

Zonal features of phytodiversity and regeneration

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Looking for literature concerning zonal features of phytodiversity, an interested party is confronted with the following problems: Although vegetation scientists offer ample material on specific characteristics from different ecozones, comparative data is lacking. Thus, methods of evaluating diversity should be standardized if there is a desire to compare it on a global scale. Furthermore, there is a need to define and localize different regeneration systems since many ecologists often describe similar effects in different parts of the world with different terminology; or they have different connotations for identical terms; one example of this is the very common expression "gap".

Earlier papers presented the author's ideas about zonal features of regeneration regimes including different types of disturbances and processes of mosaic cycles (BÖHMER & RICHTER 1997), as well as of phytodiversity patterns (RICHTER 1998). The following is an attempt to clarify whether species richness of stands depends on regeneration processes. Before this step, the first part of the paper points out a typological overview of regeneration and phytodiversity. Special effort has to be given on a classification of different dimensions of regeneration processes considering not only the spacial extent, but also the origin of impact. However, it is noteworthy to keep in mind that „...any classification forms always a crutch to understand reality as it considers only an anthropocentric vision“ (WIEGLEB, 1986).

1 Regeneration processes

The survey in fig. 1 presents four regeneration types covering one part of patch dynamics within six different aspects of vegetation dynamics. Only autogenesis, an equivalent to the traditional „climax-theory of self-preservation“, does not belong to disturbance processes. In contrast, the other three types of regeneration depend on such events with different levels of impact and with different origins. In this context, volcanic eruptions, hurricanes or landslides have certainly to be considered as destructive exogenous processes with regard to any ecosystem exposed to such an event. In contrast, processes reacting as driving forces of non-destructive cycles within an ecosystem might be assumed as endogenous or „internal processes of change“ (PICKETT & WHITE, 1985), here designated as „disturbance-like event“ (REMMERT, 1985). As part of the same author's umbrella concept of mosaic-cycles, it describes more or less inconspicuous impacts promoting the shift of mosaics of species caused by retrogressive and successive stages as vital parts of an ecosystem. In these cases climax must be defined as a final stage of succession within a „climax-theory of continuous cycles“.

According to this approach, the smallest dimension of disturbance refers to spot dynamics, including perturbation with key organisms of the system adapted to the resulting effects. In steppes or grass tundras for instance, piles of earth thrown out by burrowing rodents might proliferate the appearance of low frequent satellite species by spot dynamics within a surrounding of more or less high frequent core species on undisturbed ground. A system with a cycling mosaic of core and satellite species without exogenous disturbance can be expressed as „carousel“ (VAN DER MAAREL & SYKES, 1993). It describes a “merry-go-round“ migration of most if not all herb and grass species, causing a high probability of recolonization by any of the species for each microsite (fig. 2). In these cases, annual climatic variations or different amounts of consumption by phytophages may be regarded as triggers for the changing abundances of the

key species. Small openings by cryoturbation within alpine mats and turfs may be regarded as endogenous disturbance-like events too (BÖHMER, 1999)

Concerning medium sized processes, i.e. the „mesolevel“ in fig. 1 gap dynamics are the most conspicuous processes driven by exogenous forces. In hardwood forests, fast lateral ingrowth by neighbouring trees competing for open spaces may fill up partial crowns-breaks within a few months. Above all, this is true for protracted partial crown die-backs as known from stands of southern beeches in Western Patagonia (REBERTUS, 1994). These cases of limited space do not tend to offer harsh deviations from previous microclimatic conditions and hence do not create patches for additional taxa. So, gaps must have a minimum size to warrant an increase of species richness; it depends on solar inclination as a function of season and latitude, as well as on height of the tree stand. Influence on α -diversity is given preferably where an uprooting of tree towering above a canopy and where domino-effects cause extensive breaks („trees kill trees-effect“, VAN DER MEER & BONGERS, 1998). Under these circumstances, tropical rain forests seem to be more vulnerable than most other woodlands. However, as the major killing agents play a decisive role, regions subject to rare events like extraordinary storms and accumulations of snow or icefalls seem to be most affected.

Although less considered in geobotanical literature, large sized natural clearings, i.e. the „macrolevel“ in fig. 1, are much more significant for regenerative processes than gaps. According to HARPER (1977), disastrous impacts comprise events confronting an ecosystem with high probability within a few plant generations. This applies to large fires as a driving force of vegetation cycles in boreal coniferous forests, mediterranean shrubland, as well as in savannas or steppes, to hurricanes in various tropical and subtropical rain forests or to denudation by floods in deserts. In this case, exogenous processes act as „inherent disturbances“ (BÖHMER & RICHTER 1997), providing the revival of a system and thus, forms part of it („destructive system“, KIMMINS 1987). Instead, cohort senescence or mortality must be judged as endogenous processes responding to nutrient deficits and to a loss of plant productivity on leached soils. This „chronosequential biomass hypothesis“ (MUELLER-DOMBOIS & KITAMAYA 1996) refers in particular to monodominant stands of old growth trees containing the same structure of age. The extreme El Niño-event in 1982 / 83 illustrates an instructive example by causing widespread cohort mortality of the predominant *Scalesia pedunculata* on the Islands of Galapagos. There is evidence, that the same species follows cyclic recoveries reacting upon a declining incorporation of carbon while growing up (ITOW & MUELLER-DOMBOIS 1988). On the other hand, heavy rainfalls by ENSO-phenomena may provide progressive cycles too. Thus, in the Sechura Desert of Northern Peru, the 1998 event locally resulted in an extraordinary dense coverage of herbs and grasses, as well as an enhanced sprouting of tree seedlings (KRÜGER & RICHTER, in press). While in this case occasional peaks of booming effects are not at all destructive on slight elevations, floodings by the same event are to be regarded as disturbances for neighbouring ecosystems in depressions.

Furthermore, the schemes in fig. 2 imply that exactly the same disastrous event is able to cause different dimensions of disturbance dynamics. This is true for an extraordinary large avalanche that devastates the outer border of a coniferous forest resulting in a natural clearing. The same event may create gaps within a neighbouring alder-formation that might only be adapted to smaller avalanches. Finally, herbaceous communities in a gully experience a spot- or carousel-type superimposition by delayed melting of snow. In this case, three different types of regeneration-processes are initiated by just one exogenous disturbance-impact. Only if the avalanche is sized on an average it might be regarded as an „inherent disturbance“, establishing a system composed by key organisms adapted to the effect; this gives reason to put the

expressions „exogenous“ and „endogenous“ in parentheses (fig. 1). However, if the avalanche is outsized, the result is a completely alternating species-pattern within the clearing of the former forest, a partially alternating structure within gaps of the alder-thicket and a cycle of migrating species in the herbaceous gully-community, as shown in fig. 2.

