SPATIAL AND TEMPORAL DIMENSIONS OF BIODIVERSITY DYNAMICS

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Summary

In all its facets, biodiversity is strongly determined by spatial heterogeneity and temporal variability of the environment. Populations, communities, and ecosystems are constantly changing over a broad spectrum of geographic scales and over both short-term ecological time scales and evolutionary-relevant scales. Therefore, biodiversity is in a continuous flux. Spatial heterogeneity at the habitat, landscape and continental levels plays an important role in controlling biodiversity dynamics. Dynamic biotic processes such as interspecific competition and mutualistic interactions are important for the generation and variation of biodiversity. However, the individual importance of controlling factors and the relationship between ecosystem functioning and biodiversity dynamics are still a matter of debate.

The survival of species is strongly controlled by stochastic extinction and colonisation processes in habitat patterns that are governed by, for example, the number of occupied sites and their degree of isolation. Worldwide, increasing fragmentation of formerly contiguous ecosystems poses a severe threat to species forming metapopulations when extinction rates of local populations exceed colonisation rates. Lack of knowledge about central processes determining the spatial distribution of species in communities and ecosystems is a serious problem for planning conservation measures to counteract the effects of fragmentation (e.g. edge effects, genetic impoverishment).

Temporal fluctuations of environmental factors are likewise of importance for the regulation of biodiversity dynamics. Of particular importance are disturbances which can cause a mosaic of different successional stages occurring side by side. Temporal fluctuations in the spatial extent and severity of disturbances produce a shifting mosaic of adjacent patches of different successional stages which tends to support a maximum of species diversity at intermediate levels of disturbance. At an evolutionary time scale biodiversity dynamics are influenced by a complex interplay of biotic (e.g. competition, dispersal) and abiotic (e.g. climate, soils) factors.

1. Introduction

Biodiversity is constantly changing over different scales. The influence of regional, biogeographical, historical and evolutionary processes occurring at large spatial and temporal scales determines biodiversity dynamics on a broad spectrum of time and space. "Biodiversity dynamics" refers to the natural turnover of populations and communities on the one hand, and of taxa on the other hand, whereas turnover means origination and extinction at predominantly continental to global scales, and colonisation and disappearance at local to continental scales.

The factors, processes and principles that are fundamental for the comprehension of this dynamic nature of biodiversity occur on a wide range of scales in biotic and abiotic conditions, like the influence of geological transformations of the Earth's surface, speciation, habitat patch dynamics, interspecific interactions, mutation, genetic drift, and many other features. Also large temporal and spatial ranges have to be considered if one wishes to unveil this dynamic aspect of nature.

Interactions among species, like interspecific competition and mutualism, play an essential role in the generation and in the dynamics of biodiversity. On an ecological time-scale interspecific competition can restrict the number of co-existing species, but simultaneously lead to a diversification of species' traits. Even though predation has direct negative effects on the prey consumed, it can cause a notable increase in prey diversity. Such interactions and many more functional relationships are widespread in most ecosystems and vital for dynamics of biodiversity.

As these relationships link species to each other, a loss of one species could easily cause the loss of other species and changes in the ecosystem in a kind of a domino effect. At an evolutionary time scale, interspecific interactions account for the evolutionary generation of biodiversity; in the course of the coevolution of species new biological traits develop continuously.

Spatial heterogeneity and temporal variability of the environment rigorously determine biodiversity dynamics at the community and ecosystem levels. Temporal changes of the environment enhance the potential for the co-existence of species like in gap-forming processes that provide species requiring open space with new potential habitats. This interplay of recurrent disturbance and (re)colonisation creates a shifting mosaic of patches at different successional stages. Many systems tend to show highest species diversity at intermediate disturbance intensity and frequency.

To date, biodiversity research has primarily focused on the assessment and description of existing biodiversity patterns and on the rapidly advancing biodiversity decrease due to anthropogenic impact. Knowledge on the dynamics of biodiversity has predominantly been derived from data assessed by the classical disciplines of biogeography, geobotany, population biology, evolutionary biology, and genetics, often before biodiversity research was established as a discipline.

This chapter concentrates on the natural causes and consequences of biodiversity dynamics at different spatial and temporal scales. One section focuses on temporal dimensions, another on spatial dimensions. This aims to facilitate the conception and to highlight the importance of each dimension, though they are often linked to a lesser or higher degree. The subsequent discussion of the interrelations of biodiversity dynamics and ecosystem functions is related to the temporal dimension; this is a complex matter that has to date been recognised only in some qualitative aspects. A separate section considers dynamics across ecological, geological and evolutionary scales, discussing diversity dynamics across historical time periods and at a global level.

