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Cover photograph: Giraffes on the game farm Omatako Ranch (Observatory S04 Toggekry) in the Namibian Thornbush Savanna.
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Life forms along the BIOTA transects—new perspectives on biomes in southern Africa

Jens Oldeland*, Ute Schmiedel & Norbert Jürgens

Summary: The concept of life form is one of the cornerstones in ecology. Insight into the relationship between life form and climate leads to the classification of biomes, which is largely based on the dominance of plant life forms. The BIOTA Observatories along the southern African transects covered six different biomes in southern Africa. After nine years of observation, data from these Observatories were analysed for patterns of relative cover and richness of the five basic life forms of Raunkiaer as well as extended life forms along the major climatic gradient. Our findings partly confirmed, and to some extent modified existing biome classifications for southern Africa. Furthermore, the relationship between life form composition and precipitation along the transects was analysed in a direct gradient analysis using fuzzy set ordination. The gradient analysis revealed species richness per life form as a suitable proxy to quantify life form occurrence in relation to annual rainfall. Finally, it was shown that not all proposed biomes can be separated clearly regarding richness or relative cover of life forms.

Introduction

Climate is known to be a major determinant of the distribution of plant life on Earth. Early approaches to classify macroecological units were mainly based on climate (Schimper 1898, Köppen 1936, Holdridge 1947) or on soil-climate interactions (Walter & Box 1976). The widely applied biome concept classifies major landscape units on the basis of dominant plant strategy types (Odum 1945, 1971), which are understood as a response of the vegetation to macroclimatic conditions. Thus, it is not surprising that large scale climate models use the distribution of biomes to project possible effects of climate change on the biota (Claussen 1994, Cramer et al. 1999).

The definition of biomes is based on the composition of dominating plant strategy types or life forms. However, due to a limited set of life form types employed, a limited number of their combinations make an objective classification a challenging task. In particular, the definition of the term 'dominant' remains vague.

The classification of the seven biomes of southern Africa (Rutherford & Westfall 1994), for instance, is based on the ordination of life form combinations in their relation to rainfall and temperature. A similar approach was applied by Irish (1994) for Namibia, resulting in four biomes there. Both classifications rely on a database consisting of hundreds of vegetation relevés from various sources, which rely largely on unpublished data or semi-quantitative information such as personal communications and photographs. From these various sources, the dominating life form combinations were identified for areas where no other information was available. For example, a combination defined as "phanerophytes and hemicryptophytes" would result in the typical composition for the Savanna Biome (Irish 1994). Hence, the resulting borders of the biomes are still based rather on interpretation than on an objective classification, making decisions on boundaries hardly reproducible.

It is widely accepted that classifications based on quantitative data result in better representations of the real world than presence and absence data (Fielding 2007). Hence, a more quantitative definition of dominance, related to a standardised area, would contribute to a better and more objective biome classification. Furthermore, such quantification in terms of species richness or abundance of a particular life form could also serve as an indicator for potential changes in the environment. For example, climate change is more likely to drive gradual changes in the dominance of certain life forms than their mere presence or absence. Therefore, we apply our quantitative life form data, i.e. both cover and species richness on standardised Observatory plots, along the BIOTA transects to compare them with the description of the existing biome classifications. This will provide a quantitative verification of previous findings or might even lead to local adjustments. Our data may also help to detect possible intersections or gradual transitions of biome borders.

Identifying fuzzy boundaries has become an important task for dealing with uncertainty in ecology in order to describe gradual transitions between two or more states (Regan et al. 2002). Hence, the application of Fuzzy theory was assumed to have a large impact on vegetation science (Mucina 1997). Recent applications in a wide range of ecological studies confirm this statement. For example, Fuzzy theory helped to improve the classification of vegetation communities (Moraczewski 1993, Zhang & Meng 2007), identify ecotones in vegetation dataset (Arnot & Fisher 2007, Mahecha et al. 2009) and allowed better classification of remotely sensed images (Foody 1992, Lucieer 2006, Oldeland et al. 2010). Fuzzy set ordination (FSO), invented by Roberts (1986), allows testing a-priori hypotheses of climate-vegetation interactions with multivariate datasets. This approach inverts the exploratory character of com-

mon ordination techniques, such as PCA or CCA, where the observer is subjectively looking for patterns in ordination space. FSO has already been applied in several gradient analysis studies (Banyikwa et al. 1990, Boyce 1998, Boyce et al. 2005, Zhang & Meng 2007). However, all of them were focussed on species rather than on life form composition.