2 Phytodiversity patterns

With regard to zonal biomes, the different types of diversity may vary considerably, depending on community structure and topographic variety. In the following explanation, only "typical", i.e. predominant life-form patterns and formations of lowland ecosystems that occur in nine ecozones are of interest here. In this sense, the idea of comparing phytodiversity patterns must be based on "models", that take into account species numbers, as well as community diversity within plots of the same size and of typical situations at respective locations. The samples in fig. 3-5 are derived from different sites in three ecozones and are considered to describe representative formations. The examples are basing on personal experiences by the author; further information on locations in the remaining six ecozones is presented in a former paper (RICHTER 1998).

Of course, problems arise from the considerable differences in taxonomic diversity given by varying evolutionary progress in the world's floristic regions (WHITTAKER 1975). Thus, a map of endemic genera based on notes by TAKHTAJAN (1986) and a recent map of species richness (BARTHLOTT et al. 1996) do not necessarily coincide. RICHTER (1998) pointed out the possibility that taxonomic diversity at the genera level corresponds with evolutionary developments over a long period of time, whereas taxonomic diversity at the species level corresponds with parameters of abiotic heterogeneity caused by orographic, geomorphological and mesoclimatic differences. In the table of diversity patterns (fig. 6), these problems are not completely disregarded, as hints of possible derivation are given there.

All the more this is necessary, as most ecozones display their specific diversity patterns dependent from their successional steps within the prevailing regeneration cycles. In case of the mediterranean ecozone, for example, the influence of large ground fires as well as of crown fires creates disastrous clearings with successional stages from garrigues to evergreen pine forests or oak woodlands (fig. 3). In the first case, open scrub on heavily eroded rocky ground like Greek phrygana reveals the highest level of α -diversity within Europe, holding sometimes more than 100 species within an area of 150 m² (BERGMEIER 1994). There is evidence that some garrigues, tomillares or phrygana of thermo- or xeromediterranean sites are likely to be fire ecosystems adapted to frequent burning. In the second case of a final stage of succession, woodlands show an apparently limited species richness (CARL & RICHTER, 1989). So, ecotope diversity in fig. 3 indicates a patchy community system derived from South African (COWLING, 1992) or Baja Californian mediterranean areas (MINNICH, 1998) that are a kind of theoretic conception for European mediterranean landscapes prior to man's influence. The patchwork of different successional stages is responsible for an elevated β -diversity with a high standard derivation in species numbers. It should also be mentioned that human impact by clearing forests and agricultural expansion, additionally supported the evolution of a large number of annual plants for thousands of years in the Mediterranean of the Old World (fig. 3; PIGNATTI & PIGNATTI, 1984). This historical factor of species promotion is missing in equivalent zones of the Cape Province, South-West Australia, Central Chile and California, where an effect of „phyt globalization“ by invasive aliens suppresses trends of adaptive radiation.

Another important observation is that fire-ecosystems do not necessarily cause an evolved species richness. Boreal forests have even fewer species per plot than most tundra sites, although coniferous forests may be replaced by fireweed, birch and willow stands as well as by mires and even by episodic aquatic formations when burned. The patch-work of different communities shown in fig. 4 are considered to indicate a typical pattern in boreal Canada (TRETER, 1993). Here, an elevated β -diversity does not lead to an increased α -diversity within the different succession stages.

Finally, a limited β -diversity, like in most tropical rain forests (fig. 5), must not coincide with a diminution of species richness. The high level of α -diversity here is caused by an extraordinary high number of trees, epiphytes and lianas, but certainly not by patchiness, as might be concluded from an over-estimated gap-theory.

3 Extratropical features of phytodiversity and regeneration

After this general introductory part it is possible to give a short overview of phytodiversity and regeneration in each of the nine ecozones following the system developed by SCHULTZ (1995). Fig. 6 presents α -diversity separated in five groups based on species numbers per 100 m², including the possible range of deviation. The index of β -diversity is given by the community number per 25 hectares. As a result, γ -diversity is the total of α - and β -diversity and expresses a landscape's diversity (WHITTAKER 1972) that might be characterized by the species number of a defined region (BEIERKUHNLIN 1998).

Therefore, at least in most of its humid sections the ecozone of subpolar tundra shows a higher landscape diversity than the boreal zone due to a greater species richness per plot mostly combined with a dense pattern of ecotopes. The reason for this varying community-structure lies in the arctic topography. It causes a small-scale variety of permafrost phenomena like frost boils, polygons, pingos or palsa and furthermore affects the distribution of soil moisture, soil types, and snow coverage. All of this might be finally superimposed by bird nests, lemming burrows, musk-ox dunghills, or lichen pastures of reindeer (THANNHEISER 1988). Most of these small patches can be considered as episodically cycling communities. Consequently, tundra ecosystems are dominated by spot dynamics, as assumed in fig. 7, where gelifluction, burrowing mammals and small processes of denudation make up a great portion of regeneration events at the micro-level.

Further south in the mid-latitudes, the conditions for species richness remain comparable with the differences between tundra and coniferous forests of high latitudes. Once more, the open systems of steppe are strongly influenced by spot dynamics with triggers like burrowing mammals, drought and additionally, sometimes salinification in shallow depressions. Although fires are likely to occur frequently, their impact on regeneration processes is less dominant than in boreal forests, since surface fires prevail. While delimited spot dynamics are of priority in steppes, nemoral deciduous forests show various types from micro- up to macro-disturbances. The range of differently sized destructive cycles extends from partial die-back caused by phytophages over gaps created by storms (REMMERT 1991) to clearings by blowdowns (REBERTUS et al., 1993). Furthermore, cohort-senescence due to soil nutrient metabolism takes part in mosaic-cycles (WELSS, 1985). Despite the respectively high variety of exogenous influences (fig. 7), the main regeneration type of nemoral forests seems to be an autogenetic one. Therefore, in most cases both species richness and β -diversity remain respectively low (fig. 6).

