FUNCiTREE

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Trait-based models for single AFS functions

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Contents

Contents **2**

1 Functional ecology and ecosystem services **3**

2 Functional traits, tree functional groups and AF functions **5**

3 Bayesian Belief Networks: Linking functional groups and responses **6**

4 The tree-grassland interaction function **7**
4.1 AF functional groups that affect tree-grass interactions 7
4.2 Linking grassland responses to AF tree functional group 7
4.3 Functional group - environment interactions on grassland productivty 8

5 The soil fertility function **10**
5.1 Functional characeristics of AF associated with soil chemical properties 10
5.2 Linking soil responses to AF tree functional group 10

6 The fodder quality function **11**
6.1 AF functional groups related to fodder quality 11
6.2 Linking livestock preferences to fodder quality traits 11

7 References **13**

1 Functional ecology and ecosystem services

The concept of ecosystem services (ES), i.e. the contributions of ecosystems to human well-being (TEEB-Foundations 2010), has emerged from the need to integrate economic development and sustainability by bridging ecological and economic values. Currently, the interface between ecology and economics is a dynamic research area; however, the development within the specific research fields has not followed the same pace. Whereas a strong focus has been dedicated to questions about economic valuation and accounting, the assessment of ecosystems' capacity to provide ecosystem services and the identification of indicators of the critical functions that underpin service provision (the service provision function) are still major research challenges. In order to adress these challenges, it is necessary to develop comprehensive programs to monitor the services provided by different ecosystems and species (de Bello et al. 2010). The role of natural science and the scientific development of the ecological dimension in the ES paradigm are essential both for the overall theoretical progress in this cross-disciplinary research field and for the operationalization of the ES framework, which can lead to ways of using natural resources that are more compatible with life systems. Two important tasks ahead are: (1) to identify the critical and most proximate functions that sustain a particular ES and (2) to search for indicators or proxies that can describe the capacity of the natural system to maintain these functions.

In order to deal efficiently with these broad challenges, it is critical to better understand the mechanisms behind the relative effect of environmental and land-use factors, and its feedbacks to ecosystem functioning. In this context, in the last few years, ecologists are increasingly using approaches based on the functional traits of organisms, i.e. measurable characteristics of species linked to their fitness and their effects on ecosystems, as a means to address some of the most fundamental and applied questions in ecology (Díaz et al. 2007). The approaches developed in the area of functional ecology aim to characterise organisms according to traits with good correspondence to eco-physiological functions, such as those involved in carbon and nutrient acquisition, and life-history characteristics associated with reproduction and dispersal in plants. The framework, further proposes that species or individuals can be grouped according to their traits and that groups that share the same attributes are expected to have similar responses to the environment, for example strategies to cope with drought, nutrient scarcity and disturbances. Groups of species with similar trait values (attributes) can also be linked to specific effects on other organisms, through food webs and through changes in bio-geo-chemical processes that affect, for example, carbon storage and nutrient mineralisation and availability in soils, all of which have a direct link to the provision of ES. As a result, these approaches provide a more mechanistic point of view than the use of species identities alone, and allow the comparison between different ecosystems, which is necessary in order to predict the effects of different management alternatives on the provision of ES (Lavorel et al. 2007).

Studies in this field have mostly focused on trait indicators of plant growth, persistence and recruitment, but the approach has also been applied to other ecological functions, for example the characterisation of pollinating insects, soil decomposer organisms and river sediment micro-fauna. By analogy, and with a broader scope, the relationship between structural characteristics of organisms and/or organism groups and particular functions that support the provision of ES can be explored. Although differences in trait values between organisms come from various sources, which can be roughly classified as interspecific (among species) and intraspecific (among individuals within species) differences, a vast majority of the approaches followed in trait-based ecology have focused only on the former, considering only a single mean trait value for each species, thus neglecting the importance of intraspecific variability in trait values. Considering only interspecific variability assumes that intraspecific differences are much smaller than interspecific differences, but this point of view has recently been challenged by several studies that indicate that intraspecific variability can have a considerable importance (de Bello 2013) and claim for an ecological science based on individuals rather than on species. As a consequence of the bias towards a trait-based ecology focused on interspecific differences, there is a plethora of studies considering species mean trait values, while practically no study has considered intraspecific trait variability (but see Mouillot et al. 2005; de Bello et al. 2013), especially to assess the provision of ES.