2. Temporal dimensions of biodiversity dynamics

2.1. Biodiversity dynamics at the population level

2.1.1. Succession

By the early eighteenth century, the phenomenon of directional change in vegetation composition over the years was raising scientific interest, and in 1806 the term ‘succession’ was introduced in its present meaning. Succession goes along with notable diversity changes and is thus an important natural cause for biodiversity dynamics at local to regional levels. Two main types of succession can be distinguished: (i) primary succession which starts on uncolonised or redeposited bare substrates, and (ii) secondary succession which starts on sites where the former vegetation cover has been destroyed or severely disturbed, but soil formation processes have already taken place and soil seed banks are still present.

Primary succession has been described for sand dunes, alluvial deposits, young glacial retreat zones, and volcanic deposits. Indispensable for primary succession is an import of diaspores, mainly as seeds conveyed by wind or water from other sites, subsequently leading to an increase in diversity. Nomadic plants with anemochoric seeds are often the first colonisers of these areas. During primary succession initial soil formation occurs, facilitating the establishment of further species due to improved site conditions. Besides the numbers of species, biodiversity increases in many other aspects like the variety of life forms and functional relationships and the spectrum of plant dispersal types.

These include an augmenting variety of animal-dispersal modes by, for instance, birds, ants, rodents or other mammals. The time span until the end of the primary succession phase depends on climate, substrate, and species immigration onto the site. On lava deposits in southwestern Japan, a forest vegetation dominated by the tree *Machilus thunbergii* (Lauraceae) established after 700 years, whereas nutrient-poor quartz-sand dunes at Lake Michigan were colonised by oak forest after some 1000 years.

During secondary succession, the velocity of biodiversity dynamics is generally higher, compared to primary succession. Soil formation has already taken place and the soil seed bank and an often considerable amount of vegetative propagules accelerate the (re)establishment of secondary vegetation. In both types of succession the quality of the adjoining habitat types and the size of the succession area influence the temporal dynamics: the smaller the distance from a seed source the faster the succession and diversity dynamics will be.

Severe soil degradation can lead to a major drawback in secondary succession, and the return of the original habitat type can be awkward. A prominent example is the Mediterranean low shrub formation Garigue, which forms a final successional stage after the evergreen sclerophyllous *Quercus* forests that originally had surrounded nearly the entire Mediterranean were cleared in Roman times and soils severely degraded. Under these circumstances, biodiversity dynamics are lower for several decades to centuries after disturbance.

Biodiversity dynamics during primary and secondary succession are largely determined by the life histories of the colonising species. Colonisers can be classified as the ecological types of selection r and K, according to the logistic rates of population growth. R-selected species maximise the intrinsic rate of population increase (r). Every time favourable conditions become effective in an unsaturated community (e.g. sufficient light, heat, and moisture in a newly created habitat) the species immediately colonise the area with great numbers of individuals that quickly complete a short reproduction cycle. Such species are vagile opportunists, favoured in rapidly changing environments as in the early stages of succession. It follows that at first, biodiversity is immediately raised due to the increase in species number. As subsequently equitability and structural heterogeneity of the young community rapidly decrease, biodiversity dynamics temporarily decelerate until the next community turnover occurs.

In contrast, K-selected species maximise their competitive ability in response to stable environmental resources that are exploited to a relatively high degree. This implies selection for low birth rates, high survival rates among offspring, and prolonged development times of the growing individuals and the entire populations, i.e. a strategy of equilibrium species. K represents the carrying capacity of the environment for species populations showing an S-shaped population-growth curve. In consequence, these are late-successional species that cause a steady increase in species number, equitability, and structural heterogeneity after the short-living r-selected species have receded. As these two types of selection represent contrasting extremes, most species are located somewhere along an “r-K continuum”, causing biodiversity dynamics to vary in every single case.

Results from old-field studies on secondary succession have shown distinct shifts in vegetation composition, often starting from a herbaceous stage, followed by grass dominance which gives way to shrubland stages due to the slow invasion of woody species, eventually leading to a forest. As the physiognomic changes during this successional sere occur abruptly, the term ‘relay floristics’ developed, referring to the functioning of an electronic relay. According to this theoretical framework, biodiversity dynamics display sudden changes, interrupted by phases of stagnation.