4 Subtropical features of phytodiversity and regeneration

Three subtropical (sub-)zones are distinguished here: First, the mediterranean regions at the western rim of continents with a climate dominated by humid winters; second, the laurophyllous regions at the eastern rims where the climate is mostly affected by humid summers; and lastly, the arid parts toward the equator. The warm deserts on the western sides cause a more obvious disruption between extratropical and tropical flora than the transitional monsoonal domains on the eastern sides do. Due to these facts, mediterranean subtropical zones show more similarities to the extratropical complex, whereas tropical elements are to a certain degree able to enter the laurophyllous woodlands, creating a higher level of diversity, especially among tree species.

The relation to mid- and high-latitude-forests, at least in the Mediterranean of the Old World, is evident by the apparently limited species variety of pine and oak woodlands. On the other hand, the high level of α -diversity in European open scrub communities, in South African fynbos and in some Californian chaparral must be considered as well. Finally, it should be emphasized that the Old World's Mediterranean forms the most important genetic pool from which weeds originate. This fact we have to keep in mind as it implies that frequent low level disturbances enhance the diversity of short-lived species, like therophytes, geophytes and hemicryptophytes (CARL & RICHTER 1989).

Concerning the arid interruption between the subtropics and tropics by deserts, it is difficult to present diversity patterns due to the following three principal factors of influence. First of all, referring to the flora, small deserts seem to be much more diverse than large deserts due to the existence of neighbouring effects. This is valid for the comparatively small Nama Karoo, as well as for the Sonora or Mohave and even for the extremely dry and very narrow coastal Deserts of Atacama, Peru and Sechura. Here, the entire species ranges are the same or even higher than in the much larger Saharo-Arabian region and the Australian Desert. Secondly, comparisons basing on releves are difficult as species numbers consist of mostly absent therophytes and geophytes. Thirdly, variations in space as in the coastal Atacama (RICHTER 1995), as well as variations in time as recently caused by the ENSO-phenomenon in the coastal Sechura (s.a.) reduce the items in fig. 6 to a speculation.

The case of El Niño shows that self-preservation constitutes a great part of regeneration processes in deserts. Though frequent droughts affect the long-term mortality through progressive aridity, in extreme cases leading to extinction, it is mostly an ineffective supporter of destructive cycles. Therefore, patch dynamics in deserts seem to be limited to denudation and flooding or wind, including friction effects or accumulation due to shifting sand dunes.

Subtropical summer- or evergreen woodlands of monsoonal character will not be considered in this paper, because they show similarities to nemoral or tropical formations, depending on their latitudinal position.

5 Tropical features of phytodiversity and regeneration

Within the tropics beginning with the semi-desert subzone to savannas and deciduous dry forests up to evergreen rainforests, species numbers increase with the gradient of humidity in most cases. However, it should be noted that extraordinary species richness may occur in neotropical communities of semi-arid and semi-humid stands too, as SILBERBAUER-GOTTSBERGER, I. & GOTTSBERGER, G. (1984) mention for tree-stands of Brazilian cerrado. In contrast, apart from floristic differences, decreasing α -diversity in the seasonal tropics of Africa may result from direct man-made desertification and natural overgrazing by wild game for millennia.

Nevertheless, β -diversity may reach higher levels in drier subzones. An explanation might be found in the wide system response of the very sensitive vegetation related to the many slight variations in land forms, soil moisture and soil properties. Vegetation there ranges from species-rich wet gallery forests to species-poor xeric habitats with a fragmentary cover of lichens and cyanobacteria on the rocky outcrop of inselbergs (POREMBSKI et al. 1994).

Furthermore, savannas seem to form a changing mosaic of temporary sites (SINCLAIR 1979). There is a strong interaction between perennial grasses and elephants, giraffes (both of which have an important impact on woodlands) and wildebeests. Fire has a more pernicious widespread effect. It particularly prevents young trees from growing up into the canopy. This results in an uneven age distribution and tree populations may become highly unstable. Decennial or secular fluctuations in this mosaic-cycle lead to the fact that α -diversity varies within the same ecosystem.

Even evergreen rain forests, normally ranking as models for extreme heterogeneity may vary considerably (GENTRY 1982). Supported generally by the diversity of trees, the African Paleotropics profit from a great number of stem-climbers, whereas in the Neotropics, epiphytes play the most important role. Concerning epiphytes, a striking difference between lower and higher elevations should be pointed out: while epiphytism in lowlands is quite limited with only a few larger examples of vascular plants and a low number of bryophytes, there is an increasing epiphytic diversity found at higher elevations (RICHTER 1996).

It should be emphasized at this point that too much relevance is put on gaps by falling trees as sources of regeneration in rainforests, because gap-forming processes are only frequent in regions to which they are prone. According to WHITMORE (1989), the mosaic of structural phases caused by catastrophic impacts like cyclones, earthquakes, or periodic fires is coarse in Papua New Guinea, whereas in Borneo only fine structural mosaics or non-gaps are the standard because of minimal destructive effects. Apart from the relatively rare toppling over of towering trees in primeval forests of tropical flat lands, it is more common to find partially collapsing crowns or rotten tree trunks falling over. It is much more characteristic for trees to die in a standing position than to crash down and create gaps. This might have inspired LIEBERMAN et al. (1993) to entitle a paper "Forests are not just Swiss cheese"...

Therefore, we should consider autogenesis as the main regeneration-type in tropical rainforests as WHITMORE (1990) does. This fact implies that neither gaps, nor clearing-dynamics caused by fires during El Niño-drought, nor hurricanes regionally promote regional tropical heterogeneity. Likewise, we cannot decisively explain species richness of rain forests in the tropics by the niche diversity, because the canopy-structure there does not create a much more differentiated micro-climatic variation than that of extratropical forests. So it seems that there is no correlation between tropical heterogeneity and any type of regeneration or any given specific habitat-structure.

6 Conclusion

As fig. 6 and fig. 7 comprise the status of different types of disturbance and diversity per ecozone, some statements are notable:

1. The kinds of disturbances vary in different ecozones. An additional proof of this fact is given by WHITE et al. (in press) by evaluating some 70 papers on natural disturbances in North America.