FUNCiTREE made a broader application of the framework of comparative ecology using architectural and eco-physiological traits of individual trees in agro-pastoral systems to explore three key ecological response functions with a direct link to grassland productivity, soil formation and the provision of fodder. We applied the model with data from a seasonally dry agro-silvopastoral system in West Africa.

2 Functional traits, tree functional groups and AF functions

We based the analysis on data from the FUNCiTREE database on 106 individuals of 23 tree species occuring in the area of Potou (Senegal), under two different environmental conditions, in salty soils and in non-salty soils.

The trees were clustered in functional groups according to different traits, which were associated with the three selected ecological functions: grassland productivity, soil properties and fodder provision (Table 1). Traits related with grassland productivity and soil properties were measured on each individual tree, thus allowing us to take into account intraspecific variability in trait values both within and across soil classes. Individual trees were classified into Plant Functional Groups (PFG), which were built using hierarchichal clusterings based on the among-trees dissimilarities for the selected traits. In contrast, for traits related with fodder provision, i.e. indicators of nutritive quality, digestibility and toxicity, only a single value per species was considered. Given the high number of indicators measured for this function and the high levels of correlation between them, a Principal Component Analysis (PCA) to the species x traits matrix allowed to obtain two orthogonal axes: the first one was related to the digestibility of the plants and the second to its chemical composition and toxicity. Afterwards, a cluster analysis based on these PCA axes was performed to produce PFG for fodder provision.

Table 1: Traits used to group trees according to their potential to affect understorey productivity, fodder quality and soil chemistry

Grass productivity	**Soil properties**	**Fodder provision**
Specific leaf area (SLA)	Tree height	Acid detergent fiber
Maximum Leaf area index (LAI)	SLA	Acid detergent lignin
Minimum LAI	Legume /non-legume	Crude protein
Leaf phenology		Gas test value
		Neutral detergent fiber
		Soluble N
		Total P
		In vitro degradation of OM
		Tannins

3 Bayesian Belief Networks: Linking functional groups and responses

Bayesian networks (BNs) represent systems as a network of interactions between variables. They are probabilistic graphical models that represent random variables and their conditional dependencies. They are structured as nodes (variables) and their interrelationships through conditional probability tables.

Several characteristics of BNs make these models a powerful tool to assess and represent ecosystem service provision functions. First, they enable to establish relationships between characteristics of a system and functions, even when data are incomplete, which makes it possible to overcome limitations of traditional statistical models that rely on large amounts of empirical data to be built. In our case, we established the conditional probabilities of the different functional groups to produce a response on grassland productivity, on the chemical properties of the soil and on the preference of fodder by livestock (cattle, sheep and goats).

Second, conditional probability tables can be built from different data sources such as primary empirical data, data retrieved from the literature and expert opinions; and can make use of both quantitative and qualitative data. In our case, we used different data sources and quality for the functions modeled. In the case of grassland productivity and soil properties functions, we used primary data of traits and responses collected by the FUNCiTREE project. In both cases, traits and functional responses were observed at the individual tree level; therefore, the analysis could account for intra-specific variability in trait composition and responses, and for possible differential responses as a result of the interaction of trait composition and the physical environment. In the case of the fodder provision function, we used data retrieved and prepared from the CIRAD data bases on chemical analyses of Sahel tree species, and on expert opinions about the preference of the fodder by livestock.

4 The tree-grassland interaction function

4.1 AF functional groups that affect tree-grass interactions

The PFG related with the grass productivity function were based on four traits. These traits were indicators of the phenology of the tree crown (the degree of deciduousness), of the resource-use strategies (SLA and LAI) and of the size of the tree. All these traits are likely to impact the performance of the herbaceous vegetation under the tree canopy.

Based on the hierarchical clustering described above, four AF tree functional groups were identifed (Fig.1). The different features of the trees in the different PFG had important implications in their abundances on the two studied environmental conditions. For example, the deciduous strategy of trees in the PFG4, as well as their low SLA values indicated that these trees are able to undergo the rough environmental conditions associated to salty soils; consequently, 41% of the trees in salty soils were classified in PFG4, while less than 10% of the trees in other soils belonged to this group. On the other hand, the conditions of trees in the PFG3, which keep a high canopy cover during the dry season, and of those in the PFG2, with high SLA values, makes them to be much more abundant in benign conditions, where 31.7% of trees belong to PFG2 and 24.1% to PFG3 than in salty soils (12.1% and 5.7%, respectively).