The question at which instant a species actually arrives at an old field is a matter of controversy. The model of initial floristic composition postulates that most late successional species (like shrubs and trees) are already present at the beginning of the regeneration process. They are either part of the soil seed bank or present with vegetative propagules, rhizomes, or a sapling bank. This model suggests comparatively low species dynamics during secondary succession.

The organismic concept of plant succession analogises succession with the convalescence of an organism to reach the climatic climax vegetation and, in consequence, a concomitant biodiversity climax at the end of a succession. This monoclimax theory was rejected and amended through the polyclimax theory into an individualistic concept. New models, like obligatory succession and competition hierarchy, were derived from the probability theory, supposing that in the course of succession an equilibrium would be reached that also stands for a certain diversity level. The focus was moved from simplifying explications for complete successional lines to the differentiation of causes and mechanisms of succession.

The controversy about the contiguity of succession and stability resulted in a more sophisticated view on stability of ecosystems, differentiating in resilience and resistance. In this context resistance is the ability of an ecosystem to maintain itself and its biodiversity after the occurrence of a relevant impact, i.e. disturbance. Resilience is the ability of returning into the original state after a moderate temporary change has occurred due to disturbance.

This distinction in conjunction with the accentuated view on the mechanisms of succession helped the disentanglement from older ideas about a final stable state of succession and diversity, characterised by low entropy, high degree of organisation, high resistibility against environmental changes and highly linked-up food chains. The former deterministic and idealised view has been replaced by one that is orientated on probabilities. Here, disturbance plays an important role as it most commonly influences biodiversity dynamics due to the creation of spatial heterogeneity in time (see Box 1).

Disturbance

Various definitions exist for disturbance. They all have in common any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment. The key issues are that disturbances are discrete in time, in contrast to chronic stress or background environmental variability, and that they cause a notable change in the state of the system. Disturbance has variously been defined in terms of the effect on demography, community, and ecosystem.

1. Demographic definition—an event that causes death to one or more dominant individuals.
2. Community definition—an event that causes alteration of composition or structure of the vegetation.
3. Ecosystem definition—an event that causes a release of a previously unused resource.

Disturbance increases the spatial heterogeneity in the availability of nutrients, light, moisture and space for new growth by existing or replacing species. A disturbance can have a major effect on biodiversity dynamics due to changes in successional pathways as a consequence of changed species interrelationships at the site; these can be ephemeral or long-lasting. In some ecosystems like floodplains or closed forests of the non-tropics, natural disturbance is a crucial factor for maintaining the coexistence of certain species and, thus, a higher biodiversity.

Box 1. Disturbance

On a regional scale important parameters determining diversity dynamics include local community size, immigration and emigration rate, and abundance of species within the metacommunity. Disturbance frequency and intensity account for extinction as well as the isolation degree, leading to a low immigration rate.

2.1.2. Genetic diversification

Speciation and extinction rates determine biodiversity dynamics up to the global level. Natural causes for species extinction and hence losses in biodiversity span fire, hurricane, freeze damage, fluctuating water levels in basins, landslides, lava flows, as well as biotic causes like insect calamities, disease, predation, burrowing animals, and many others.

Speciation is the process of formation of isolated reproductive populations. As habitat fragmentation can lead to the genetic isolation of formerly connected populations, it can cause speciation. Animal populations often occur in scattered colonies forming a mosaic.

Regular seasonal disturbances lead to predictable fluctuations in population size and distribution. Unpredictable regional and temporal disturbances lead to reductions in population size and even to local extinctions. If there is no evolutionary pressure (e.g. selection, mutation) the genetic variance will remain quite stable in large populations. In small, isolated populations, an overall reduction in genetic variability occurs due to stochastic changes in gene frequencies (genetic drift).

Following disturbance these populations undergo stages of critical population sizes exerting a bottleneck effect on genetic diversity. Also founder colonies start with a rather low genetic variability and have to pass a bottleneck stage.

One consequence of a small population size is a higher degree of inbreeding, causing low genetic variability within individuals and reducing the fitness of the entire population—the so-called inbreeding depression. The reduced fitness can result in smaller seed size, reduced fertility and/or reduced germination rate compared to the parent generation.

