

1 Why Study Inselbergs?

W. BARTHLOTT and S. POREMSKI

1.1 Inselbergs – Model Ecosystems for Biodiversity Studies

The study of islands has provided fundamental insights for our understanding of ecological and evolutionary processes that affect the biodiversity of ecosystems. Experimental studies and observations on islands have a long tradition, with Darwin (1859) and Wallace (1881) advancing the ideas of evolution and speciation. More recently, the island biogeography theory of MacArthur and Wilson (1967) provided an important boost for ecology which became increasingly important in view of the rapidly increasing fragmentation of habitats all over the world. Current investigations on islands take different aspects of biodiversity research into consideration, such as species-area relationships and patterns of species richness (for survey see Adersen 1995; Vitousek et al. 1996).

In addition to oceanic islands there exist terrestrial habitats which are ecologically isolated from the surrounding area and which either form fragments (i.e., surrounded by a mosaic of habitats at least partly tolerable by fragment species) or islands (i.e., surrounded by an inhospitable matrix). Comparative research on their diversity used different types of habitat isolates, such as caves, mountains, and even individual plants. One of the most advanced projects devoted to understand the consequences of fragmentation of formerly contiguous ecosystems is the Biological Dynamics of Forest Fragments Project which is located to the north of Manaus (Amazonas, Brazil). This long-term study measures the relationship between tropical forest remnant size and their species diversity (survey in Bierregaard Jr. and Stouffer 1997).

Granitic and gneissic inselbergs (from German Insel = island and Berg = mountain, a term coined by Bornhardt 1900) form naturally occurring terrestrial islands or fragments depending on the habitat requirements of the species considered. Since granite is the main component of the Earth's continents, granite outcrops are landforms which have developed under a wide range of climates (Campbell 1997; Myers 1997). In both temperate

and tropical regions granite outcrops attracted the interest of early naturalists. For example, in the southeastern USA and in Australia the study of the biotic and physical characteristics of plant communities on inselbergs has a long tradition and has provided detailed insights into, e.g., composition and structural and functional aspects (see the contributions of Wyatt and Allison, Chap. 10.10, and Hopper, Chap. 10.9, this Vol.). However, despite their widespread occurrence in many tropical regions, inselbergs were largely ignored as subjects of ecosystem research. Only rarely could tropical inselbergs attract the interest of early naturalists. For example, Alexander von Humboldt (1819), while traveling along the Orinoco in southern Venezuela, provided us with first descriptive accounts of the blackish crust on the rocks of inselbergs.

It is only since a relatively short time that the global importance of inselbergs for several aspects of biodiversity research has been recognized. In being scattered like islands throughout a matrix of, e.g., forest or savanna, inselbergs offer excellent research opportunities for addressing different topics of biodiversity research and conservation management. The complexity of most ecosystems is an important obstacle to their understanding. In contrast to this, the comparatively low structural richness of inselbergs makes quantitative and qualitative assessments of their inventory easier. However, despite their relatively limited structural richness they comprise a broad array of life-forms. Because of the particular growth conditions on inselbergs, both nonvascular and vascular plants are represented by specialized species adapted to drought stress, heat, and high irradiation (see Büdel et al., Chap. 5, and Biedinger et al., Chap. 8, this Vol.). In this context, it is important to note that the harsh environmental conditions on outcrops have been the driving force in the evolution of poikilohydric vascular plants on inselbergs (i.e., the complete desiccation tolerance of vascular plants, see Kluge and Brulfert, Chap. 9, this Vol.), whereas this ecophysiological trait plays at best a minor role in other ecosystems.

Inselbergs occur in a broad range of sizes and in highly varying degrees of isolation throughout all major biomes and allow for the rapid experimental testing of hypotheses. Unlike most other ecosystems, inselbergs maintain their typical attributes irrespective of geographic location, thus enabling broad-scale comparisons between very different regions (i.e., different in diversity, vegetation type, etc.). In forming original habitat islands, inselbergs offer the opportunity to compare fragmentation effects, which are a usual precondition here, with the consequences of fragmentation in formerly contiguous ecosystems. Moreover, one has to note that in many regions inselbergs belong to the least-disturbed ecosystems and are therefore of special interest. This is in strong contrast to most oceanic

islands, which were severely affected by human influences already long ago. However, inselbergs too are not free from signs of human impact, as is demonstrated by the invasion of weeds on rock outcrops located near settlements. Similarly to oceanic islands, inselbergs form useful models for analyzing the dynamics and consequences of plant invasions because of their relatively low complexity, which is an important prerequisite for a regular monitoring.

In contrast to a number of comprehensive accounts on the geology and geomorphology of inselbergs (e.g., Bremer and Jennings 1978; Thomas 1994), no such contributions are available on the biology of this ecosystem to date despite a considerable number of individual publications. This disregard is even more remarkable because other rock outcrop formations, e.g., cliffs (Larson 1990; Matthes-Sears et al. 1997; Larson et al. 1999) and tepuis (i.e., sandstone table mountains), have attracted much scientific interest over the past years. A symposium on granite outcrops held at the University of Western Australia (Perth) in 1996 brought together a considerable number of researchers concerned with a broad spectrum of different aspects of inselberg research. This meeting formed an important milestone toward this first comprehensive treatment of inselberg studies.

