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Inselberg vegetation and the biodiversity of granite outcrops

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Abstract

Granite inselbergs occur as mostly dome-shaped rock outcrops in all climatic and vegetational zones of the tropics. Consisting of Precambrian rocks, they form ancient and stable landscape elements. Due to harsh edaphic and microclimatic conditions, the vegetation of inselbergs differs markedly from those of the surroundings. Well defined inselberg habitats (*e.g.* cryptogamic crusts, rock pools, monocotyledonous mats, ephemeral flush vegetation) can be distinguished based on physiognomy. Plant diversity of inselbergs is influenced by both deterministic processes and stochastic environmental disturbances. The latter promote higher species richness due to the prevention of competitive exclusion. Considerable regional differences in floristic composition, life forms and species diversity exist concerning both the vegetation of whole inselbergs as well as those of individual habitats.

Introduction

Introduced by the German geologist Bornhardt (1900), the term "inselberg" has achieved general acceptance in international literature. As solitary, usually monolithic mountains or groups of mountains, they rise abruptly from the surrounding plains (Fig 1). Consisting of Precambrian granites and gneisses, inselbergs are old landscape elements that may possess an age of more than 50 million years. Bremer & Jennings (1978) and Thomas (1994) provide detailed surveys of their geomorphology. Inselbergs are widely distributed on the old crystalline shields and occur particularly in tropical and subtropical regions but can also be found in temperate zones (*e.g.* southeastern USA, southwestern Australia). Due to harsh edaphic (*i.e.* more or less devoid of soil cover) and microclimatic (*i.e.* high degree of insolation and evaporation rates) conditions, the vegetation of inselbergs differs markedly from that of the surroundings. In contrast to their temperate counterparts (for surveys of literature, see: Australia; Ornduff 1987; Hopper 1992: USA; Quarterman *et al.* 1993), tropical inselbergs have not yet attracted many biologists. In North America and Australia the interest in rock outcrop vegetation is well established and consequently there has been an impressive number of ecological studies, including reproductive ecology (*e.g.* Hopper 1981; Wyatt 1983), competition (*e.g.* Sharitz & McCormick 1973; Ware 1991) and speciation (Hopper & Burgman 1983; Moran & Hopper 1983). Apart from regional, rather descriptive studies for tropical inselbergs (*e.g.* Adjanohoun 1964; Bonardi 1966; Fleischmann *et al.* 1996; Granville 1978; Hambler 1964; Ibisch *et al.* 1995; Porembski 1995; Porembski *et al.* 1994, 1996a; Reitsma *et al.* 1992; Richards 1957; Sarthou 1992; Villiers 1981), comparative analyses of their vegetation are rarely available.

Since 1991, the vegetation of African and South American inselbergs has been the focal point of research at the Botanical Institute, University of Bonn. Within the frame of this project, primary emphasis has been both upon a comparative floristic analysis of tropical inselbergs and on the identification of ecological factors responsible for regulating the species richness of inselberg plant communities. The objective of the present paper is to provide a general overview of plant communities on tropical inselbergs in combination with some comments on the relation between regional floristic richness and species numbers on inselbergs.

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Flora and Vegetation of Inselbergs

Floristically, inselbergs in different geographical regions are clearly distinct. Apart from families that are of certain importance in regard to species number on inselbergs throughout the tropics (*e.g.* Poaceae, Cyperaceae, Rubiaceae), there are also region-specific families. For details on temperate inselbergs see Ornduff (1987), Hopper (1992) and Quarterman *et al.* (1993).

- **African inselbergs:** Fabaceae, Scrophulariaceae and Lentibulariaceae belong to the most species- rich families. The percentage of endemics is comparatively low. Therophytes are the predominant life form. Floristic differences are low on a local scale (low β-diversity).
- **South American inselbergs:** Melastomataceae, Orchidaceae, Cactaceae and Bromeliaceae are the most species-rich and characteristic families. The percentage of endemics is high. Phanerophytes are the predominant life form, whereas therophytes are far less important. Local floristic differences vary greatly (high β-diversity).
- **Tropical Asian inselbergs:** These are particularly well represented on the Indian subcontinent (Krebs 1942). However, information about the floristic composition of their vegetation is very sparse (Bharucha & Ansari 1962; Willis 1906). From consideration of these works and of several local floras (*e.g.* Matthews 1991), it can be assumed that the vegetation of Indian and Ceylonese inselbergs is close to their African counterparts at the family and genus level.

The vegetation of granite outcrops harbours a high percentage of highly adapted functional plant groups.