Cross-breeding, on the other hand, results in progeny showing increased performance, like vigorous growth or increased seed production. This heterosis occurs as a result of high heterozygosity—being one measure of genetic diversity. Heterosis is one of the stabilising forces maintaining biodiversity. A genetically higher variation in a population reduces the risk of inbreeding depression and increases the fitness up to a limited extent (Figure 1).

In consequence, the genetic variability within a population, the biotic diversity of species per given area, and the diversity at various taxonomic levels are not constant characteristics inherent to certain natural entities, but are continuously subject to change at various scales.

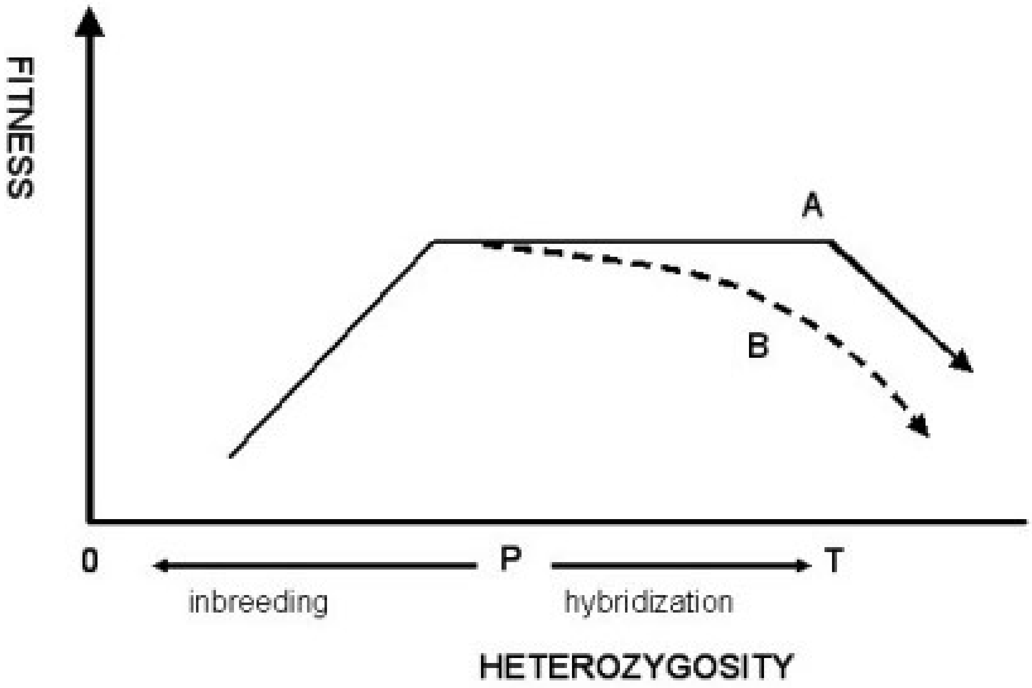

Figure 1. Degree of fitness with respect to heterozygosity.
P: threshold value for heterozygosity, left of P: inbreeding depression with a loss in fitness, dashed line: accelerated decline in the fitness of recombinant progeny, right of point T: decrease in fitness due to incompabilities between highly integrated development programs. After Vrijenhoek R. C. (1985). Animal population genetics and disturbance: the effects of local extinctions and recolonisation on heterozygosity and fitness. In: Pickett S. T. A. & White P. S. (eds.): The ecology of natural disturbance and patch dynamics: 266–286. Academic Press, London.

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Biographical Sketches

Dethardt Goetze was born in Braunschweig, Germany. He studied botany, zoology, limnology, soil sciences and geology at the Universities of Braunschweig and Freiburg/Breisgau and accomplished his doctorate at Darmstadt University of Technology. He developed a method for surveying and analysing biodiversity at different organisation levels of ecological systems in typified landscape sections in southwestern Germany. He also managed conservation projects for an environment protection organisation in central Germany. Currently, he is a postdoctoral assistant at the Department of Botany of the University of Rostock and coordinator of a botanical project of the interdisciplinary BIOTA Africa research programme (Biodiversity Monitoring Transect Analysis in Africa), focusing on the implications of global change on habitat fragmentation to develop guidelines on a more sustainable use of biodiversity in West Africa. His fields of research are the analysis of habitat patterns, landscape metrics, landscape diversity, and their dynamics.

