Testing a functional type approach for modelling and understanding the relationship between structural diversity and species diversity (Work package 5, Subproject 09 of BIOTA SOUTH)

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This workpackage is divided in two parts: In the first part we developed a generic functional type model for vertebrate animal species to assess their response to changes in vegetation structure. In the second part, we developed a functional type model for herbaceous plants to assess their response to grazing.

1 Animal functional types

The response of animal species to changes in vegetation structure depends on species specific habitat requirements, but also on a variety of other traits such as the scale at which animals perceive their environment, behavioural traits and general demographic features. Here, we developed a generic population model for vertebrate species to test how these traits determine the response of species to changes in vegetation structure.

The model describes a species by a set of functional traits (traits related to spatial scale and habitat use, demographic traits, behavioural traits and dispersal related traits) and simulates the spatial population dynamics in response to vegetation structure. It consists of two steps: in the fist step a map of habitat structure is translated into a map of potential homeranges for the animals. This step considers the habitat requirements of a species. In the second step, population dynamics is simulated in the basic processes reproduction, survival and spatially explicit dispersal, considering behavioural and demographic traits of the species.

We have applied the model for assessing the sensitivity of tree nesting species to a loss of large trees due to tree logging. Tested traits were: reproductive success, lifespan, trade off between reproductive success and life span, home range size, maximum dispersal distance, degree of philopatry and survival of floaters. We found that the most influencing traits were homerange size and maximum dispersal distance, followed by the basic demographic traits reproductive success and life span. The effect of all other traits was marginal, and the main results were robust against changes in the spatial pattern of trees.

These results have two implications: First, they indicate that the "obvious" traits, large homerange, good dispersal abilities, and high population growth rate are in fact the most important ones. More subtle behavioural traits may play a role in specific cases, but are of minor importance in a broad classification. A functional classification for the response of species to a loss of trees may therefore broadly be based on these basic traits. Second, the result that large home ranges and dispersal distances are most important traits indicate that large animals and in particular birds are comparably safe under a loss of trees, whereas small animals, in particular small tree living mammals or reptiles, may be threatened. This result may contradict the general thought that large animals are more threatened by habitat loss than small species because of their higher demand of space.

The model analysis was accompanied by a literature survey to perform a functional classification of bird, mammal and reptile species in the study area, based on the traits that are used in the model. A table of traits was completed as far as literature data are available. A second literature review was done on the application of functional type approaches in animal ecology. It showed that while the functional type concept is well developed and widely applied in plant ecology, similar approaches in animal ecology are mostly restricted to the concept of feeding guilds. A further development of the functional type approach in animal ecology may be challenging, but highly valuable.

2 Plant functional types

We developed a dynamic plant functional type model specifically for herbaceous vegetation, to understand the role of functional traits for the response of plants to grazing.

Plants are described by 6 basic functional traits (life span, seed bank strategy, seed mass, specific leaf area, plant height and plant diameter) (Table 1) from which 7 further traits are derived (germination rate, seed survival, growth rate, palatability, reproductive allocation, seed number, dispersal distance) following known positive relationships or trade offs. These traits were selected to include traits that are considered important for a plant's response to grazing (based on a literature survey) and all important demographic traits (Figure 1). The 6 basic traits were assembled to 26 PFTs (Figure 2), excluding those that do not occur in the Kalahari vegetation (following results of WP9.4) or that contradict well known trade offs.

The model is spatially explicit and simulates the life cycle of PFTs in yearly time steps. Individual growth is simulated in an explicit submodel on a finer time scale, including competition between plants on a local scale. We tested the effect of grazing on the abundance of PFTs by dividing grazing in two components: (a) "grazing" itself; individual plants are reduced in size but survive, and (b) "disturbance"; individual plants are killed. As the model does not result in coexistence of the PFTs, we accomplished a basic analysis with all PFTs with an analysis of dominance rank patterns, where we remove stepwise the most abundant PFT from the model.