The major aim of this study was to analyze the distribution of life forms on the Observatories along the BIOTA transects covering both summer and winter rainfall regime. For this approach, we used the widely applied life form concept of Raunkiaer (1934), which was also employed by Rutherford & Westfall (1994) as well as Irish (1994) for their biome classifications in southern Africa. In addition we used an extended life form concept (sensu Ellenberg & Mueller-Dombois 1965) in this case proposals made by Jürgens (1986, 1990), which further subdivide the basic life forms of Raunkiaer into finer size classes. In addition to the classification by Rutherford & Westfall (1994) and Irish (1994), we employed four quantitative categories regarding life forms: i.e. 1) richness of basic life forms, 2) abundance of basic life forms, 3) richness of extended life forms, and 4) abundance of extended life forms. First, we analyze our quantitative categories for each Observatory along the transects and compare our findings with those of Rutherford & Westfall (1994) (for South Africa) and Irish (1994) (for Namibia). Secondly, we apply FSO in order to test which of the four quantitative descriptors best explains the life form distribution along the rainfall gradient. Finally, reproducibility of biomes according to FSO results is tested in a post-hoc analysis approach.

Material and Methods

Among the many proposed life form concepts, the system of Raunkiaer (1934) is still the most frequently applied. Raunkiaer classified plant species based on the height of their perennial buds relative to the ground surface and defined five categories: **phanerophytes**, **chamaephytes**, **hemicryptophytes**, **crypto-** or **geophytes,** and **therophytes**. Apart from

Table 1: Subdivision of extended life form categories according to height classes (ranges in cm); C = Chamaephytes and P = Phanerophytes; sub = submerged, nan = nano, mic = micro, mes = meso

	Csub	Cnan	Cmic	Cmes	Pnan	Pmic	Pmes	Pmac
Height [cm]	< 1	< 5	5–15	15–50	50–200	200–500	500–2000	> 2000

these five basic life forms, a further subdivision of phanerophytes based on size classes exists. For this study, we used the vegetation data, comprising information on basic (Raunkiaer 1934) and extended life form types (Jürgens 1986, 1990, see Table 1), gathered on the 32 Observatories along the BIOTA transects, which extended across summer and winter rainfall regime. Cover relative to the total cover per plot (in the following "relative cover") and mean species richness per basic and extended life form category were calculated for the 20 m x 50 m permanent plots of all BIOTA Observatories. Cumulative species richness per life form category as well as average cover values were calculated for each Observatory over all years where data existed, using the software BIOTABase (Muche et al. 2009).

We followed Irish (1994) and Rutherford & Westfall (1994) in our definition of biomes, i.e. biomes are labelled "Desert" (D), "Fynbos" (F), "Nama Karoo" (NK), and "Succulent Karoo" (SK). To avoid having 12 of the Observatories fall into the broad category "Savanna Biome" and to reflect the difference between the dense woodlands in the north and the open savannas in central Namibia, we followed Mendelsohn et al. (2002) and further distinguished between "Thornbush Savanna" and "Woodland Savanna".

The information on annual precipitation was extracted from the Worldclim 30 arc-second raster dataset "BIO12" (Hijmans et al. 2005), representing the mean annual precipitation from 1950–2000. Values were extracted at the centre coordinate of each permanent plot, of which 20 existed per Observatory (compare Volume 1, Part II). In order to differentiate between summer and winter rainfall regime in the ordination space, values for winter rainfall areas were assigned a negative algebraic sign.

Fuzzy set ordination (FSO) is a direct gradient analysis, which allows the a-priori testing of relationships between one single gradient and a multivariate dataset. This is achieved by hypothesising a relationship between a certain factor and the vegetation. In our case, we hypothesised that 'annual rainfall' as a major gradient is responsible for the differences in life form richness and abundance, the latter expressed as relative percentage cover per 20 m x 50 m. In order to construct a FSO, five iterative calculations were carried out in which membership values, ranging from 0–1, were assigned to each plot. First, plots with high summer rainfall were assigned high membership values, expressed as fuzzy set $\mu_A(x)$. Then, plots with high winter rainfall were assigned high membership values, leading to the fuzzy set $\mu_B(x)$. This means that in set $\mu_B(x)$, the plot with the highest winter rainfall (i.e. most negative) precipitation was assigned a '1' and the plot with the highest summer rainfall precipitation is assigned a value of '0'. Then, the similarity of the life form composition between the plots in set $\mu_A(x)$, called $\mu_C(x)$, was calculated as:

$$\mu_C(x) = \frac{\sum_{y \neq x}[S_{xy}(\mu_A(y))]}{\sum_{y \neq x}[\mu_A(y)]}$$