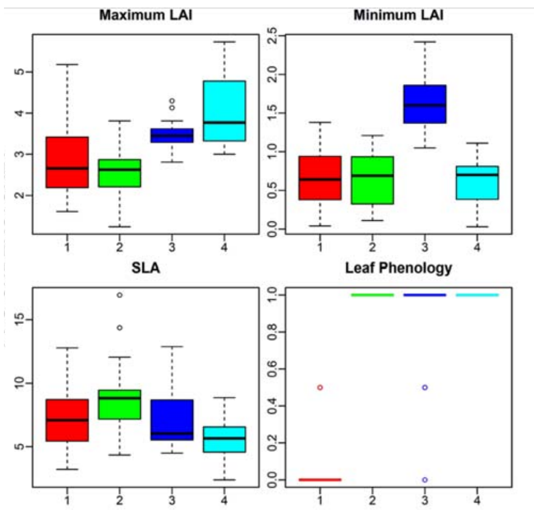

Figure 1: Mean trait values of the four tree functional groups associated with level of grassland productivity.

4.2 Linking grassland responses to AF tree functional group

The BN model was built following the assumption that the effect of the trees on the herbaceous understorey can be positive (facilitation), negative (competition) or neutral, depending on two interacting features: i) the characteristics of the tree functional group; ii) the environmental characteristics. Therefore, the final outcome of the tree-understorey interaction can be either positive or negative, depending on the balance between the magnitude of facilitative and competitive effects. According to the 'Stress Gradient Hypothesis' (Bertness & Callaway 1994; Maestre et al. 2009), facilitative effects are expected to be predominant in harsh environmental conditions and competition when resources are more abundant, but little is known about the effects produced by different functional groups.

The responses of the grassland were assessed by measuring above ground productivity, grass cover and grassland species richness in paired samples, both under the tree and in an adjacent area of grassland, beyond the influence of the tree crown. We used the Relative Interaction Index (RII; Armas et al. 2004), to quantify the net effect of the tree on these response variables. RII values can range from -1 (complete dominance of competitive interaction) to +1 (complete dominance of facilitation effects). We divided the RII value observed in the trees into 5 possible categories of grassland response, which were determined depending on the predominance of competitive or facilitation effects:

1) RII < -0.2 Strong competition
2) -0.2 < RII < -0.05 Moderate competition
3) -0.05 < RII < 0.05 Neutral effect
4) 0.05 < RII < 0.2 Moderate facilitation
5) RII > 0.2 Strong facilitation

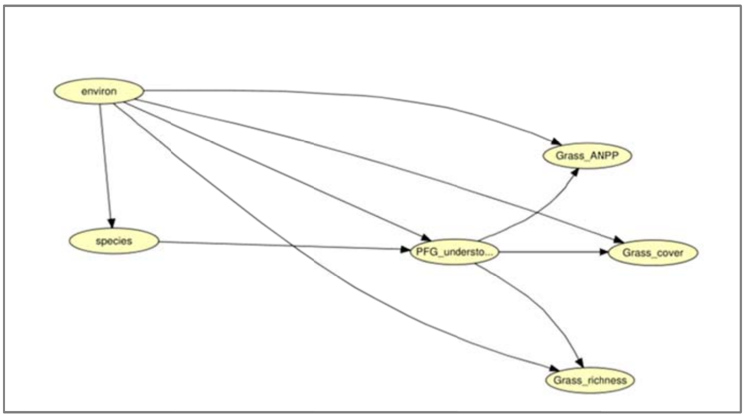

Figure XA: Bayesian Belief Network (BBN) of the effect of trees on grassland productivity.

4.3 Functional group - environment interactions on grassland productivty

Grassland productivity was affected differently by the different 'Grassland productivity' functional groups. For instance, trees in PFG2, which were mostly located in non-salty soils, had predominantly a facilitative effect on the grassland, i. e. in about 90 % of the cases, trees in this group increased grassland productivity (Fig. XBa). In contrast, trees belonging to PFG4, had either a strong facilitative effect or moderately negative effects (Fig. XBb).