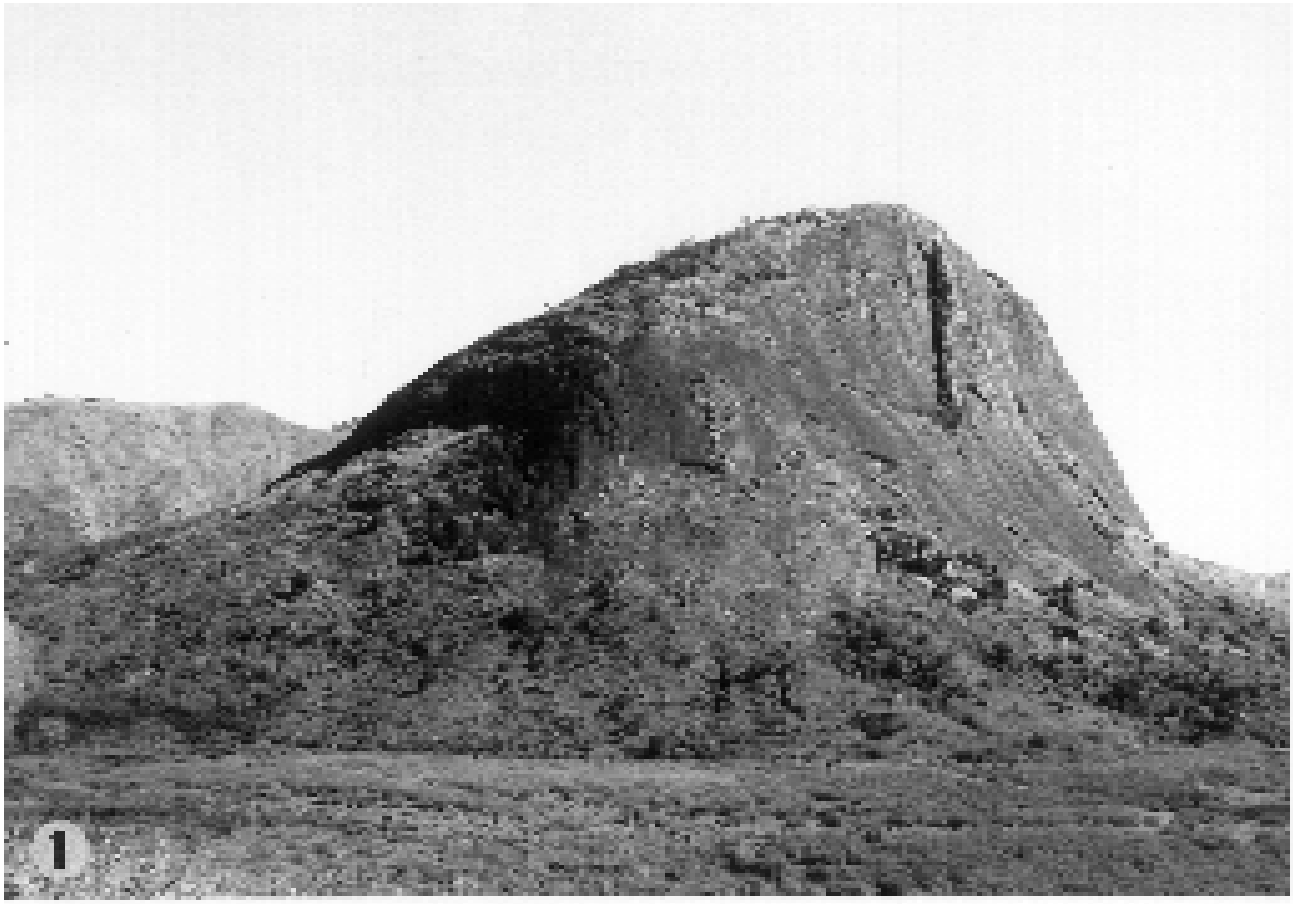

Figure 1. Dome-shaped granite inselberg in Brazil (Minas Gerais, near Camponario).

Above all, poikilohydric vascular plants (*i.e.* "resurrection plants", providing many examples of convergently developed taxa) are exceptionally well represented. Additional quite typical plant groups are succulents (Barthlott & Porembski 1996) and carnivorous plants (Seine *et al.* 1995).

Inselbergs form isolated insular ecosystems that host a vegetation consisting of physiognomically defined and well delimited habitats. Most characteristic are cryptogamic crusts, seasonally water-filled rock pools, monocotyledonous mats, ephemeral flush vegetation and wet flush vegetation. In the following, short characteristics of these habitats are given. A more detailed description is in preparation.