Where S_{xy} is the similarity between the plots x and y, $\mu_A(y)$ is the membership of plot y in the set of high precipitation plots, and $\mu_C(x)$ is the membership of plot x in the set of plots similar to high precipitation plots. For calculating the similarity between the plots we chose Euclidean Distance because of its good interpretability and the fact that we had less than 5% zeros in our life form dataset. In the next step, $\mu_D(x)$ was calculated in a similar manner, by just substituting μ_A with μ_B. Finally, a fuzzy set μ_E was calculated by addressing a "while-not" relationship,

i.e. the set of plots similar to high precipitation plots "while not" similar to low precipitation plots. This relationship was called the anti-commutative difference (Roberts 1986) and was calculated as;

$$\mu_E(x) = \frac{\left\{1 + [1 - \mu_D(x)]^2 - [1 - \mu_C(x)]^2\right\}}{2}$$

For full mathematical details see Roberts (1986). The final fuzzy set μ_E can be described as 'apparent precipitation' indicating plots with a similar richness or abundance of specific life forms at high or low precipitation values. The 'apparent precipitation' μ_E can be plotted against the actual precipitation μ_A in order to determine how much variation in life form composition is explained by precipitation. Pearson r between μ_E and μ_A was used to quantify the correlation between μ_E, i.e. for relative cover and mean richness per basic and extended life form, and precipitation expressed as μ_A.

In order to test whether biomes differed significantly in their mean membership value distribution of μ_E, we used Tukey's post-hoc test of "honest" significant difference. Differences between groups below the 5% level were considered as significant. All calculations were carried out in the R-software environment (R Development Core Team 2010); fuzzy set ordination was applied using the additional package 'fso' (Roberts 2007).

Results & Discussion

Distribution of life form richness and relative cover along the transects

Mean relative cover and mean richness of life forms per Observatory were plotted for each biome by following the BIOTA transects, e.g. from areas of high summer to high winter rainfall (Fig. 1). In the following subsections we will compare the results presented in Fig. 1 with the classifications by Rutherford & Westfall (1994) and Irish (1994).

Our findings confirm the existing biome classifications only to a certain extent. We found that in nearly all cases the relevance of the therophytic component was underestimated compared to our data. This might be due to the nature of the data used by Rutherford & Westfall (1994) who used different kinds of information. Our data was gathered over several years based on a standardised permanent plot design. Although the permanent plots covered less total area, they allowed a more detailed description of the long-term vegetation composition. The repeated measurements also allowed capturing the variability in cover and richness of plant species and hence life forms over the years. It appears that applying permanent sampling of plots improves the identification of the role of life forms in the vegetation structure.

The reverse situation was found for the Desert Biome, where we found that therophytes were overestimated by Rutherford & Westfall (1994). Jürgens (1991) and Irish (1994) disagree with their statement and showed that chamaephytes may play an important role in the Desert Biome as well. This is especially true for those coastal and winter rainfall parts of the Desert Biome, which are showing a gradual transition to the neighbouring biome, i.e. the Succulent Karoo (Jürgens 1991, 2006). Vegetation data were collected for two Observatories in the Desert Biome, however, life form cover was only included for Wlotzkasbaken Observatory (S16). Here, chamaephytes dominated while nanophanerophytes also contributed to cover. These life forms dominate the aspect of the vegetation throughout the year. Only after rare rain events, the desert aspect changes completely due to the mass occurrences of therophytes, which only lasts for a couple of weeks. These rare events have to be differentiated from the general aspect of plant strategy types that are able to survive the regional environmental conditions all. Thus, our data support the statement that therophytes are not as important as chamaephytes for the Desert Biome in terms of relative cover.

The biome classifications according to Rutherford & Westfall (1994) and Irish (1994) did not subdivide the Savanna Biome into separate classes. The two dominant life forms for savannas in general are phanerophytes and hemicryptophytes, i.e. mainly perennial graminoids, while chamaephytes do also occur but are of minor importance (Irish 1994). Our data confirm the prevalence of phanerophytes and hemicryptophytes for both the Woodland and the Thornbush Savanna in terms of relative cover. However, therophytic species play an important role in the richness and cover of these two biome subtypes. Our findings thus show only subtle differences between the two Savanna types that might have been easily overlooked if a standardised design was not applied. However, beyond the basic and extended Raunkiaer life forms considered in this study, Woodland Savanna in northern Namibia is well distinguished from Thornbush Savanna based on leaf morphology (i.e. broad-leafed versus fine-leafed) and on the biogeography of phylogenetic units (Jürgens, unpublished data).

