Rhizomatous graminoid

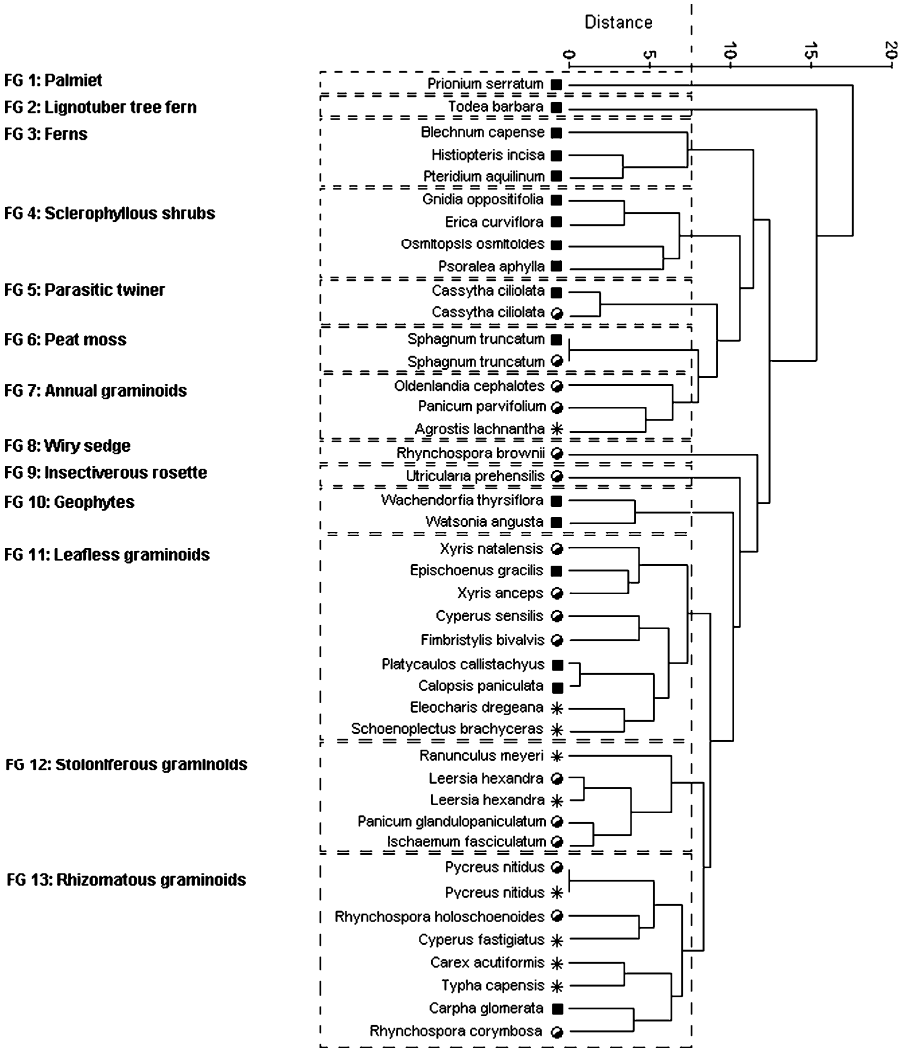


Fig. 3 Dendrogram indicating the functional classification. The symbols indicate in which wetland the species was collected: * indicates species recorded in Wakkerstroom, ■ species in Goukou, and ◕species in Mfabeni

A summary of the parameters of interest per peatland can be seen in Table 2. Most indicators display that Goukou is by far the most functionally diverse wetland, although it is dominated strongly by a single species which belongs to its own functional type. Mfabeni Swamp and Wakkerstroom wetland are both dominated by more or less the same functional groups, namely rhizomatous graminoids, stoloniferous graminoids, and leafless graminoids.

Calculation of the FD and the weighted FD illustrates clearly that Goukou wetland is functionally more diverse than the others and that Wakkerstroom is the least functionally diverse. The three dendrograms for the different peatlands are illustrated in Fig. 5. An interesting picture emerges when considering the dominants and co-dominants within this dendrogram. Within Wakkerstroom wetland and Mfabeni wetland, the dominant species belongs to the same group, and all dominant and co-dominant species are functionally quite similar, belonging to three different closely resembling functional groups.

In Goukou wetland, however, the dominant species belongs to the functionally most divergent group. The only other species that may locally achieve dominance within the wetland are restios belonging to the leafless graminoids. So, Palmiet (*Prionium serratum*), the dominant species in Goukou wetland, has no functional equivalents, and is competitively successful, so it only leaves niches open for functionally dissimilar species, which only occasionally achieve local dominance.