2. Smaller spot dynamics are prevailing in extratropical grasslands, i.e. the subpolar tundra and the temperate steppes.
3. Gap dynamics may play an important role in most forest ecosystems but seem to be overestimated as initial triggers for regeneration processes.
4. Large clearing dynamics are a most significant ecofactor in boreal forests, mediterranean shrubs, pine forests, as well as in subtropical resp. tropical deserts.
5. Autogenesis must be considered as the main regeneration type in nemoral hardwood forests, laurophyllous forests, tropical rainforests and temperate semi-deserts.
6. Species richness of vascular plants per plot is greatest in tropical and subtropical rainforests and in tropical savannas, smallest in deserts and boreal coniferous forests.
7. Due to the predominance of fire-events maximum patchiness is obvious in tropical savannas, mediterranean shrubland and boreal forests; on a smaller level, β -diversity is high in the tundra too.
8. There is no significant correlation between the type, size, or frequency of disturbances and the status of diversity on a global scale. For instance, the tropical rainforests as the most prominent example of high diversity can not be explained by an extraordinary high rate neither the low diversity of boreal forests by a low rate of disturbances.

If species richness of different vegetation zones is not ruled by disturbance regimes as a worldwide superimposing significant factor, we have to look for another straggling effect and / or for a framework of formation factors at least responsible for differences in diversity patterns within the ecozones. As for the global aspect of diversity the so-called „Rapoport's Rule“ might be helpful, which states that latitudinal ranges of animal or plant species increase towards the poles (narrow definition of the term by ROHDE 1996). With regard to the zonal gradient of phytodiversity, this rule provides an explanation for the tropical species richness and vice versa, extratropical species poverty:

1. Greater effective evolutionary time, which is defined as a factor that comprises greater evolutionary speed at tropical temperatures and longer contemporary evolutionary time under relatively constant thermic conditions, is the primary cause of greater species numbers in the tropics (ROHDE 1992). FRÄNZLE (1994) considers tropical rainforests as highly developed systems with a most efficient entropy flux displaying a maximum stability by homogenous climatic and edaphic environments.

2. Low-latitude species typically have less environmental tolerances than high-latitude species. Furthermore, a larger number of "accidentals" (i.e. species that are poorly suited for different habitats) occur in tropical communities. The constant input of these accidentals artificially inflates species numbers in the tropics (STEVENS 1989).

3. Present seasonal variability between sites separated by latitude or elevation drives the Rapoport phenomenon, because low-latitude species are less capable to tolerate seasonal temperature fluctuations than high-latitude species, which sustain a more violent competitive evolutionary pressure (Seasonal Variability Hypothesis, according to STEVENS 1996). This phenomenon includes a phenological synchronization that triggers the reduction of both differentiation among species and opportunities for regeneration (RUNKLE 1989).

Consequently, Rapoport's Rule provides an initial explanation for the geographical pattern that marks the two extremes of diversity: "a chemostate-like system tending to become monospecific, and a Noah's ark or museum situation with an infinite number of species each represented by just one specimen" (MARGALEF 1994). The same concept applies to the principal pattern of increasing species richness from the poles towards the equator, only interrupted by the hydroclimatic stress within the arid transition zone.

On the other hand, zonal features of diversity do not at all follow continuous gradients. In fact, within the Extratropics and Mediterranean species numbers of vascular plant communities seem to show a correlation between different types of regeneration. There is evidence that open stands are connected via spot dynamics and thus, micro-climatic as well as pedogenetic niche-heterogeneity provide a higher α -diversity. In contrast, forest stands with a closed canopy are connected via constant self-preservation or large clearing-effects and thus, micro-climatic as well as pedogenetic niche-homogeneity cause a lower α -diversity.

This concept is to underline by species numbers in anthropogenic ecosystems:

1. In every ecozone the degree of α -diversity in natural stands differs from that one of man-made-ecosystems, generally on a diametrical basis (fig. 6).
2. The low α -diversity in natural extratropical forests leads to decreased species richness after abandonment of fields, just the opposite to the situation in the tropics (RICHTER 1998).

However, an apparently negative correlation between biomass of vascular plants and phytodiversity in the Extratropics and Mediterranean can not be regarded as a direct dependance: The fact that phytophage- or drought-caused disturbances controlling the type of regeneration are more frequent and of greater impact in open stands than in woodlands has to be considered as a *functional factor* within an ecosystem. In contrast, the fact that open stands are mostly combined with a higher niche-heterogeneity providing phytodiversity is given by the *spacial structure* within an ecosystem.

The dimension of β -diversity shows relation with different disturbance patterns. For example, fire- or plague-induced boreal or mediterranean woodlands include more successional stages and therefore as well a higher patchiness as self-preserving systems like nemoral woodlands. Even in tropical rainforests, β -diversity remains low in case of rare disturbance impact that promotes uniformity by self-preservation, whereas in savannas, different scaled destructive cycles keep the patchiness higher.

It should be pointed out, that a pure ecological view of defining diversity patterns only by aspects of actual processes of vegetation dynamics must be completed by two further approaches. At first one should keep an eye on the evolutionary status of an ecosystem. A second aspect is even more neglected by vegetation scientists: The different types of disturbances or disturbance-like events have to be considered together with their spacial dimensions, combined with the respective type of plant formation.

As various causes of accidents lead to disturbances of different dimensions we can distinguish between macro-, meso- and microdisturbances. Although classifications as shown in fig. 6 and 7 can never fit reality, it might - when founded on the models mentioned above - provide a basis to understand the immensely complex range of ways in which regeneration and diversity can take place. Considering the zonal features of disturbances and diversity, fig. 8 gives an idea of the importance of spacial aspects all the more, as they must be combined with different frequencies and time scales of regeneration processes. This viewpoint might be helpful for those ecologists doubting whether the „Intermediate Disturbance Hypothesis“ makes sense or not. The argument of diversity being highest at an intermediate rate of disturbances (GRIME 1973; CONNELL 1978; HUSTON 1979; VAN DER MAAREL, 1988) „is circular and not particularly usefull ... unless the ‘intermediate` frequency of disturbance can be defined independently of its effect on species

diversity“ (HUSTON 1994, 122). Actually, such a definition must base on a geographical point of view, i.e. the analysis of the time and spacial structure of regeneration processes.