Ursula Karlowski was born in Oberhausen, Germany. She studied Biology at the Universities of Bielefeld and Bonn and her dissertation subject was the secondary succession of old-fields in the afromontane region of Uganda. The influence of animal-dispersal on the regeneration process as well as the implications of her results for the management strategy of Mgahinga Gorilla National Park was one of the focal points of her study. She has been engaged in rain forest conservation in eastern and central Africa since 1988, especially in southwestern Uganda in close cooperation with the Mgahinga Gorilla National Park Project. She continued her vegetation studies and assessments on the conservation status in Kahuzi-Biega National Park and in high altitude regions of the Parc National des Virunga, D.R. Congo.

Currently she is working as a scientific assistant at the Institute of Biosciences at the University of Rostock. As a specialist in vegetation ecology her special interests are studies of vegetation change and nature conservation strategies. She has been given grants from DAAD, FES and from animal and environment protection NGOs like Friends of the Earth, berggorilla&regenwald direct aid, and Diane Fossey Gorilla Fund.

Klement Tockner is an Associate Professor for aquatic ecology at ETH (Swiss Federal Institute of Technology) and head of the research group "Floodplain Ecology and Biodiversity" at the department of Limnology at EAWAG (Swiss Federal Institute for Aquatic Science and Technology). He received his PhD degree in 1993 at the University of Vienna. After one year of work as a limnology consultant in East Africa, he coordinated the Danube Restoration Project in Austria. In recent years, he has been a visiting scientist at the Tohoku University (Sendai, Japan), the University of Montana (USA) and the Institute of Ecosystem Studies (USA). Klement Tockner has experience of both fundamental and applied scientific investigations of European river systems. In particular, he has worked on several large Alpine river systems, and has been involved in the scientific investigations underpinning restoration of parts of the Danube. He leads an international and interdisciplinary research team at the Tagliamento River in NE Italy, which is a key reference ecosystem of European importance.

Aparna Watve is working at Agharkar Research Institute Pune, India, on a project to document plant communities on rock outcrops in Northern Western Ghats. The rock outcrops are rich in endemic plants which are in immediate need for conservation. The present project aims at identifying appropriate management strategies for conservation of the outcrop habitats. Her doctoral work was on spatial distribution of plant species and communities in the Mulshi area of the Western Ghats. She has worked in Botanical Surveys of India for documenting the floristic diversity of national parks, and became engaged in developing web based electronic catalogues of Indian organisms at the Centre for Biodiversity Informatics. Her main interests are documentation and dissemination of knowledge regarding biodiversity, especially of specialised habitats such as sacred groves and rock outcrops. She is also working as a consultant for non-formal, unsupervised environment education programmes.

Klaus Riede studied zoology and biocybernetics in Frankfurt and Tuebingen, Germany. After his dissertation in Zoology, at the Max-Planck-Institute for behavioural physiology, he studied the species-rich grasshopper fauna of South America. He continued field studies in Malaysia, combining them with neuroethological laboratory experiments about hearing physiology in Orthoptera. Since 1997, he designed and managed two major biodiversity informatics projects at Museum Koenig, Bonn: the "Global Register of Migratory Species" (www.groms.de) and the "Digital Orthoptera Access" project (*www.dorsa.de*).

Stefan Porembski was born in 1960, in Berlin (Germany). He studied Biology with Chemistry and Physics at the Freie Universität Berlin and at the University of Bonn, and his dissertation subject was functional aspects of the morphology and anatomy of succulent plants with particular emphasis on Cactaceae.

He was a Postdoctoral and Scientific Assistant at the Botanical Institute of the University of Bonn, and since 1998 has been Professor and head of department at the Botanical Institute and director of the Botanical Garden of the University of Rostock, where he created a working group on terrestrial habitat fragments (inselbergs, miniature dunes, forest islands, and temporary pools).

His main fields of research are tropical ecology and biodiversity (the vegetation of inselbergs, forest fragments, desiccation-tolerant vascular plants, carnivorous plants, succulents, and epiphytes), and systematics of angiosperms. He has concentrated especially on the analysis of spatial and temporal dynamics of plant communities by using permanent plots placed in different tropical ecosystems. Several of his projects are concerned with the consequences of changing land-use activities for the species diversity of tropical ecosystems. He has researched mostly in South America (Brazil), West Africa (Ivory Coast, Benin), and India, and has received grants from, among others, the DFG, BMBF, and DAAD. He is Vice-President of the International Organisation for Succulent Plant Study (IOS).