A rather unclear situation in terms of life form dominance arises in the Nama Karoo Biome. The Nama Karoo, a grassy dwarf shrubland (Edwards 1983) is dominated by chamaephytes and hemicryptophytes. Rutherford & Westfall (1994) noted that the high variability of the hemicryptophytic and chamaephytic components is heavily influenced by grazing pressure. Grazing related patterns were found on six of the seven Observatories. All but Observatory S12 in the Nama Karoo were installed as pairs in order to investigate the influence of landuse, mainly in terms of grazing pressure. The Observatory pairs in the Nama Karoo are S39/S40, S08/S09 and S10/S11. We identified differences between Observatory pairs mainly in the relative cover of phanero-, chamae-, and hemicryptophytes. For example, at the Observatory Gellap Ost (S10) with moderate grazing pressure, relative cover of hemicryptophytes was about 35%, whereas at the adjacent Observatory Nabaos (S11) with high grazing pressure, it dropped to almost 1%. This contrast shows the difficulty of obtaining an objective classification also of macroecological units when the human induced variability is not taken into consideration.

The winter rainfall biomes show characteristic differences when compared to the summer rainfall biomes. In particular, the increase of cover and species richness of geophytes has to be noted. While geo-

phytes were not considered in the original classification due to a lack of data, the standardised permanent plot design allowed gathering precise information on richness and abundance of this life form. According to Rutherford & Westfall (1994), the dominant life forms are mainly leaf-succulent chamaephytes. Our data clearly confirms the high dominance of chamaephytes. Additionally, we observed an almost linear increase in richness and relative cover for chamaephytes with increasing winter rainfall. Rutherford & Westfall (1994) list phanerophytes, chamaephytes and hemicryptophytes as the main life forms for the Fynbos Biome. Again, our data confirm their classification. However, due to the extended life form system that we used, it becomes clear that only nanophanerophytes contribute to the phanerophytic component. This information might be important in comparisons with the other biomes as it characterises the uniqueness of the Fynbos Biome. Indeed, Rutherford & Westfall (1994) comment that the phanerophytes in the Fynbos Biome are typically less than 2–3 meters tall and larger phanerophytes are rare, even in areas with higher rainfall.

The extended life form system, as demonstrated here, offers some new insight into the biome classification but also shows some limitations. A better discrimination due to the additional differentiation in height, especially of phanerophytes, has proven to be meaningful for the Fynbos and the Woodland Savanna. However, when relative cover or species richness per life form is compared, subdivision of phanerophytes, for instance, into subclasses leads to a different ranking of the life form; mostly resulting in an underestimation of the phanerophytic layer.

Relationship between life form composition and precipitation

We tested whether relative cover or mean species richness as a quantifying value applied to either the Raunkiaer or the extended life form classification better reflected the biomes along the precipitation gradient (Fig. 2). The Pearson correlation between the actual precipitation μ_A and the membership values μ_E of the

anti-commutative fuzzy set were highest for species richness as a quantifying value in general and for the extended life form system in particular. Relative cover for the extended life form system showed only slightly higher correlation than the basic Raunkiaer system.

In other words, for the analysed dataset, the actual precipitation seems to be able to explain variations in species richness per life form better than variations in mean relative cover. Furthermore, this implies that species richness per life form might be a better proxy for distinguishing biomes along the considered precipitation gradient than their relative cover.

Several possible explanations can be highlighted to explain the differences in the correlation values between species richness and relative cover as quantifying values. Species richness as a quantifying value for life forms is less prone to possible observer bias than estimation of cover, although the ability to identify or find rare species depends on the experience of the observer (Kercher et al. 2003). A more important source of bias is the variation in sampling time, i.e. the time span after 'biologically important' rain events (Ogle & Reynolds 2004). These rain events stimulate plant growth and reproduction. Depending on the time when sampling is conducted, the vegetation aspect and thus cover can dramatically change within a few weeks, leading to differences in cover estimates over time. However, the same holds for species richness per life form, although again less severely. Finally, within a given Observatory, the intra-annual variation in relative cover seems to be stronger than the variation in species richness, possibly due to habitat specific variations. This seems to be especially true for the Desert and Nama Karoo Biomes, where species richness shows very little variation but a large discrepancy is found in relative cover between single plots.

Differences in biomes according to life forms

The Tukey HSD post-hoc test was applied to the pooled membership values per biome for the two quantifying values (i.e. species richness and relative

cover) and the two life form systems, in order to test whether biomes can be differentiated according to their mean 'apparent precipitation' (Fig. 3). For species richness per life form, five groups (Fig. 3a–e) were distinguished, while for relative cover only four groups were found (Fig. 3a–d). Interestingly, only the variant 'richness of basic life forms' was able to significantly distinguish between Woodlands and Thornbush Savanna. In contrast, this was the only variant in which Desert and Nama Karoo were not considered as significantly different.