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Figures

Fig. 1: Types of vegetation dynamics (top) and types of regeneration (highlighted).
(fig. 1: 1-regmod fh5)

Fig. 2: Steps of regeneration processes within various vegetation types.
(fig. 2: 2-treefi. fh5)

Fig. 3: Illustration of plant distribution (left: 100 m²) and community patterns (right: 2.5 km²) in a highly heterogeneous semiarid Mediterranean garrigue. In contrast to the species-rich type of garrigue in the left figure, the one on the right shows a typical homogenous distribution of evergreen forest communities (models left, upper row: Circea / Latio, and right: Mani / Pelopones; left, lower row: Cinque Terre / Liguria and right: Kistenbosch / Cape Province).
(fig. 3: 3-meddiv.fh5)

Fig. 4: Illustration of plant distribution (left: 100 m²) and community patterns (right: 2.5 km²) in boreal coniferous woodlands (models: Fiby / Sweden and Kitwanga / British Columbia).
(fig. 4: 4-bordiv. fh5)

Fig. 5: Illustration of plant distribution (epiphyte patterns at lower left: 4 m², pattern of lower strata upper left and pattern of canopy strata upper right: 100 m²) and community patterns (lower right: 2.5 km²) in a tropical rain forest rich in epiphytes (models upper row: Huixtla / Chiapas; left, lower row: Zamora / Southern Ecuador and right: Leticia / Amazonia).
(fig. 5: 5-trodiv. fh5)

Fig. 6: Hypothetical evaluation of various diversity parameters under mean site conditions and an assessment of diversity change in the course of secondary succession influenced by human impact in different ecozones.
(fig. 6: 6-divzon.fh5)

Fig. 7: An attempt to allocate the extent of disturbances and self-preservation in various ecozones.
(fig. 7: 7-regzon.fh5)

Fig. 8: Space / time dimensions of different levels of disturbances.

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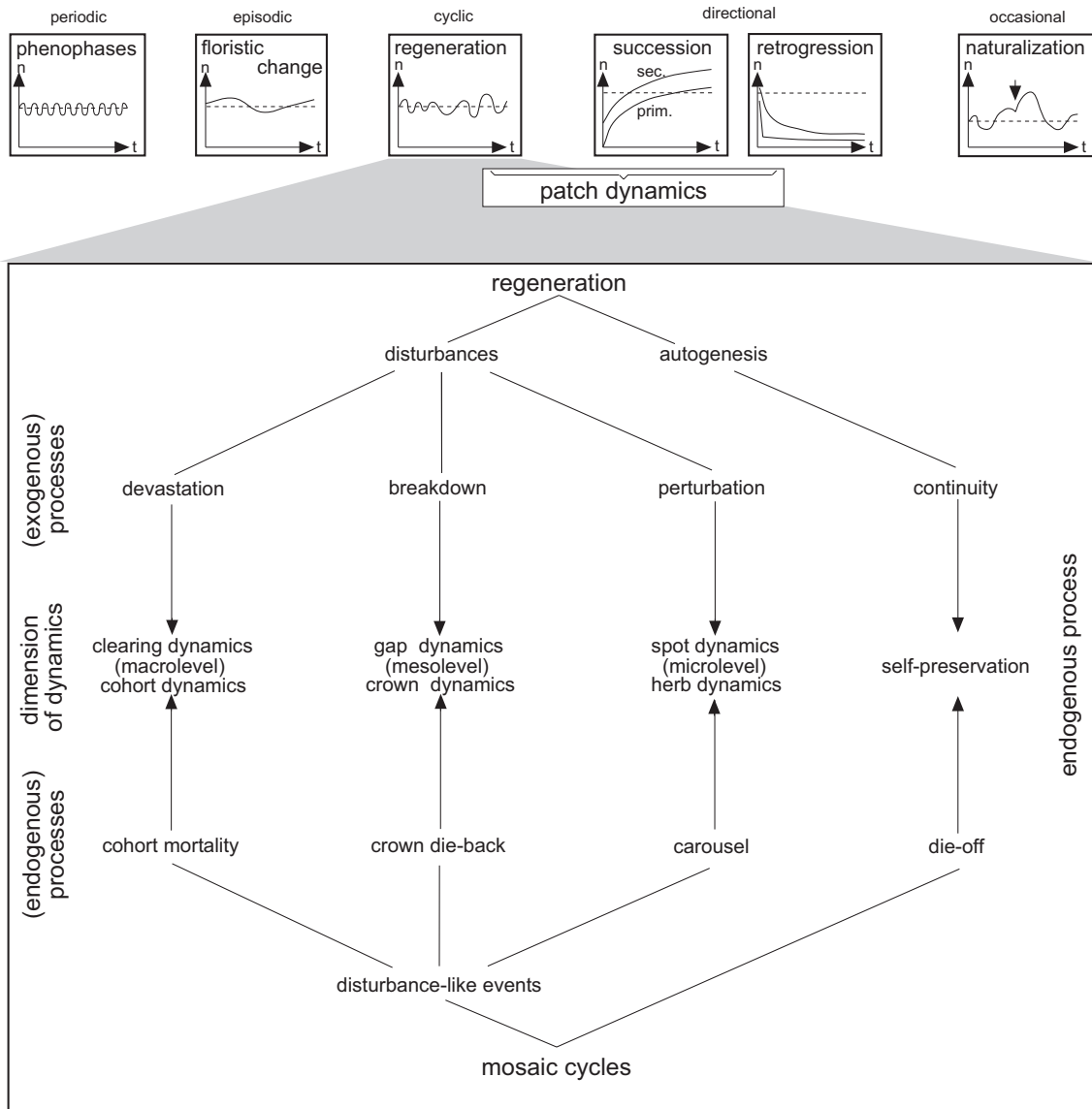
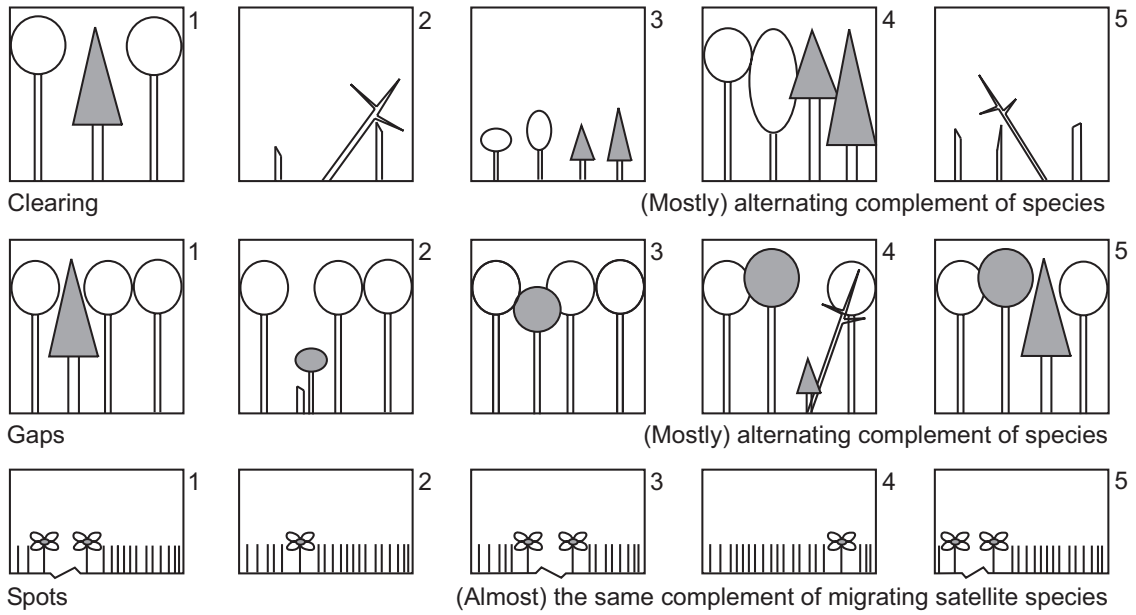