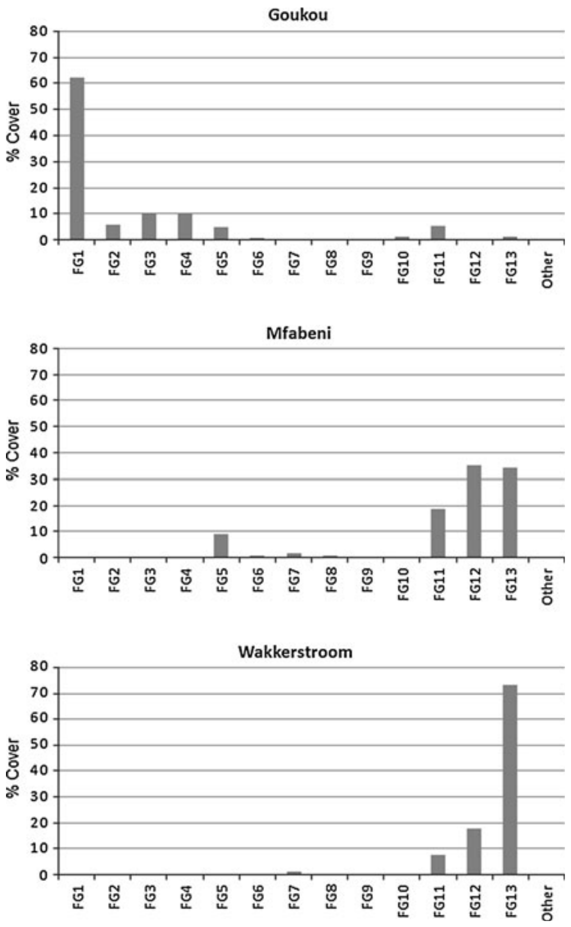


Fig. 4 Prevalence of the different functional groups in the three different peatlands, based on the occurrence of plants in small plots in transects made in each of them. Some functional groups are not mentioned in the text due to their low proportions in the vegetation, for example FG 9 (Insectivorous rosette plants)

Discussion

The dominant species in the transects in Wakkerstroom and Mfabeni belong to the same functional group, namely the rhizomatous graminoids. This group, together with the two closely related groups of stoloniferous graminoids and leafless graminoids, largely coincide with Boutin and Keddy's (1993) definition of matrix dominants. It is clear that this is the typical growth form of a "helophyte" and a successful growth form in permanent wetlands across the world (Cronk and Fennessy 2002; Cook 2004).

Although the main three functional groups in Mfabeni and Wakkerstroom are similar, it is obvious that Wakkerstroom has most of its species (72%) in only a single functional group, namely the rhizomatous graminoids, whereas the abundance of the different functional groups is more evenly distributed in Mfabeni. The impression exists that this most likely also means that in Mfabeni, the co-existence of many species together is more stable, because species-rich communities stretch over large extents in the wetland. This situation is different in Wakkerstroom wetland, where four functionally similar species (*Typha capensis*, *Carex acutiformis*, *Pycreus nitidus*, and *Cyperus fastigiatus*) compete with each other, but where a single species (*Typha capensis*) is a clear winner in large stretches of the wetland and achieves virtual monodominance. This demonstrates niche separation between divergent functional types with functionally similar species occupying the same niche (Tilman 1994). This means that competition between species that are functionally similar is more likely to drive out one of the competitors, whereas co-existence is more likely among functionally dissimilar species (Weiher and Keddy 1999; Pugnaire and Valladares 2007).

The dominant species in Goukou wetland is a unique species that has been allocated to a functional group of its own. This makes the situation in Goukou different from the other two peatlands, because the most effective competitor—*Prionium serratum*, a sedge-like plant on a woody stem—is also functionally the most divergent species.

The traits that make this species stand apart from all other species in the analysis are its rooting depth and root/shoot ratio. The relative abundance of this species in Goukou is much higher than that of any of the dominants in Mfabeni and Wakkerstroom, whereas simultaneously the species and functional diversity in Goukou wetland is higher than in the other two peatlands.