Cryptogamic crusts

Exposed rock surfaces are almost completely covered by either specialized cyanobacterial lichens (typically *Peltula* spp) or cyanobacteria (frequently *Stigonema* spp and *Scytonema* spp; Büdel *et al.* 1994), which are responsible for the characteristic brownish or greyish colour of inselbergs. In seasonally dry, savanna regions, cyanobacterial lichens dominate on granite outcrops, whereas under rain forest climates the rocky slopes are commonly covered by cyanobacteria. Particularly where seepage water is available, moss cushions (in West Africa, frequently *Bryum arachnoideum*) may establish (Frahm & Porembski 1994).

Seasonally water-filled rock pools

These pools, water-filled after rainfall, soon dry out if not replenished by subsequent rain, and form temporal habitats. Short-lived herbs predominate. Besides species which are otherwise widespread on marshy ground (*e.g. Cyperus* spp, *Ludwigia* spp), there are specialists which are restricted to this habitat both on tropical and extra-tropical rock outcrops. Prominent examples are richly represented within the Scrophulariaceae, such as the Namibian *Chamaegigas intrepidus*, *Amphianthus pusillus* (southeastern USA) and species belonging to the genera *Lindernia* (*e.g. L. monroi* and *L. conferta*, Zimbabwe), *Dopatrium* (*e.g. D. longidens*, West Africa; Fig 2), *Glossostigma* (*e.g. G. drummondii*, Australia). Interestingly, there is a high percentage of poikilohydric species amongst these. Widespread on East African inselbergs are geophytic waterplants of the genus *Aponogeton* (*e.g. A. stuhlmannii*, Zimbabwe). Characteristic but frequently overlooked are geophytic *Isoetes* species (*e.g. I. nigritiana*, West Africa) that have also been recorded from extra-tropical inselbergs, like *I. melanospora* (Georgia, USA) and *I. australis* (Australia). These terrestrial species can be considered to be Gondwanan elements which have only