Fig. 2: Steps of regeneration processes within various vegetation types.

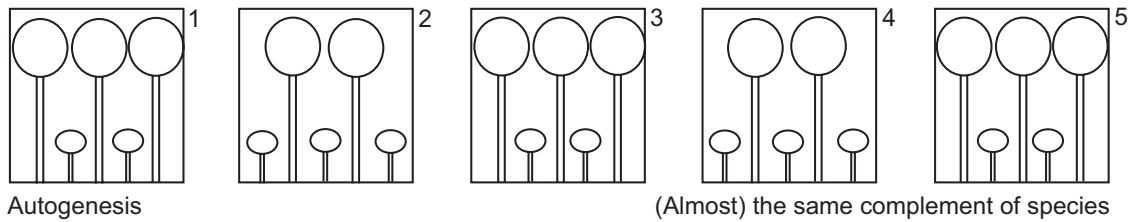
Disturbances:

Regeneration-types caused by exogenous processes:



Mosaic cycles:

Self-regeneration:



Regeneration-types by endogenous processes:

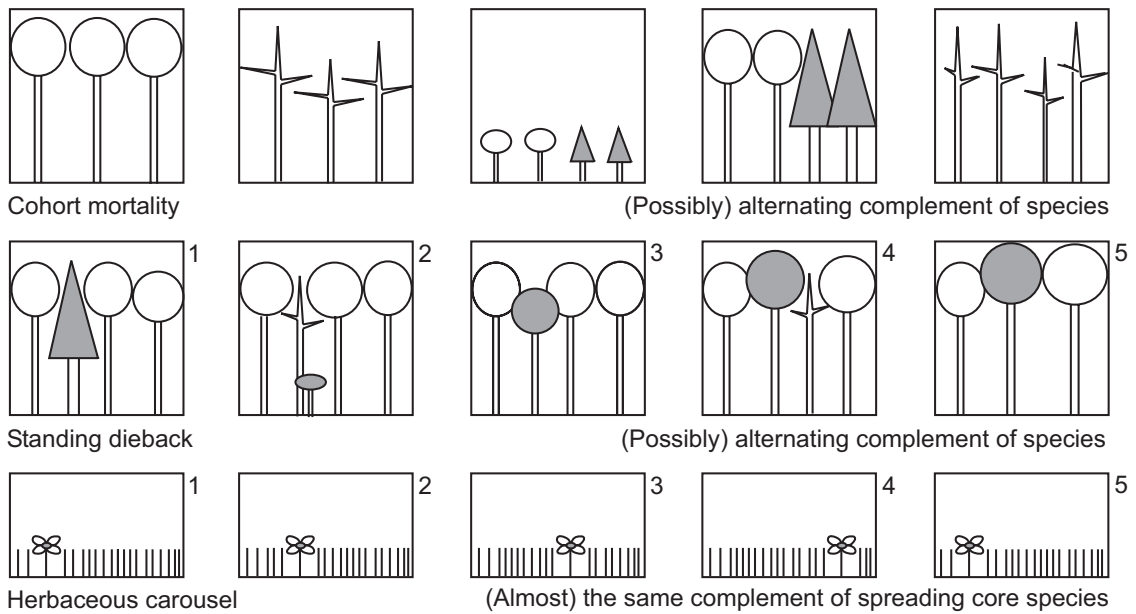


Fig. 3: Illustration of plant distribution (left: 100 m²) and community patterns (right: 2.5 km²) in a highly heterogeneous semiarid Mediterranean garrigue. In contrast to the species-rich type of garrigue in the left figure, the one on the right shows a typical homogenous distribution of evergreen forest communities (models left, upper row: Circea / Latio, and right: Mani / Pelopones; left, lower row: Cinque Terre / Liguria and right: Kistenbosch / Cape Province).