In both life form systems, cover-based quantifying values did not separate Thornbush and Woodland Savanna nor Fynbos and Desert in terms of their membership values to a significant extent. While the low separation of the first pair is understandable due to the minor differences in spread, the statistical insignificance for the latter pair (Fynbos vs. Desert) is not that easy to comprehend. Firstly, the variation for Desert is very large, compared with Fynbos, and especially when compared with the very low variation for richness-based quantifying values for the Desert. The large variation in cover values for life forms in the Desert Biome (Fig. 3), leads to different membership values. However, it has to be noted that we applied relative cover (i.e. related to total area covered per plot) instead of absolute cover (related to total area of the plot) in order to stress differences in life form composition rather than general differences in vegetation density.

Conclusions

The aim of this study was to analyse patterns of species richness and relative cover per life form along the BIOTA transects. In particular, we compared mean values from nine years of observations from 32 Observatories with existing biome classifications. Interestingly, with a relatively small set of 32 samples from six different biomes, we were able to confirm and (partly) suggest some adjustments for these classifications. Furthermore, we quantified the
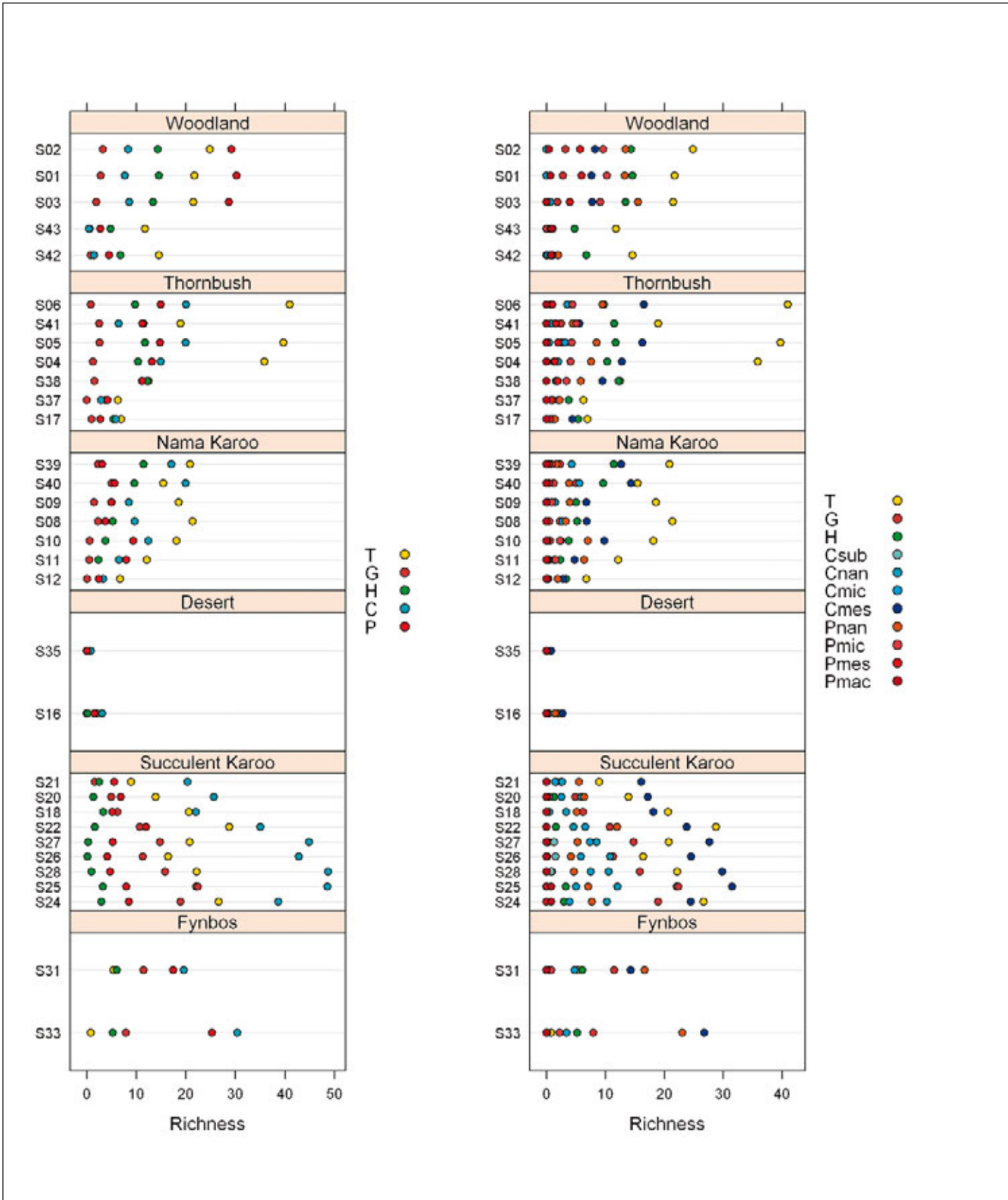
Fig. 1: Richness and relative cover of life forms along the precipitation gradient. For each biome, richness and relative cover of Raunkiaer's simple and extended life form