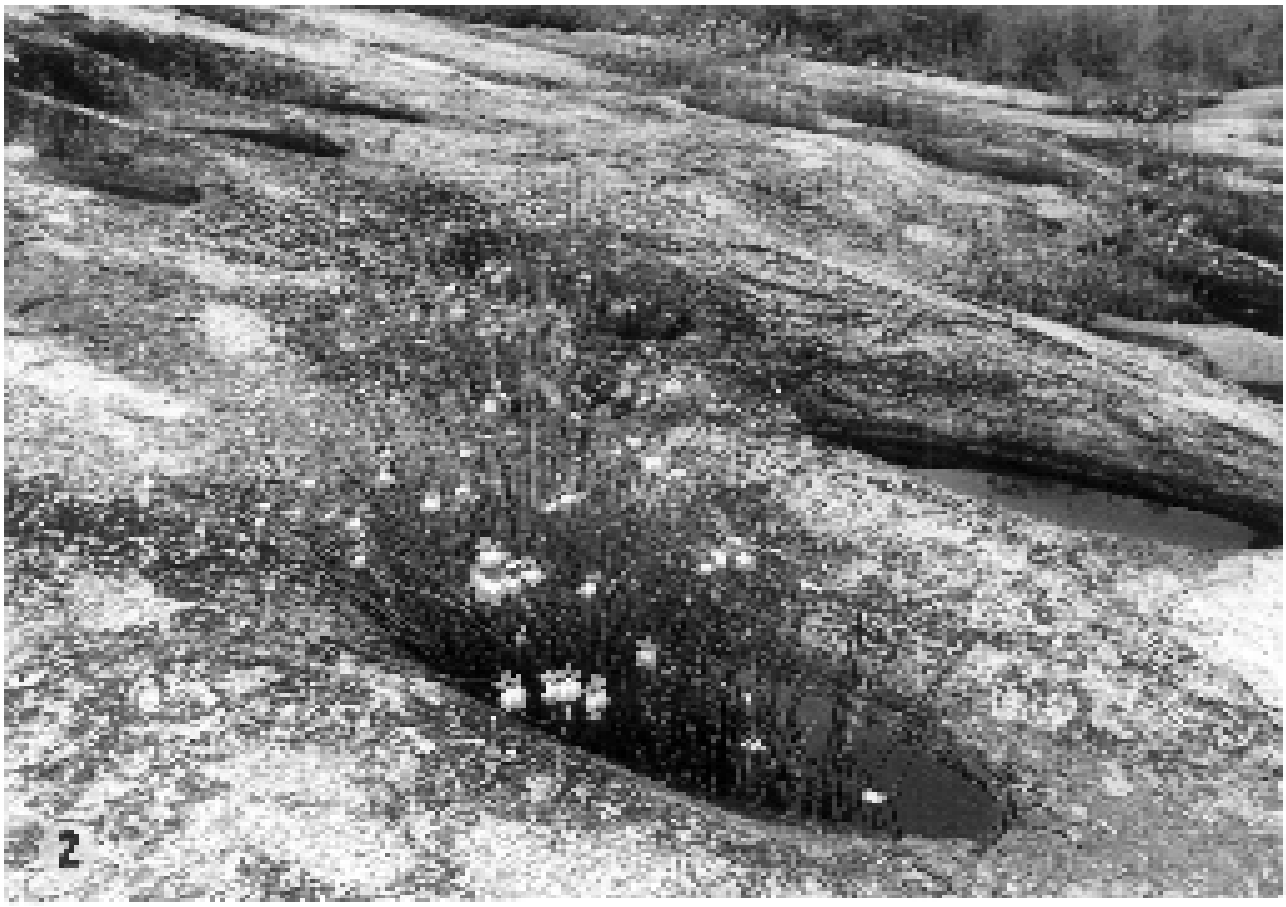

Figure 2. The Scrophulariaceae *Dopatrium longidens* is a characteristic colonizer of seasonally water-filled rock pools on West African granite outcrops. Photograph by Nadja Biedinger.

little or no long-range dispersal ability (Taylor & Hickey 1992).

Monocotyledonous mats

Soil cover is usually absent. However, a substrate mainly consisting of decaying plant material is present. Carpet-like mats formed by Bromeliaceae, Cyperaceae and Velloziaceae cover even steep rocky slopes (Fig 3). In tropical Africa and Madagascar, Cyperaceae dominate (*Afrotrilepis* in West Africa; *Coleochloa* in East Africa and Madagascar) and Velloziaceae (Xerophyta) sometimes attain the status of co-dominants. On neotropical inselbergs, Bromeliaceae (*e.g. Pitcairnia* spp, *Dyckia* spp, *Vriesea* spp) and Velloziaceae dominate, whereas Cyperaceae (*Trilepis* spp) are of minor importance. On granite outcrops in southwestern Australia, several poikilohydric species of the genus *Borya* (*e.g. B. constricta, B. sphaerocephala*) form dense mat-like stands on exposed slopes. Mat-forming Cyperaceae and Velloziaceae possess convergently developed morphological (treelet-like habit), anatomical (roots possessing a velamen radicum; Porembski & Barthlott 1995), and physiological (poikilohydry) adaptations in order to withstand the harsh ecological conditions on inselbergs. Remarkably, most mat-forming species host a highly specific set of epiphytic orchids (*e.g. Polystachya microbambusa* on *Afrotrilepis pilosa* in West Africa).

Apart from monocotyledons, only a few other groups of vascular plants occur as mat formers on inselbergs, for example the poikilohydrous shrub *Myrothamnus* (*M. flabellifolia* in East Africa; *M. moschata* in Madagascar) and a number of likewise poikilohydric species of the fern genus *Selaginella* (*e.g. S. niamniamensis, S. dregei* in East Africa; *S. convoluta, S. sellowii* in Brazil).

Ephemeral flush vegetation

This term was introduced by Richards (1957) and denotes a vegetation type developing at the base of steep slopes over thin soil where water continuously seeps during the rainy season. Poaceae and Cyperaceae make up the largest part of the phytomass. Most striking are tiny ephemerals with members of Eriocaulaceae, Xyridaceae, Burmanniaceae and carnivorous plants (Fig 4; Droseraceae and Lentibulariaceae; *Utricularia, Genlisea;* Seine *et al.* 1995). In tropical Africa, this community is especially well developed (*i.e.* most rich in species) on inselbergs situated in savanna zones (Dörrstock *et al.* 1996).

Wet flush vegetation

This occurs on inclined, bare rocky slopes where water flows continuously during the rainy season. Typical are small-sized annuals, in particular *Xyris* spp and *Utricularia* spp, which are attached to cyanobacterial

Figure 3. Mat-forming monocotyledons (here a bromeliad *Encholirium* sp) are a typical element of the vegetation of tropical inselbergs. Photograph by Nadja Biedinger.

crusts. Occasionally, small patches of mosses can be found which provide establishment sites for other vascular plants. This community develops best under humid tropical climates.

Despite fundamental floristic differences, the physiognomy of plant communities on inselbergs remains largely unchanged throughout the tropics. Inselbergs located in temperate regions are very similar to their tropical counterparts in regard to habitat composition. However, a major difference is evident in the widespread occurrence of monocotyledonous mats on tropical outcrops and their near absence from temperate inselbergs. The reason for this distinction is not clear yet. Presumably, climatic conditions (*i.e.* low temperatures) are responsible for the absence of slightly succulent (*e.g.* Bromeliaceae) or poikilohydric monocotyledons.