The model also showed the importance of FG –environment interactions in determining the outcome of the tree-grass interaction. In our case, the kind of effect on the grassland by trees with particular characteristics depended on whether the tree occurred in salty soils or non-salty soils. For example, the trees in PFG4 had a positive effect on grassland productivity in harsh conditions (salty soils), probably because they provide a high canopy cover during the wet season, thus offering protection and increaing the productivity of the herbaceous layer. In contrast, in non-salty soils, the effect of these trees was often negative, because of the reduction in light availability under the tree canopy during the wet season (Fig. XDa and XDb). Further, the effects of PFG1, the one with maximum LAI in the dry season, also depended on environmental conditions. In non-salty soils, trees in this group had a positive effect, because they offer protection to the understorey vegetation during the dry season, and do not cast much shade during the wet season. In contrast, in salty soils, they had a more negative effect, because they do not offer an adequate shelter in the wet season.

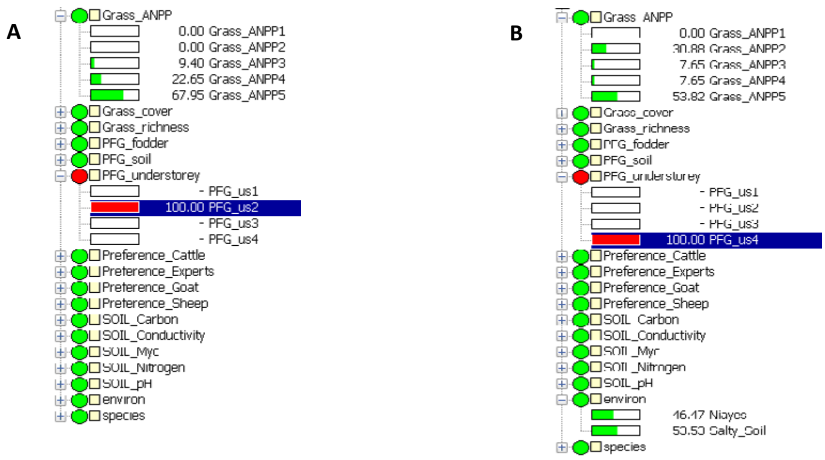

Figure XC: Image showing interactive tables in the Bayesian Belief modeling software, Hugin Expert indicating the probability of occurrences of classes of grassland response (variable Grass_ANPP) in A. Tree functional Group 2 (PFG_us2) and B: Tree functional Group 4 (PFG_us4).

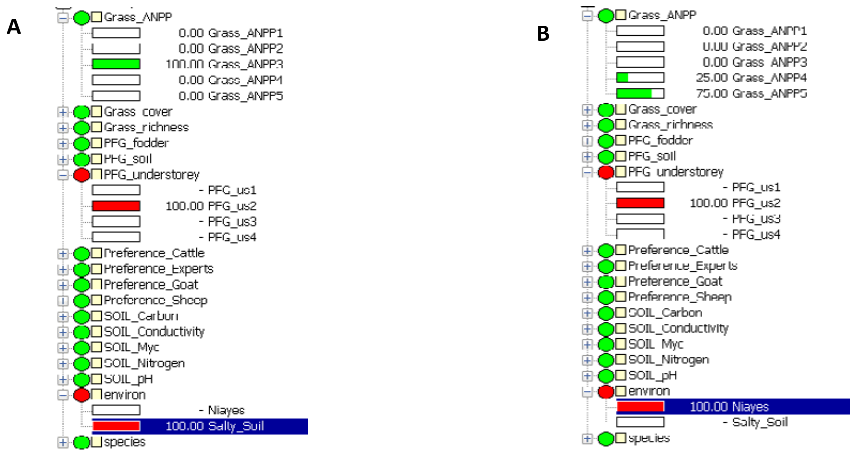

Figure XD: Image of interactive tables in the Bayesian Belief modeling software, Hugin Expert showing the probability of occurrences of classes of grassland response (variable Grass_ANPP) in A. Tree functional Group 2 (PFG_us2) and B: Tree functional Group 4 (PFG_us4).

5 The soil fertility function

5.1 Functional characeristics of AF associated with soil chemical properties

The three traits used to assess the associated of trees with soil formation processes were 1) tree height, a surrogate for biomass production and amount of litter deposition; 2) specific leaf area (SLA), an indicator of the degree of litter decomposability; and 3) whether the tree was a legume or not, a surrogate for N fixation capacity (Figure 2). Legumes, which were more frequent in non-salty soils, were classified in the PFG1. Among the non-legume species, trees in PFG2 were short and had low values of SLA, and were common in salty soils. On the other hand, trees in PFG3, which were tall and had intermediate to high SLA, were mostly located in non-salty soils.