1.2 Perspectives of Inselberg Research

Even though the number of studies concerned with inselbergs has increased over the past years, large gaps still exist in regard to our understanding of basic attributes of this ecosystem. Apart from a lack of knowledge about the basic constituents of the vegetation of inselbergs in certain regions (e.g., India), there exists an even larger deficit concerning questions of ecosystem structure and function. Moreover, even in more traditional fields of botany, like morphology and anatomy, essential functional characteristics of the sometimes bizarre growth forms (e.g., caulescent rosette trees) are barely known. In addition, important physiological properties (e.g., poikilohydry of vascular plants) of many inselberg specialists are only poorly studied.

Obviously, a positive correlation exists between outcrop size and species diversity (Porembski et al., Chap. 4, this Vol.) which apparently is a function of increasing habitat diversity. For a number of species it is known that there is a certain threshold of inselberg size below which they do not occur. An analysis of the determinants of minimum habitat sizes might offer opportunities to test hypotheses concerning the development of diversity in fragmented landscapes. Inselbergs thus offer a great poten-

tial for studying issues which today are of global concern and which might affect conservation biology.

There is still much controversy concerning the relationship between the species richness of an ecosystem and its response to disturbing effects. The examination of inselberg habitats over longer time scales might therefore provide valuable information. Experimental permanent plots which included habitats of varying diversity were established on Ivorian inselbergs in 1990. Preliminary results indicate a considerable degree of variation (i. e., local extinctions, immigrations) between individual habitats with climatic disturbances acting as a highly significant factor which controls habitat-specific turnover rates (Porembski and Barthlott 1997). However, only limited data are available in regard to differences between plant strategies (e. g., reproductive effort, population size), which might explain the long-term existence of species-rich communities in habitat fragments. Likewise, nothing is known about the dynamics of metapopulations and the number and size of subpopulations needed for long-term survival. Investigations devoted to the examination of the genetic diversity of spatially isolated inselberg populations could become very useful concerning the deciphering of the relationship among degree of isolation, population size, disturbance, and exchange rates between disjunct populations.

Granitic and gneissic inselbergs consist of a largely uniform substrate (at least from the viewpoint of plants). Large differences in location, however, provide good opportunities for comparative studies along ecological gradients. Moreover, inselbergs provide excellent opportunities to evaluate the relationship between local and regional diversity, which is still not understood (Caley and Schluter 1997). A comparison between selected inselbergs of nearly identical size surrounded by a similar matrix (e. g., rainforest) is expected to demonstrate the nature of this relationship. First results already indicate that inselberg species richness is positively influenced by a high regional diversity, as could be shown for mat communities on rock outcrops situated in Brazilian Atlantic rainforest (Porembski et al. 1998; Seine et al., Chap. 11, this Vol.). Additionally, several other aspects concerning the diversity of species communities in habitat fragments could be addressed. For example, one could ask whether habitats which are rich in plant species are more speciose on other trophic levels as well when compared to less species-rich habitats. Up to now these questions simply cannot be answered, as is the case with far more complex problems, e. g., on the level of ecosystem functions (e. g., energy and nutrient flow). Because of their simplicity in ecosystem structure, inselbergs provide good opportunities for documenting the relationship between diversity and ecosystem function. This interaction could be tested experimentally by the removal or addition of dominant species in order to

evaluate the consequences in regard to ecosystem function (e.g., resistance to alien species).

Data obtained from the hitherto established permanent plots on inselbergs in the Côte d'Ivoire have shown that their vegetation is characterized by a rapid response to environmental fluctuations. This fact and the widespread occurrence of inselbergs offer interesting possibilities for the assessment of the relationship between inselberg diversity and global environmental change. In being geologically very stable and constituting old landscape elements, inselbergs experienced in the past dramatic fluctuations of the surrounding vegetation as a consequence of climatic oscillations. In comprising a broad spectrum of plant growth forms with very different ecological affinities, future changes in seasonality, temperature, and precipitation could result in a relatively rapid shift in the composition of the inselberg vegetation. In many regions, therefore, a regular monitoring of inselbergs in different regions could contribute to the recognition of possibly changing climatic conditions.

1.3 Linking Inselberg Research to Other Ecosystems

Oceanic islands and their terrestrial counterparts have proved to be very useful in studies of biodiversity. The understanding of inselbergs with respect to population and community ecology is, however, still in its infancy. Despite this fact, certain general tendencies are already visible concerning significant factors influencing the species richness of inselberg plant communities. Future research on inselbergs would benefit considerably from a comparative analysis of other ecosystems that are characterized by similar properties and which likewise underlie extreme environmental conditions. Of particular interest in this respect are other geographically widespread azonal ecosystems which are well delimited against their surroundings, like cliffs and ferricretes. Since there is great similarity in important growth conditions, it would also be rewarding to evaluate the interactions between species richness and disturbance by comparing the vegetation of inselbergs with epiphytic plant communities in tropical forests.

Another important aim of future inselberg research is to understand the reasons for their susceptibility towards invasive weeds and, on the other hand, to identify those inselberg specialists which might develop into weeds when given the opportunity to reach habitats outside inselbergs via roads or forest clearings. In this case, a close link exists with oceanic island research, which is particularly aware of the danger of invading alien species.

Inselbergs

Biotic Diversity of Isolated Rock Outcrops in Tropical
and Temperate Regions

Porembski, S.; Barthlott, W. (Eds.)

2000, XXXII, 524 p. 15 illus. in color., Hardcover

ISBN: 978-3-540-67269-2