Species Diversity of Plant Communities on Inselbergs

Traditionally over the past, islands have played a crucial role in ecological studies designed to achieve a better understanding of those factors influencing the species richness of habitat fragments. Though the bulk of scientific interest was directed to oceanic islands, naturally occurring continental island biotas may provide even better opportunities (*e.g.* because of less anthropogenic interference) for such studies. Due to their worldwide distribution, granitic outcrops offer excellent venues for comparative phytogeographical studies as well as for research on the controlling factors of species richness in isolated plant communities. Within the frame of this paper, consequences of abiotic influences and implications of biotic interactions for the diversity of the vegetation of inselbergs will be examined (for more details see Porembski *et al.* 1995, Porembski *et al.* 1996b).

Seasonality promotes higher species diversity

Observations on inselbergs in the Ivory Coast have revealed considerable habitat-specific differences in both alpha (*i.e.* the number of species) and β-diversity (*i.e.* the degree of change in species diversity along a transect or between habitats; Magurran 1988) between *Afrotrilepis* mats extending over large areas of rock and ephemeral flush communities which usually cover only a few square meters. In contrast to the almost monospecific monocot mats, which are dominated by the highly competitive Cyperaceae *Afrotrilepis pilosa* (with stems more than 1 m high, attaining an age of several hundred years), ephemeral flush communities may harbour several

Figure 4. Tiny annuals and carnivorous species (*Drosera indica*) are the characteristic components of ephemeral flush communities on tropical inselbergs (Benin, West Africa). Photograph by Nadja Biedinger.

dozens of tiny ephemerals. Each year, with the onset of the first rains in the rainy season, the component species of the latter community must establish themselves anew, leaving much room for stochastic events. It is this abiotically driven dynamic between dry and rainy season that may prevent competitive exclusion, and therefore guarantees the persistence of a highly diverse plant community. The bulk of ephemeral flush species is very small (*i.e.* less than 15 cm in height), and most species are generally considered as weak competitors (*e.g.* the carnivorous plants). In contrast, the species-poor *Afrotrilepis* mats are in a state of equilibrium with *Afrotrilepis pilosa* which is the clearly dominating element, leaving few opportunities for the establishment of additional less competitive species.

Species diversity not only varies between different inselberg habitats, but there is also a considerable degree of within-habitat variation in species diversity along ecological gradients. For most habitats on Ivorian inselbergs, a decline in species diversity along a gradient from the seasonally dry savanna region towards the rainforest zone was observed that is in marked contrast with the diversity of the surrounding vegetation. Again, it is possible to conclude that climatic seasonality favors the maintenance of species-rich plant communities on inselbergs by preventing competitive exclusion. The declining diversity of inselberg vegetation in the Ivory Coast from savanna towards rainforest is probably enforced by increasing isolation of rock outcrops in the latter region. Granite outcrops are less frequent in the rainforest zone which, also lacks further azonal habitats such as ferricretes. In the savanna zone, the higher number of inselbergs and ecologically similar sites may serve to reduce extinction rates (via metapopulation dynamics) and thus promotes more species-rich communities.

Regional differences in plant species-richness on inselbergs

Studies on inselberg vegetation in different parts of the tropics showed large regional variations, both floristically and in regard to plant species-richness. The exact reasons for the pronounced differences in local plant species diversity on inselbergs situated, for example, in the Upper Guinea region of West Africa (low diversity) and in the Brazilian Atlantic rainforest (high diversity) have not been analyzed in detail yet. However, we assume that this difference is a consequence of the higher regional species diversity of the latter region (one of the global centers of biodiversity), resulting in a greater number of potential colonizers of inselberg habitats. This is illustrated by the considerably higher number of mat-

forming species on Brazilian inselbergs (more than a dozen species of Bromeliaceae, Velloziaceae, Cyperaceae; *unpublished data*) compared to the more or less monospecific *Afrotrilepis* mats on West African inselbergs. On the local scale the species richness of the vegetation of inselbergs is probably also influenced by processes, such as source-sink effects and metapopulation dynamics which both affect extinction rates on rock outcrops (Porembski *et al.* 1996a).

It has to be the aim of future comparative studies to explain existing floristic differentiations and the variations in plant species diversity between inselbergs located in geographically distinct areas. Because they are relatively uniform in geology, granitic and gneissic inselbergs offer a unique opportunity for the search for general determinants of species diversity in plant communities.

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