system are presented in different colors. Each line represents one Observatory, which are ordered from highest precipitation of summer rainfall to highest precipitation of winter rainfall.
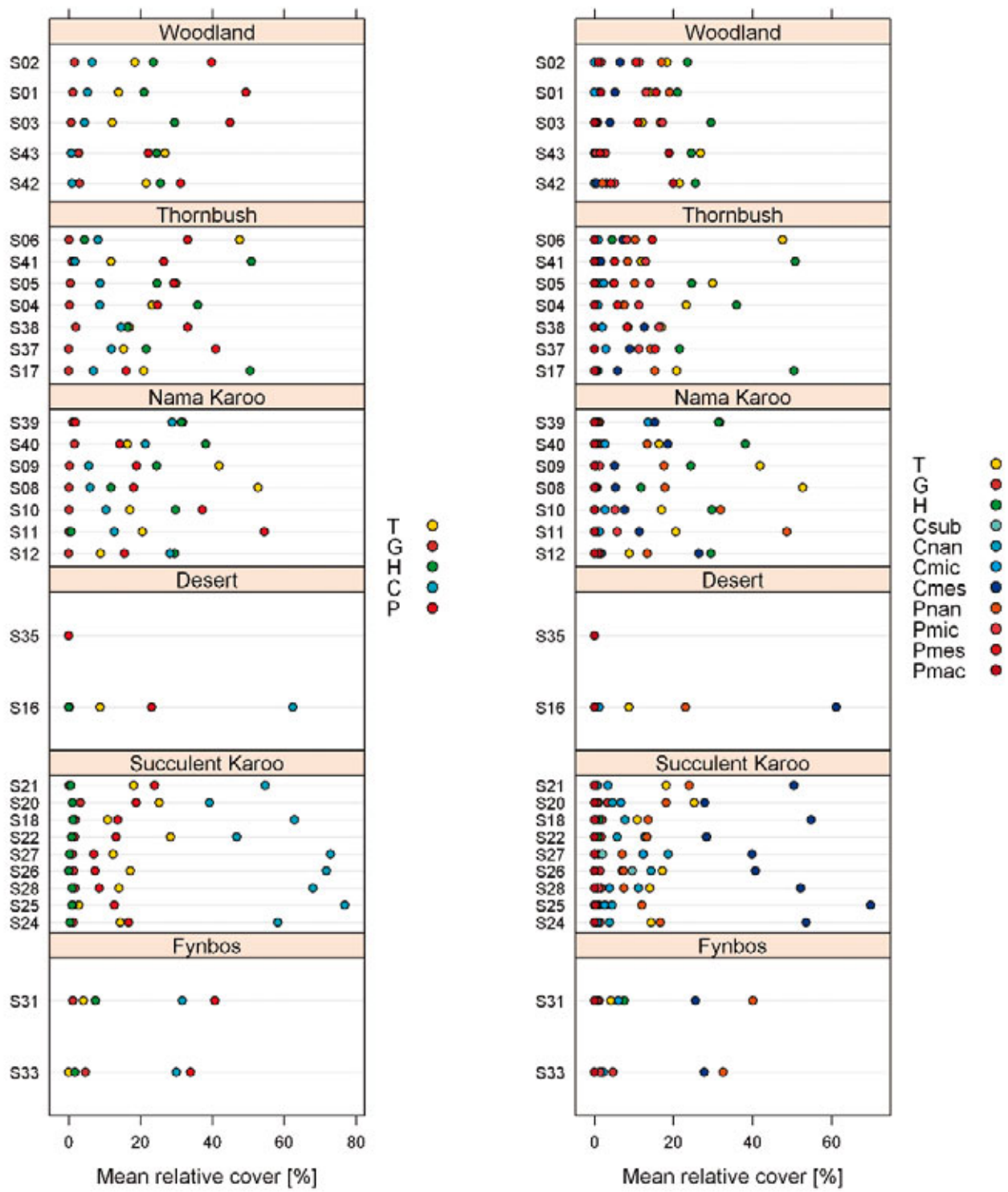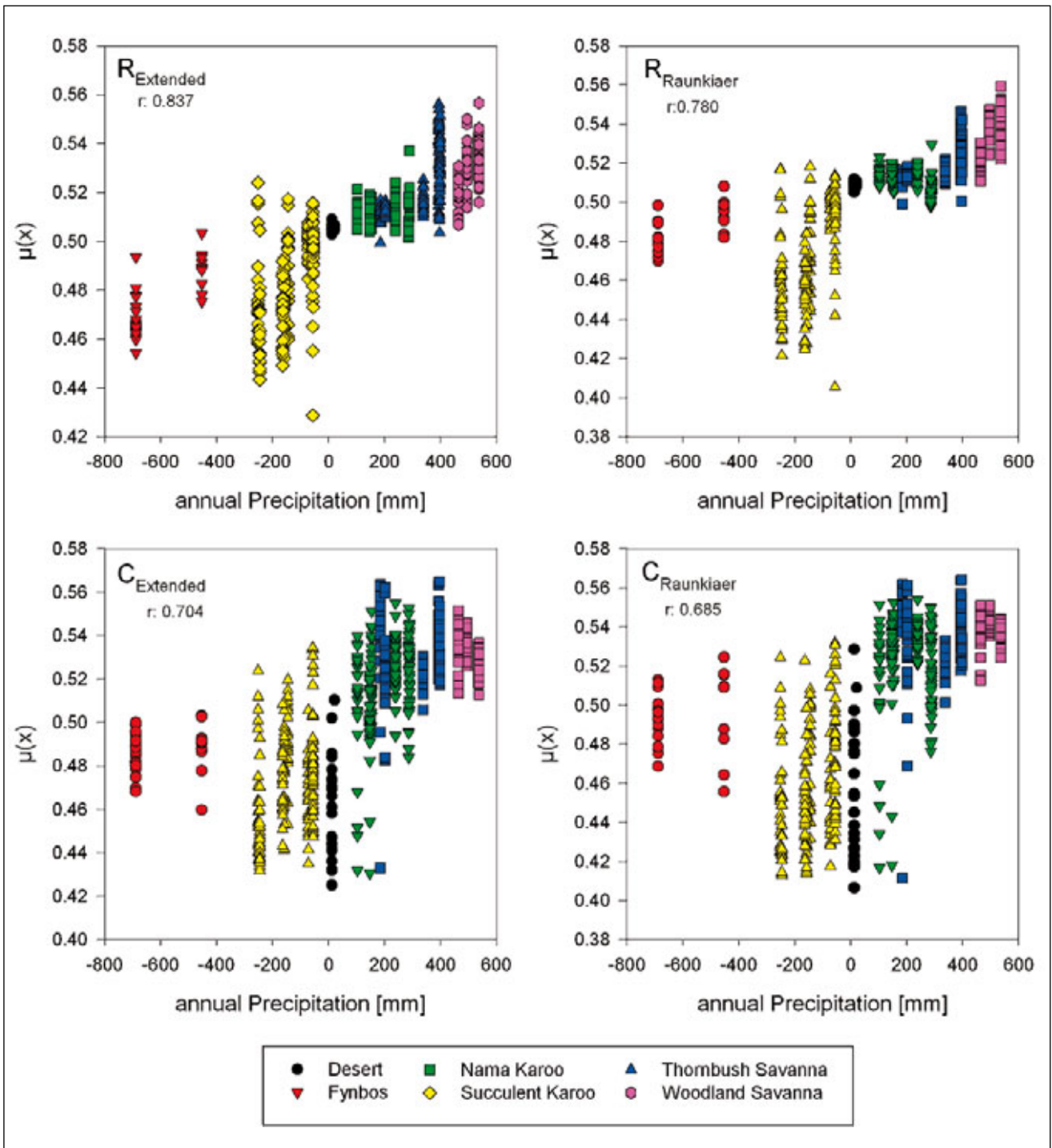
Fig. 2: Fuzzy set ordination of life form information per 20 m x 50 m plot along the precipitation gradient. Negative values on the x-axis reflect the winter rainfall, while positive values indicate a summer rainfall regime. The y-axis represents membership values for the fuzzy set μ_E. The r-value represents Pearson correlation between precipitation and membership value $\mu(x)$. Upper left: richness of extended life forms, upper right: richness of Raunkiaer life forms, lower left: cover of extended life forms, lower right: cover of Raunkiaer life forms.