The analysis allowed the identification of important and advantageous traits both in general and in the response to grazing: In the scenario without grazing, a high growth rate (correlated to SLA) and perennial lifeform were the most important traits that determined dominance (the first 4 dominance ranks had a large SLA, the first 7 ranks were perennials, Table 2). This result is not surprising, as a high SLA is in the model only traded off by palatability, and everything else being similar, a PFT with a high SLA is superior in the ungrazed scenario. Perennials perform better, as they are less dependent on recruitment in the undisturbed competitive environment. In the response to grazing, plant size and SLA (being traded off by palatability) were the most important traits. In simulations with all PFTs (Figure 2), the dominant PFTs were substituted by PFTs that had exactly the same traits, but were smaller. In the dominance hierarchy (Table 2), PFTs with a positive response to grazing were either small in height and had a medium to large SLA, or they had a small SLA and were of medium or large in height. This demonstrates two strategies of grazing avoidance: being small or being unpalatable. A tolerance strategy, having a high SLA and thus a high regrowth capability, did not emerge in the model. Grazing alone did also not promote the dominance of annuals. However, strong disturbance shifted the dominance patterns from perennials to annual plants. While these main trends of grazing effects are intuitively understood, it is interesting that besides no other traits had a strong influence on the response to grazing (e.g. seed bank persistence and seed size). This improves a previous version of the model without explicit growth of plants.

In comparison to field data, the model results match general trends of how functional traits respond to grazing well (e.g. selection of small plants, dominance of annuals under disturbance). However, the model does so far not reproduce the realistic distribution of the PFTs along a grazing gradient in the Kalahari correctly. This contrast between general validity and mismatch in the specific case indicates that the model captures general characteristics of a grazed system well, but it misses specific features of the southern Kalahari system, e.g. specific processes that occur under exceptionally dry conditions, or plant traits that are not included in the model. A further development and adjustment of the model will therefore help understanding system specific influences on the response to grazing.

