Concluding remarks on Namib Fairy Circles, their origin, phenology, ecology, dynamics, ecosystem function and similarities to other vegetation patterns

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Chapter 12   Conclusions

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This book offers diverse and comprehensive information on almost all aspects related to the core topic "fairy circles of the Namib Desert", as well as information on other types of regular vegetation patterns. The organisms associated with these patterns, ecosystems, geology, geomorphology, soil properties, functional interactions and ecosystem services are discussed by a team of 15 scientists from varied disciplines with up to 42 years of experience and competence based on studies and careful field observations in all geographical parts of the Namib Desert in Angola, Namibia and South Africa.
What are the main take-home messages resulting from the information presented, and what are some of the main research questions for future investigations?

1) The development of the various regular vegetation patterns in the Namib Desert region is controlled by a broad diversity of drivers. Interestingly, in only a few cases (e.g. clonal growth rings), the plants are the main drivers. In the majority of cases, plants play a minor or secondary role. Regular, circular gaps in the vegetation are mainly caused by the foraging and nesting behaviours of various organisms, especially termites and, rarely, ants. There is abundant evidence that the fairy circles of the Namib Desert are formed by the action of sand termites *Psammotermes* spp. over most of the Namib and by a new species of harvester termites recently discovered in the northernmost Namib of coastal Angola. Regular islands of vegetation are principally controlled by the way various animals have influenced edaphic properties. Some of these vegetation features are due to animal activities long ago that are now no longer occurring (e.g. soil alterations by burrowing mammals). Banded vegetation that follows the topographical contour line is strongly controlled by soil properties and surface hydrological processes. In some types of contour-parallel banded vegetation, plants also play an important role, and aeolian sedimentation is sometimes involved.

The hypothesis that fairy circles are formed by "self-regulation" of the vegetation, as a consequence of positive and negative feedbacks among the plants and the movement of soil water over distances of many meters, is not supported by available evidence. Termites, however, exert the strongest control on the availability of soil water through their direct removal of transpiring plants in the vicinities of their colonies. Through this process, the termites ensure the conservation of soil water required for colony survival and, at the same time, create the bare patches known as fairy circles. The spatial regularity of those structures is best explained by competition and interactions among neighbouring termite colonies.

Despite the theoretical motivation to identify a universal, underlying mechanism responsible for diverse vegetation patterns ranging from circular vegetation gaps to isolated vegetation patches, our research provides evidence for the operation of a diverse array of processes that involve animals, plants, and soil properties in arid to semi-arid environments. Some of these processes interact, and their complexity requires further detailed investigation.

2) Why does ecosystem engineering by organisms play such an important role within the arid ecosystems of the Namib Desert region? One apparent reason may simply be the high visibility of such changes in an arid environment. In dryland environments, even minor alterations in environmental conditions can amplify and accentuate other physical and biotic responses.

Examination of the structures engineered by social insects during times of extreme drought periods spanning several years or even a decade reveals the ability of social insects to survive such extreme periods. This could have evolved due to the main effects of the engineered ecosystems enabling the causative organisms to survive better than others and to expand their distribution deeper into hyperarid regions. In fact, even after ten years of well below average annual rainfall, the colonies of harvester termites in heuweltjies in the northern Richtersveld have remained active, as indicated by the collection of plant biomass by the termites and the production of frass. Similarly, after years of drought, even a small rainfall enables a large proportion of sand termite colonies in fairy circles to become active because they survived longer than would have been possible without the engineered ecosystem that was responsible for conserving scarce soil moisture resources. In both cases, heuweltjies and fairy circles, the engineered ecosystems can store rainwater over extended periods of drought.

3) While survival during extreme drought may be an important selective factor in evolution, one important ecosystem function of the engineered ecosystems is readily observed in an average year. The water-storing function of the bare patch within fairy circles buffers the extremely abrupt amplitudes of soil moisture to the advantage of many organisms. For many organisms and ecosystem processes, this simply expands the length of activity during the seasons of a year by weeks or months. For many others, the stored moisture even turns an ephemeral ecosystem with rare pulses of life into a permanently habitable one. This is obviously the case when we look at the grasses in the perennial belt, the halos and their extensions into continuous grassland between fairy circles. If we also take trophic interactions into account, many predators like aardvark are enabled to live permanently in a hyperarid desert with ephemeral rainfalls based on the combined water and biomass resources provided by fairy circles. Consequently, the engineered ecosystems expand the range of many species deeper into arid regions.

4) Fairy circles and the heuweltjies in Namibia and South Africa create new niches and the formation of complex, new biocoenoses. An example is the frequent parasitic utilisation of the bare patch of fairy circles in the Giribesvlakte by the ant *Carebara kunensis.* These ants build their nests within the bare patch and probably take advantage of the stored soil moisture. The ants are–at least during late summer–the preferred food of tenebrionid beetles. In the case of heuweltjies, colonies of the termite *Microhodotermes viator* create novel environments that are rich in nutrients and calcium carbonate within nutrient-poor landscapes that are almost free of calcium carbonate. Numerous plant species that do not occur in the surrounding landscape occur almost exclusively on heuweltjies.

5) The localised manipulation of environmental properties generates a new type of landscape: instead of a homogeneous uniform habitat, a mosaic is created with two contrasting types of environments consisting of specialised compartments next to each other. Key resources, including soil moisture (in the case of fairy circles, heuweltjies and *Macrotermes* mounds) and nutrients (in the case of heuweltjies and *Macrotermes* mounds), are constantly available in the one compartment but absent or rare for most of the time in the other adjacent compartment. The termite-driven spatial redistribution of water and nutrients turns the landscape into a pattern of steep gradients within which organisms must find their preferred combination of environmental parameters. Many organisms utilise both compartments for different services. For example, colonies of the Whistling Rat *Parotomys brantsii* may establish their warren inside a heuweltjie, but they forage primarily in the surrounding landscape matrix. The organismic, hydrological and soil chemical interactions between the core areas of the engineered system and the surrounding matrix should be studied in detail in order to fully understand the ecological functioning of the integrated landscape system. A typical question regarding fairy circles might be: how is the loss of a few sacrificed square meters of biomass production within the bare patch related to the overall ecosystem gain caused by the long-term storage of moisture beneath the bare patch and longer biomass production in the perennial belt and the halo?

6) Perhaps the most important open questions are related to the behaviour of the insects within engineered ecosystems. Why do sand termites exempt the grass tussocks of the perennial belt from their foraging? They do not attack the perennial belt, even though they forage on plants on either side, in the bare patch and the matrix. Similarly, the details of reproduction and survival during prolonged droughts require more in-depth research.