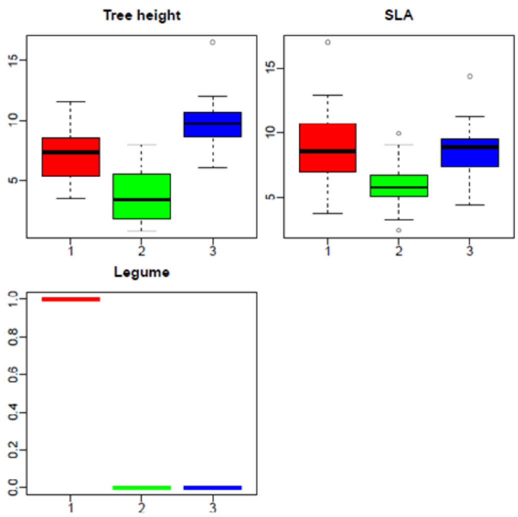

Figure 2: Mean trait values of the three tree functional groups associated with soil chemical properties

5.2 Linking soil responses to AF tree functional group

Similarly to the grassland productivity function, the BN model for the soil properties function was built following the next assumptions: i) the effect of the trees on 5 soil properties (i.e. soil pH, carbon, nitrogen, conductivity and content of mycorrhiza spores) depends on the characteristics of the tree functional group, ii) the net effect of the tree on the soil could be either positive or negative, based on the calculation of the RII, and iii) the net effect of the trees on soil properties is a function of the environment. RII values for soil responses were classified into the same 5 categories that have been described above.

The results show that trees considerably increased soil N, C and conductivity, but these effects were independent of the considered PFG and of the environment. These results are in agreement with studies in the literature and with other analyses conducted with FUNCiTREE data on the effect of trees on the soil.

6 The fodder quality function

6.1 AF functional groups related to fodder quality

The trait values in the analysis of the fodder provision function were species averages prepared from the CIRAD database prior their incorporation into the FUNCiTREE trait base; therefore intraespecific variability in trait values was not taken into account for the construction of PFG for fodder quality. We used Principal Component Analysis (PCA) to sort the species according to the trait presented in Table 1. Species were sorted into 4 areas in the ordination diagram, along a gradient of digestibility associated to PCA axis I and with content of N and tannins associated to PCA axis II (Fig. 3).

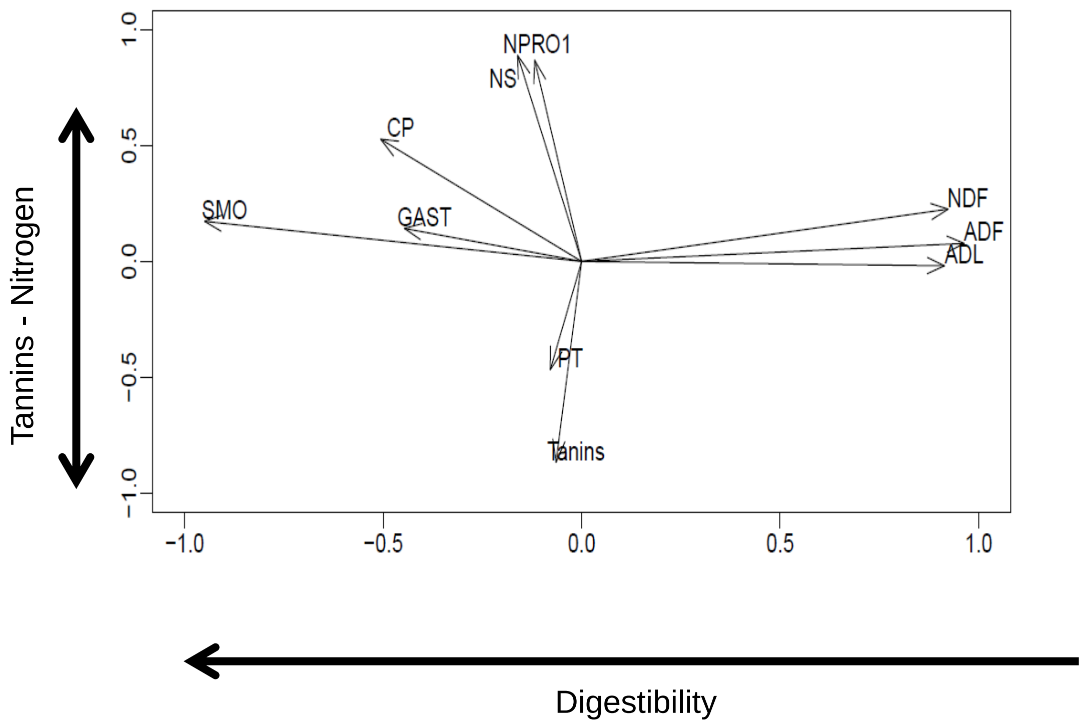

Figure 3: Ordination diagram resulting from a Principal Component Analysis (PCA) of agroforestry species based on trait values associated to forage quality.