The explanation is that Palmiet (*Prionium serratum*) is an ecosystem engineer (Jones et al. 1994, 2010) that changes its own environment to favor itself and its associates. Except for providing the organic material that builds the peatland, Palmiet also changes the hydrology of the ecosystem. Palmiet wetlands occur on a slope that is steeper than what could be expected for wetlands of a certain size (pers. comm. W.N. Ellery, but see Ellery et al. 2008; Tooth and McCarthy 2007). The occurrence and proliferation of Palmiet in foothill streams eventually "plugs" the river turning the river into a valley bottom wetland. The deep and extensive rooting system together with its clonal

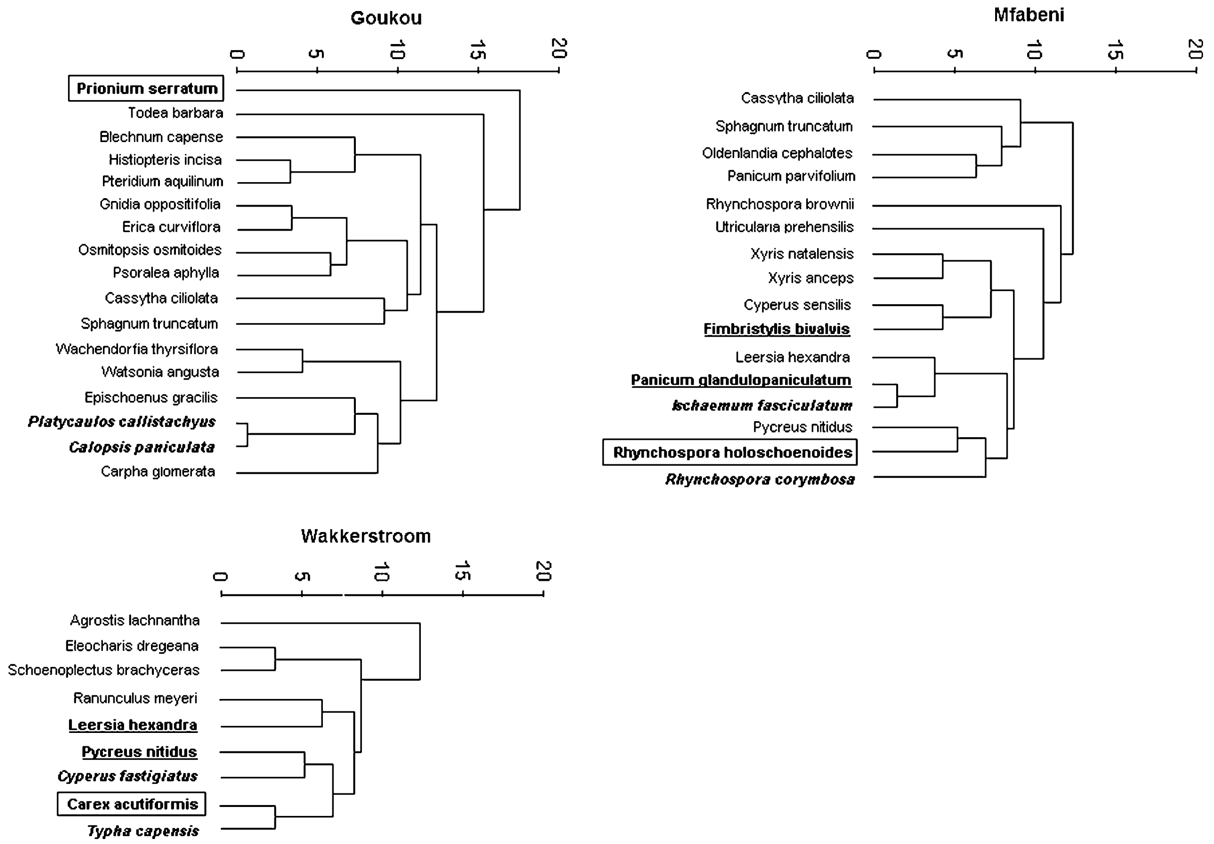


Fig. 5 Dendrograms based on functional traits of species occurring in each of the three peatlands. The values for Functional Diversity (FD) calculated in Table 2 are based on these dendrograms. The species in bold are the most important dominant species, with the species in the block the absolute dominant in the transects, the underlined species being co-dominant, and the species in italics achieving dominance only locally

growth and ability to withstand strong flood events provide the key traits that help the plant to transform its own environment. This fits the transformation of an ecosystem by an ecosystem engineer as described by Jones et al. (2010). The deep and extensive rooting system of Palmiet also possibly plays a role in "leaking" oxygen into the peat substrate which would otherwise be completely anoxic, making the habitat suitable for other species and other functional groups that do not usually occur in peatlands (Pugnaire and Valladares 2007). The root systems of the shrubby species growing in the Palmiet matrix have horizontally spreading taproots that remain shallow.