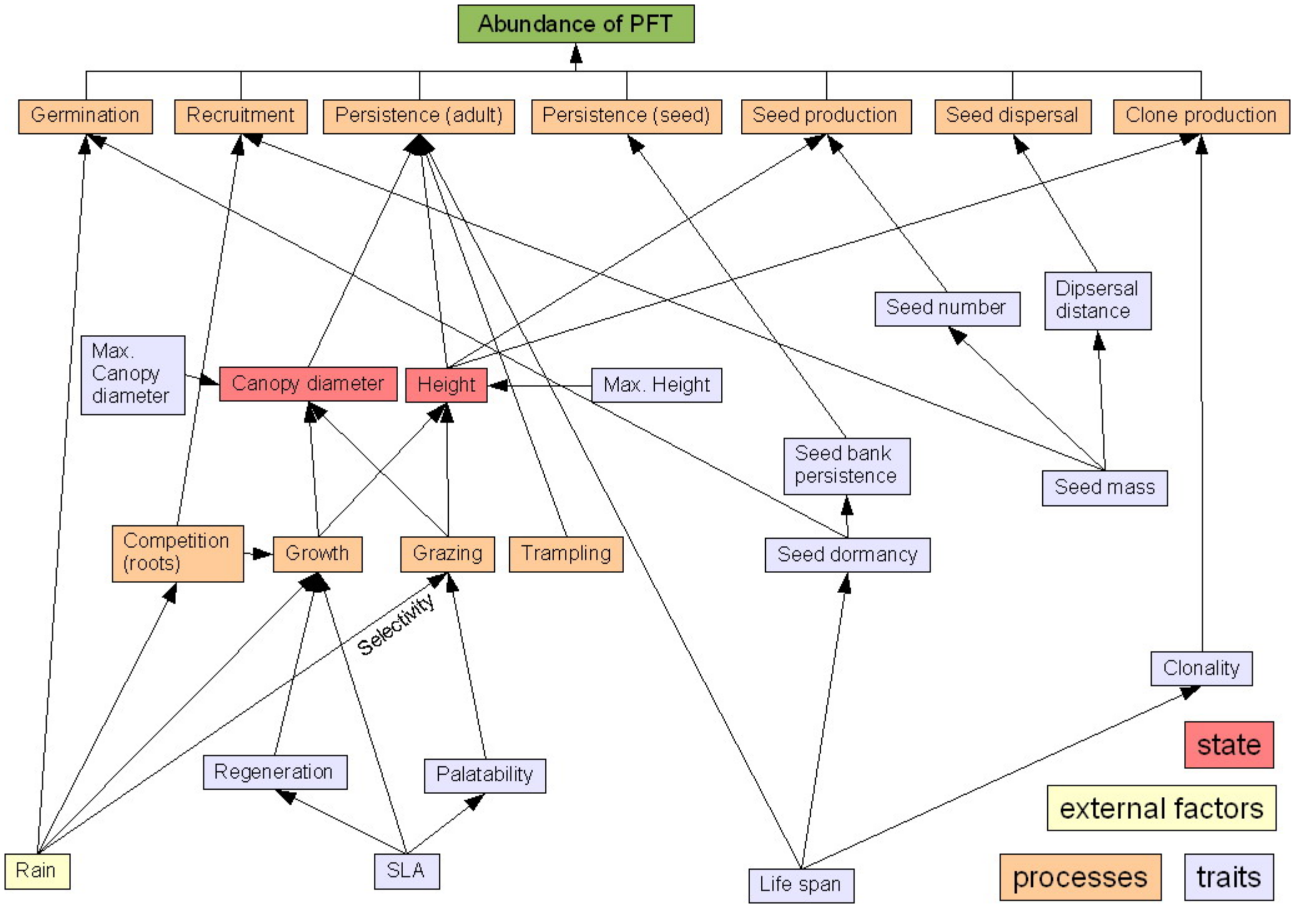

Figure 1: Causal relationships between plant traits, external factors and population processes as assumed in the model.

Life span	Seed bank strategy	Seed mass	SLA	Height	Canopy diameter
annual	transient	S	S	S	S
perennial	low persistence	M	M	M	M
	high persistence	L	L	L	L

Table 1: The 6 basic functional traits and the values they can take.