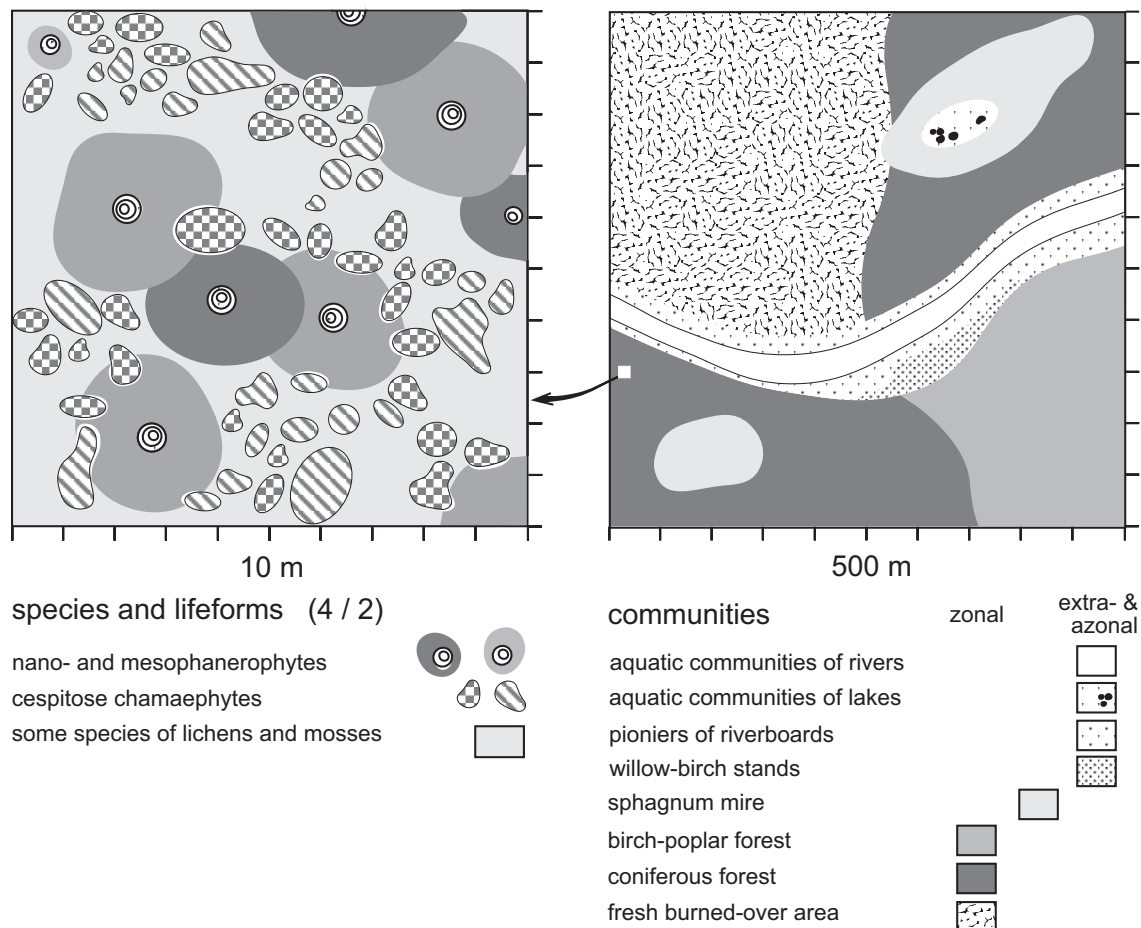
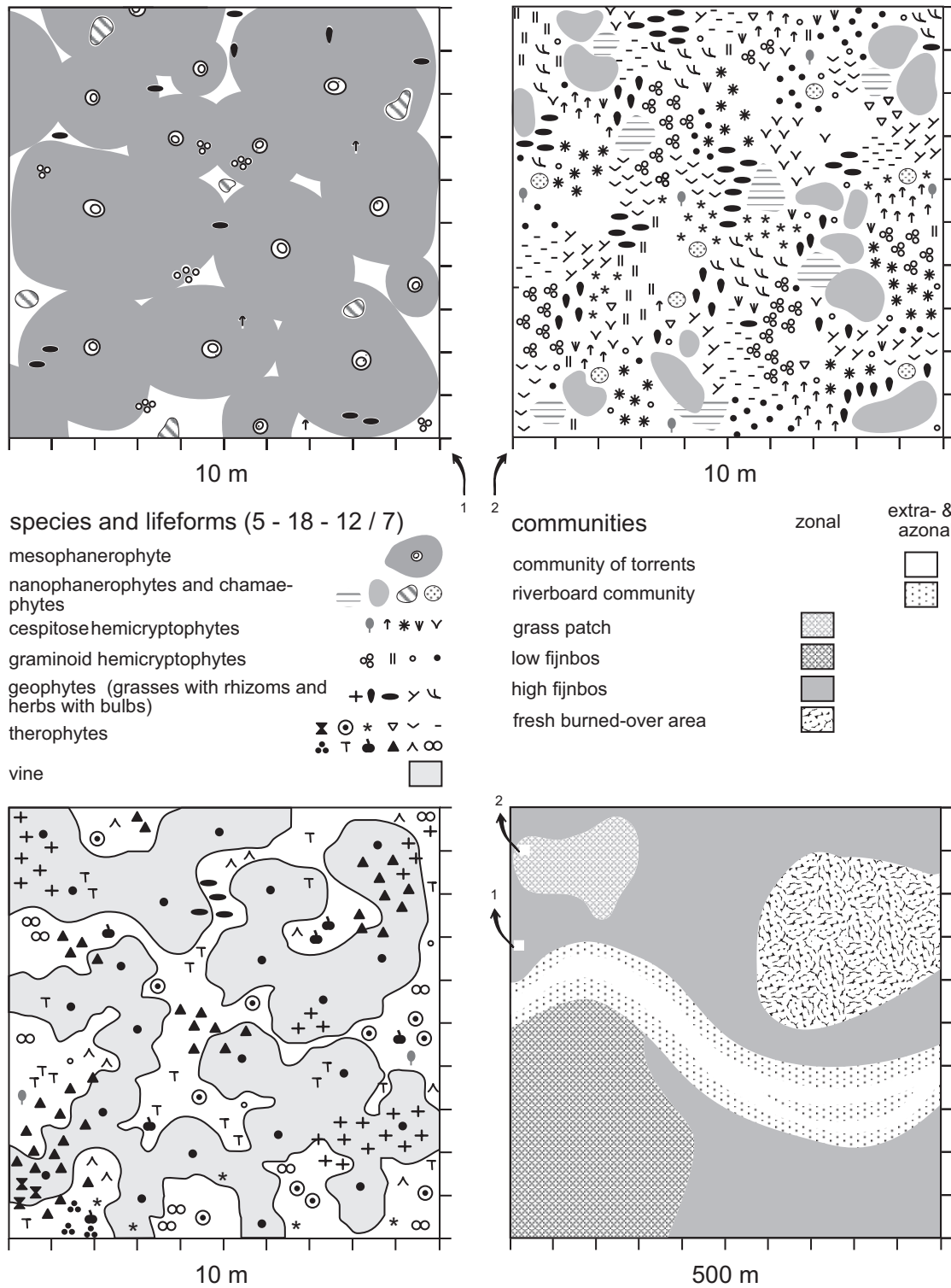
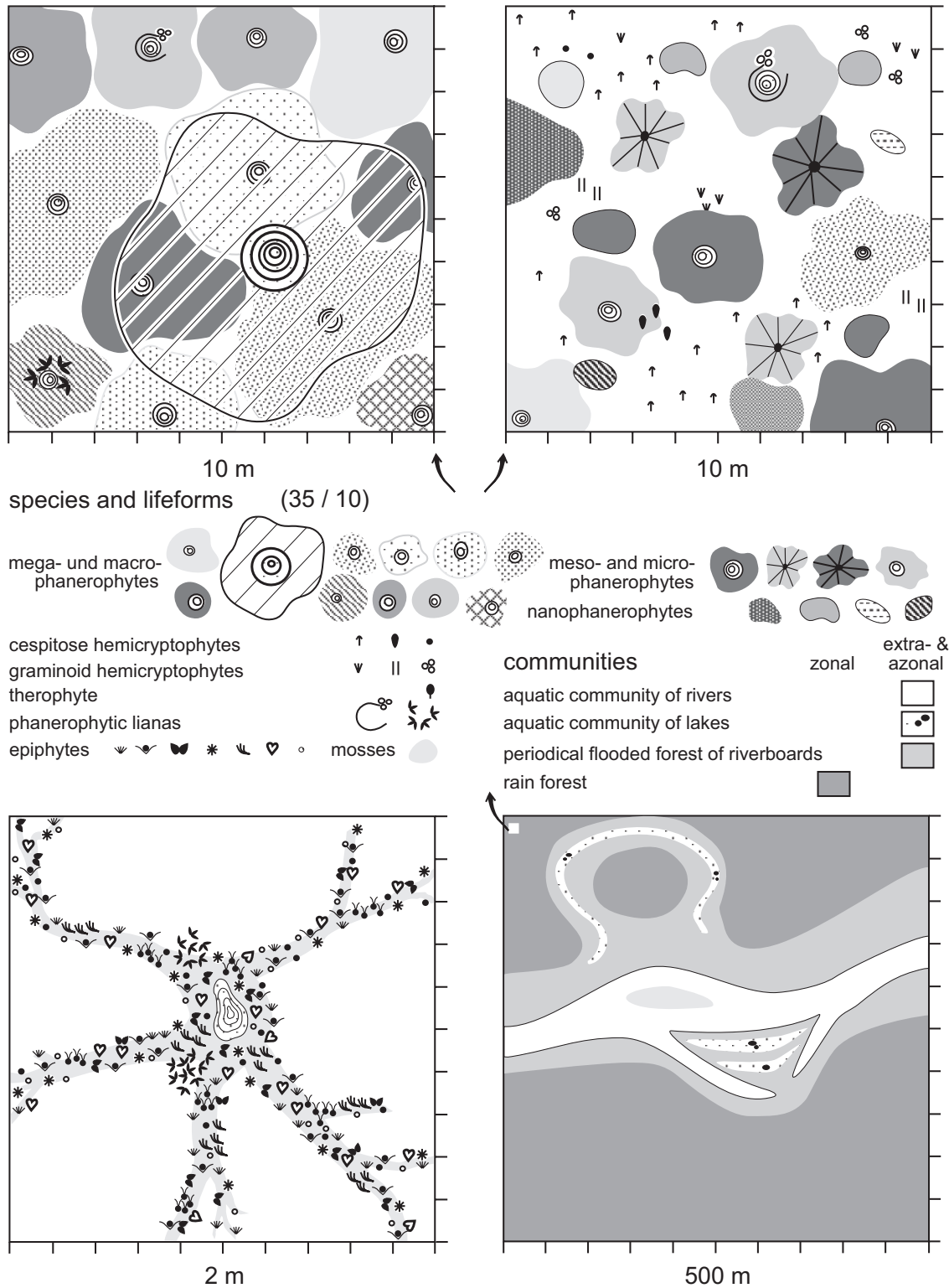