The unique ecological characters of *Prionium serratum* are partly explained by its position as an ancient lineage at the base of the clade of the Poales (Simpson 2008). The species has managed to develop an ecological strategy that has not been developed by any other species in the Poales. The age of the species also suggests that it may have occupied the niche that it does occupy today already for a long time in evolutionary history thereby constraining the development of evolutionary traits in other species that would potentially occupy this habitat. Phylogenetic isolation has resulted in a unique trait complex that no other plant has emulated (Reich et al. 2003). Because it is limited to substrates associated with very nutrient-poor quartzites in the Table Mountain Group, it has not conquered peatland habitats in other parts of the country.

If we consider ecosystem properties to be derived from the functional traits of the species and their relative abundance (Shipley et al. 2006; Vile et al. 2006), we have to conclude that peatland habitats comprise a heterogeneous group of ecosystems. Peatland habitats are all occupied by species that transform their own environment so they are all ecosystem engineers to a certain extent, but the degree in which this happens is different between peatlands and the unique properties of Palmiet in Western Cape peatlands result in a different type of peatland ecosystem than is to be expected in other parts of the country.

Another way to look at this is by considering "alternate stable states" which are to be expected in ecosystems with strong underlying environmental stresses (Suding et al. 2003; Didham and Watts 2005). In the same way, as a chance species colonizer can change the course of succession, a chance occurrence of a special functional type in a certain region will change the course of autogenic succession in a peatland. In a limited region of South Africa, succession on peatland habitats in the absence of fire proceeds toward a swamp forest, but this depends on whether the location of the peatland falls within the distribution range of the tree species that make up this swamp forest.

The emergent properties of the ecosystem are dependent on the functional types present in the peatland, for example the composition of woodland peat is different from that of sedge or Sphagnum peat (Rydin and Jeglum 2006). Also, within the present study it can be found that the peat composition of the peatlands is different for each peatland (Table 3). In general, peat developed from Palmiet decomposes slowly and has a low humification index (Rydin and Jeglum 2006).

The comparison of the three peatlands shows that the co-existence of many species can be expected both when a mixture of species from different functional groups occur together as well as when an ecosystem engineer with a unique functional type provides a niche for associate species. This validates the distinction between three different aspects of functional diversity as mentioned by Mason et al. (2005): functional richness, functional evenness, and functional divergence. In the present study, it seems that particularly functional evenness and functional divergence play a role in the co-existence of many different species. These different aspects of functional diversity complicate the comparison between different ecosystems (Petchey and Gaston 2006, 2007), and the aspects should be considered separately to obtain a full picture of what is going on in the ecosystems to be compared.

Table 3 Peat attributes for the three peatlands. Humification index (von Post humification index, see Rydin and Jeglum 2006) and peat depth are estimated from the field, whereas all other variables are averaged over a composite peat sample coming from all five transects that were sampled

Peat attribute	Mfabeni	Goukou	Wakkerstroom	Units
Humification index	H10	H4	H8	
Peat depth	>10 m	> 10 m	~1 m	
pH	4.30	3.90	4.80	
Moisture	7.89	3.97	5.06	%
Ash (A.D.)	7.5	50.8	54.6	%
Organic matter	84.7	45.2	40.3	%
Total N	2.26	0.74	0.90	%
Total C	47.08	23.67	19.08	%
C/N ratio	20.8	32.0	21.1	
Ca	0.31	0.08	0.40	%
Mg	0.210	0.106	0.270	%
P	0.033	0.039	0.072	%
K	0.015	0.192	0.323	%
Na	0.187	0.137	0.082	%
Fe	0.161	1.093	4.406	%
Cu	6.19	5.94	43.8	mg/kg
Mn	14.5	57.7	317	mg/kg
Zn	29.5	21.7	81.1	mg/kg
Al	0.198	1.296	4.343	%
S	0.707	0.291	0.453	%

Aquatic and wetland habitats contain a large number of Plant Functional Types as they require strong adaptations resulting in distinct trait complexes. In various parts of the world, attempts have been made to obtain an overview of the functional types present (Boutin and Keddy 1993; Willby et al. 2000; Cronk and Fennessy 2002; Cook 2004). Different groups of plants have been investigated and this will contribute to a global overview of a functional classification of wetland and aquatic plants.

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