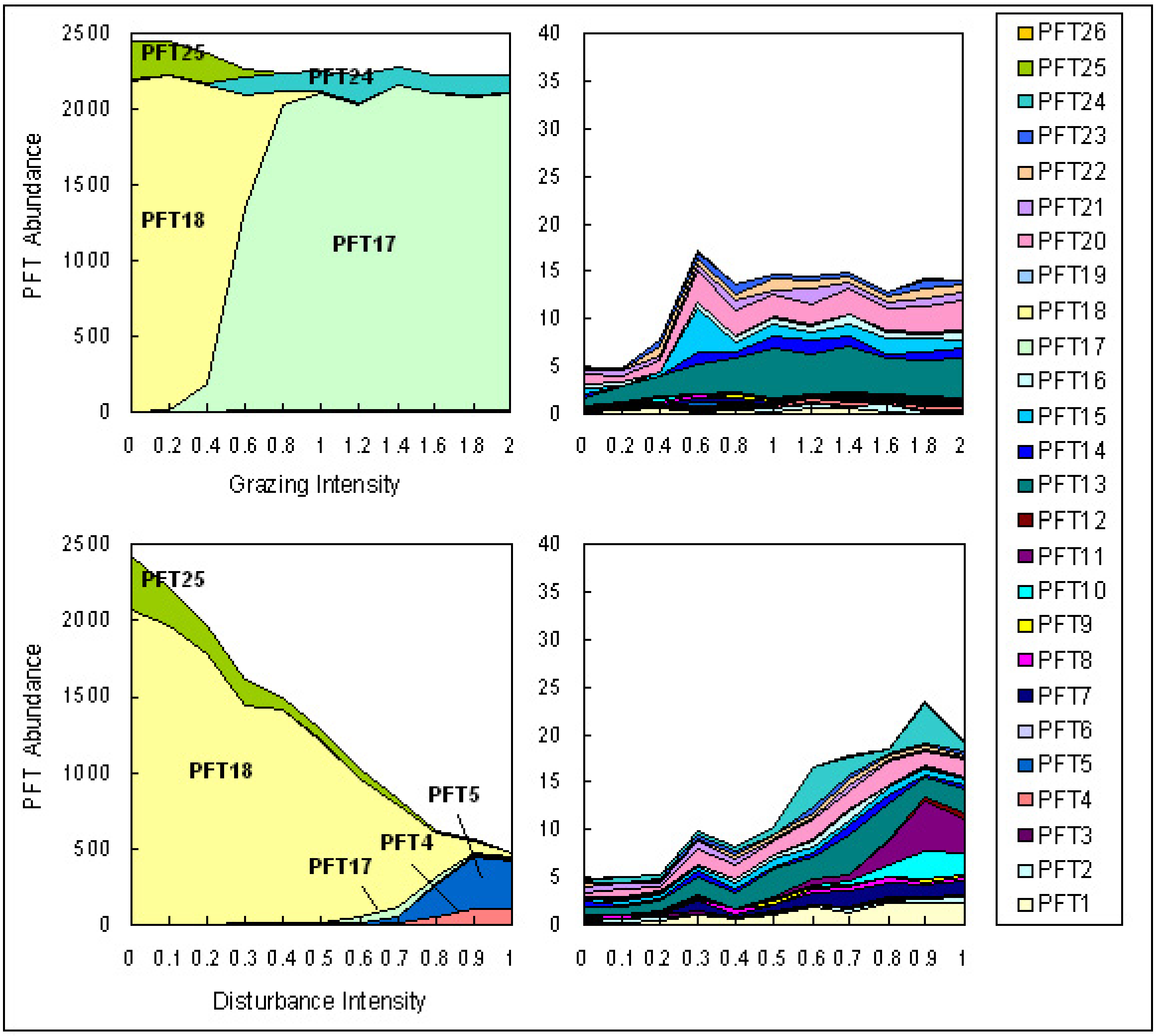

Figure 2: Abundance of PFTs in relation to grazing (top) and disturbance (bottom), as resulting from the model analysis ("grazing" reduces the size of a plant, "disturbance" kills a plant). Left: dominant PFTs. Right: rare PFTs at enlarged scale of y-axis. In the ungrazed scenario (x-axis=0), the system is dominated by PFT 18, a medium sized perennial with high SLA (fast growth rate), and by PFT 25, having the same features, but a higher seed bank persistence and lower germination rate. As grazing intensity increases these types are substituted by PFTs 17 and 24 that share the same traits, but are smaller in height. Annuals are not abundant throughout. Under increasing disturbance, PFTs 18 and 25 stay dominant up to medium disturbance intensity. Only at high disturbance intensity, two annuals (PFTs 5 and 4) substitute the perennials. These share the same traits as PFTs 18 and 17, indicating the general superiority of these types.

PFT No.	Life span	Seed bank strategy	Seed mass	SLA	Height	Canopy diameter	Dominance Rank	Response to grazing	Response to disturbance
1	annual	low persistence	S	M	M	S	19	-	0
2	*annual*	*low persistence*	*M*	*S*	*M*	*M*	*15*	*+*	*0*
3	annual	low persistence	M	M	S	S	25	0	0
4	*annual*	*low persistence*	*M*	*L*	*S*	*M*	*12*	*++*	*++*
5	annual	low persistence	M	L	M	M	11	0	++
6	*annual*	*low persistence*	*L*	*M*	*S*	*L*	*22*	*++*	*+*
7	annual	high persistence	S	M	M	S	25	-	++
8	annual	high persistence	M	S	M	M	16	-	+
9	annual	high persistence	M	M	S	S	26	0	+
10	*annual*	*high persistence*	*M*	*L*	*S*	*M*	*14*	*++*	*++*
11	annual	high persistence	M	L	M	M	13	-	0
12	*annual*	*high persistence*	*L*	*M*	*S*	*L*	*21*	*++*	*++*
13	perennial	transient	S	S	L	L	8	-	0
14	*perennial*	*transient*	*M*	*S*	*M*	*M*	*7*	*+*	*- -*
15	*perennial*	*transient*	*M*	*S*	*L*	*L*	*5*	*+*	*- -*
16	perennial	transient	M	M	S	S	17	-	-
17	*perennial*	*transient*	*M*	*L*	*S*	*M*	*3*	*+*	*-*
18	perennial	transient	M	L	M	M	1	-	-
19	*perennial*	*transient*	*L*	*M*	*S*	*L*	*20*	*++*	*- -*
20	perennial	low persistence	S	S	L	L	9	-	- -
21	*perennial*	*low persistence*	*M*	*S*	*M*	*M*	*10*	*+*	*- -*
22	perennial	low persistence	M	S	L	L	6	-	- -
23	*perennial*	*low persistence*	*M*	*M*	*S*	*S*	*23*	*+*	*++*
24	*perennial*	*low persistence*	*M*	*L*	*S*	*M*	*4*	*+*	*-*
25	perennial	low persistence	M	L	M	M	2	-	-
26	perennial	low persistence	L	M	S	L	18	0	- -

Table 2: PFTs in model analysis: Traits, dominance rank in ungrazed scenario, response to grazing and response to disturbance. Dominance ranks were determined by stepwise removing the most abundant PFT from the model. Responses to grazing and disturbance are expressed as increasing or decreasing dominance by 1-4 ranks (+/-), >4 ranks (++/- -) or indifferent response (0). PFTs with a positive response to grazing are *emphasized* (all have either Height S or SLA S). PFTs with a positive response to disturbance are mostly annuals.