relationship between life form composition and precipitation along the gradient, showing that species richness per life form is a good proxy for the rainfall gradient stretching across summer and winter rainfall regimes. Finally, we analysed the distinctness of the biomes according to life form composition. We

showed that, with the two life form systems employed in this study and the particular type of analysis, Woodland and Thornbush Savanna could not be separated except in one analysis. It might be useful to incorporate other traits of high adaptive value, like succulent organs, leaf morphology or growth form char-

acteristics that better describe the plant architecture into an adjusted biome classification.
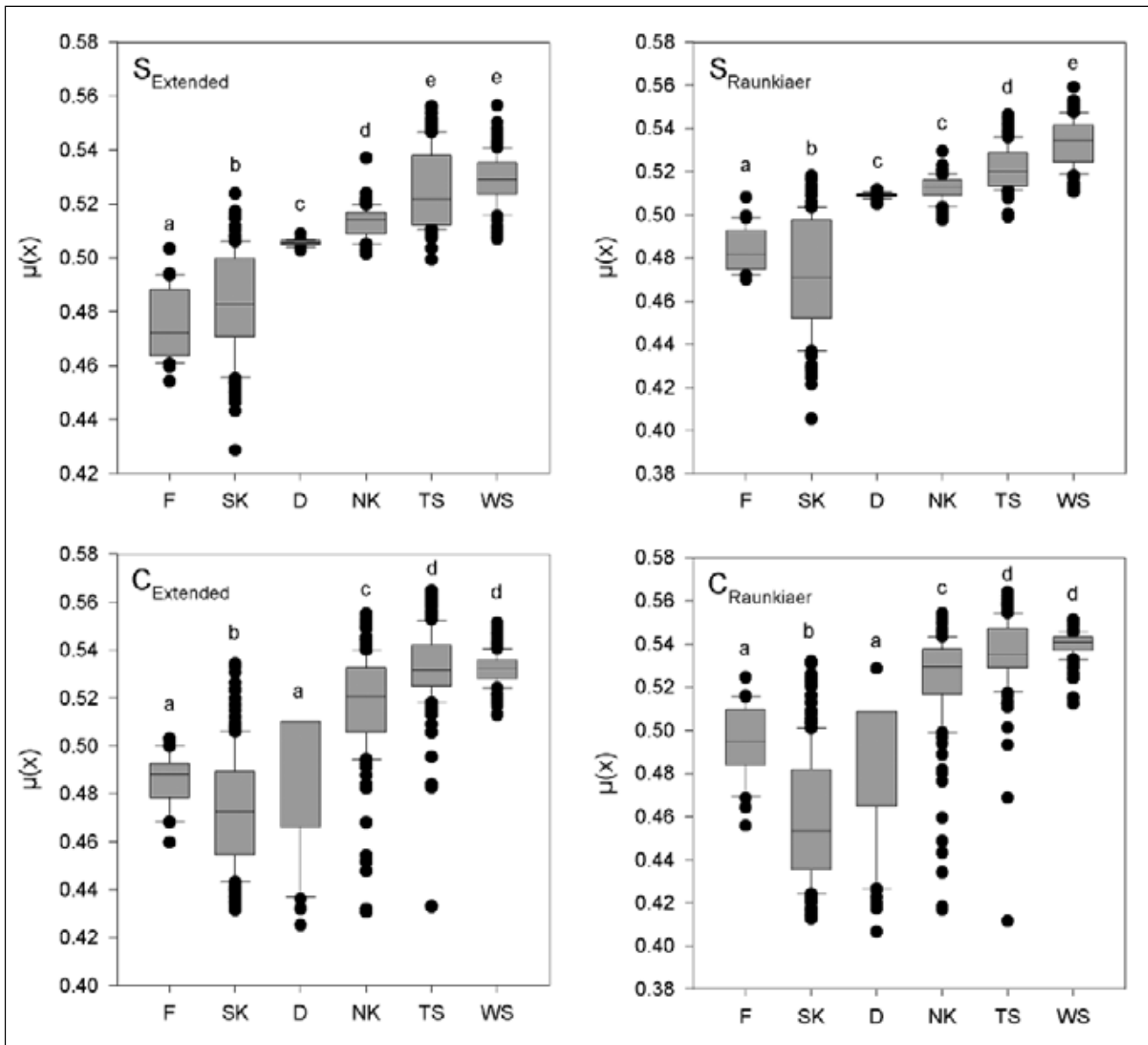
Fig. 3: Comparison of mean membership values ($\mu(x)$) per biome. Significance of differences was calculated using TukeyHSD post-hoc test. Groups with the same letters are not significantly different at the 5% level.

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