Fig. 4: Illustration of plant distribution (left: 100 m²) and community patterns (right: 2.5 km²) in boreal coniferous woodlands (models: Fiby / Sweden and Kitwanga / British Columbia).



5meddiv.fh5

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9trodiv.fh5

Fig. 6: Hypothetical evaluation of various diversity parameters under mean site conditions and an assessment of diversity change in the course of secondary succession influenced by human impact in different ecozones.

Types of diversity	Ecozones										
	1. Polar and subpolar tundra	2. Boreal woodland	3. Nemoral & austral woodland	4. Temperate steppe	5. Subtropical / tropical deserts	6. Mediterranean wood- and shrubland	7. Subtropical lauriphyllous woodland	8. Tropical savanna and deciduous woods	9. Tropical rainforest	a) extratropical	b) tropical
α -diversity (species per site)											
β -diversity (communities)											
γ -diversity (landscape)											
α -diversity trend within secondary succession	—			—							
trend of species number under human impact	—				—					—	
degree of ecosystem variability due to human impact							—				
<div style="display: flex; justify-content: space-between; align-items: center;"> <div> <p>diversity very high: </p></div> <div> <p>high: </p> <p>medium: </p> <p>low: </p> <p>very low: </p> </div> <div> <p>- + = direction of strong divergences, according to floristic regions and to disturbance systems</p> <p>p = development concerning only abandoned pastures</p> </div> <div> <p>trend strongly increasing: </p> <p>increasing: </p> <p>constant: —</p> <p>decreasing: </p> <p>strongly decreasing: </p> </div> </div>											

Fig. 7: An attempt to allocate the extent of disturbances and self-preservation in various ecozones.

		Ecozones													
		Types of disturbance		1. Subpolar Zone	2. Boreal Zone	3. Humid Mid-Latitudes	4. Arid Mid-Latitudes 4.1 Steppes 4.2 Semi-Deserts	5. Subtropical / Tropical Arid lands 5.1 Deserts / Semi-Deserts 5.2 Shrub steppes / Thorn savannas	6. Mediterranean Subtropics	7. Laural Subtropics	8. Seasonal Tropics	9. Humid Tropics	10. High mountains (above timberline) a) extratropical b) tropical		
Gelifluction		●	○	○	○	○	○	○	○	○	○	○	○	○	○
Ice / snow breakage		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Burrowing mammals		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Soil nutrient metabolism		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Game damage		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Storms / hurricanes		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Phytophages		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Frost		○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²
Flooding		○ ²	○ ²	○ ²	○ ²	○ ³	○ ³	○ ³	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²	○ ²
Salinification		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Drought		○	○	○	○	○ ²	○ ³	○ ²	○	○	○	○	○	○	○
Fire		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Denudation, incl. splash		○	○	○	○	○	○	○	○	○	○	○	○	○	○
Rapid mass movement		○	○	○	○	○	○	○	○	○	○	○	○	○	○

1 = in places devastation: e.g. hurricanes in the Caribbean or storms in western Patagonia	3 = rare, but effective
2 = frequent, but (mostly) ineffective	
Disturbative effects not present: ○ weak, seldom: ○ moderate, occasional: ○ significant, frequent: ○ severe, often: ○	

Degree of clearing dynamics	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Degree of gap dynamics	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Degree of spot dynamics	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Impact by mosaic cycles	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○

Fig. 8: Space / time dimensions of different levels of disturbances.