At a second stage, the species were grouped into four PFG using hierarchical clustering. The four groups showed clear differences in the average and ranges of scores on PCA I and II (Fig. XE).

6.2 Linking livestock preferences to fodder quality traits

The BN model was built under the assumption that the livestock preferences for the different tree species depend on its functional traits. We considered the preferences of three different livestock species: cattle, sheep and goats. Based on the expert opinions about the preference of the fodder by livestock, tree species were classified into three groups according to the preference of each of the livestock species: "Highly preferred", "Average" and "Non-preferred". It is important to remark that this model differ from the others, because it did not consider the effect of the environment on the livestock preferences because neither the trait information nor the livestock preferences information was linked with environmental data.

Almost 50 % of the species in the data set belonged to PFG2, which had intermediate scores on PCA Axis 1 and low scores on PCA Axis 2. Hence, PFG2 had intermediate digestibility and high contents of tannins. Furthermore, livestock preference data show that PFG2 is highly preferred (or consumed) by goats, whereas they are to a large extent (60 %) rejected by cattle (Fig. XF). PFG4 was the second most abundant in the dataset and encompassed trees with low average digestibility values and intermediate contents of tannins and nitrogen. Species in this group are well accepted by cattle (67 % high and 33 % average preference probability, respectively), but not particularly preferred by goats (Fig. XG, HuginExpert diagram showing probability distributions). These results indicate that a large portion of the species occurring in the area have relatively low value as fodder. This was especially so for the salty soils, where PFG3, the group with the lowest contents of tannins and relatively easy to digest, was remarkably less abundant than in non-salty soils.

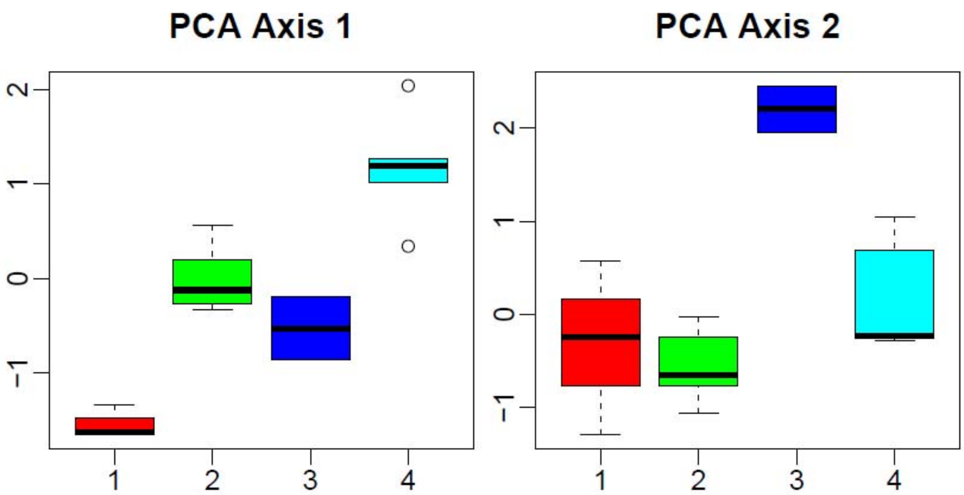

Figure XE: Mean scores on the fodder quality PCA ordingation Axis 1 and 2 in the four tree functional groups (FG) identified with hierarchical clustering. PCA Axis 1 represents a digestibility gradient and PCA Axis 2, the variability in N and tannin contents.

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Based on the principles of functional ecology, FUNCiTREE addresses the provision of multiple services of silvopastoral systems (SPS) in semi-arid regions in Africa and Central America. FUNCiTREE aims to provide farmers in the regions with a portfolio of regionally suitable tree species that are capable of providing multiple services. The project integrates theories and concepts from agroforestry and ecological science and will provide a scientifically based model for the design of modernized SPS.

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