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Reserves, Resilience and Dynamic Landscapes

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Reserves, resilience
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ABSTRACT

In a world increasingly modified by human activities, the conservation of biodiversity is essential as insurance to maintain resilient ecosystems and ensure a sustainable flow of ecosystem goods and services to society. However, existing reserves and national parks are unlikely to incorporate the long-term and large-scale dynamics of ecosystems. Hence, conservation strategies have to actively incorporate the large areas of land that are managed for human use. For ecosystems to reorganize after large-scale natural and human-induced disturbances, spatial resilience in the form of ecological memory is a prerequisite. The ecological memory is composed of the species, interactions and structures that make ecosystem reorganization possible, and its components may be found within disturbed patches as well in the surrounding landscape. Present static reserves should be complemented with dynamic reserves, such as ecological fallows and dynamic successional reserves, that are part of ecosystem management mimicking natural disturbance regimes at the landscape level.

Introduction

The Convention on Biological Diversity commits the 177 countries that signed it to conserve and sustainably use biological diversity. The long-term conservation of biodiversity requires an understanding of the processes that allow species to persist in natural as well as human-dominated ecosystems. During most of the 20th century, nature reserves and national parks have been a cornerstone in the preservation of species and natural areas. However, as more and more of the earth is modified by humans (1), the mismatches in scale between present nature reserves and the natural dynamics of ecosystems (2, 3) become more pronounced. This makes it even more difficult to achieve the goal of preserving biodiversity using reserves and national parks as the main tools.

Although reserves have been crucial for preserving species and habitats in the short term, with few exceptions they have not incorporated the long-term and large-scale dynamics of ecosystems as parts of dynamic landscapes (e.g. (2-5)). In this article, we argue that when the natural dynamics of communities and ecosystems are taken into account, a reconsideration is required of how reserves are designed and managed as parts of dynamic landscapes increasingly dominated by humans.

Reserves and national parks are geographically defined areas protected by the law in which human activities are restricted or prohibited (6). They are usually created with the intention to protect and preserve species and habitats, and are selected to maintain existing diversity and recreation values. Most reserves have been treated as static entities that should remain essentially the same and in the same place for centuries (7). Often, reserves are created to balance intensive land use in surrounding areas, and generally reserves have been placed on marginal lands (8, 9). With this approach there is a high risk of ending up with small areas of reserves as islands in an intensively managed landscape. Also, the spatial and temporal scales of organism and ecosystem dynamics in intensively managed landscapes will be determined by human objectives, often disconnected from the scales of natural processes (10).

Since less than 3 % of the earth's surface area (6.4 % of the land area (6, 9)) is protected, the traditional approach to nature reserves is unlikely to be sufficient for long-term biodiversity conservation. Neither will such a small protected area sustain the life-support systems and ecosystem services that humans depend upon. An alternative to the approach of static reserves is to recognize that

humans are a part of and not apart from nature, which implies that conservation of biodiversity and preservation of ecosystem services is of concern for all land use (11, 12). Ecosystem management has been advanced as a tool to preserve biodiversity in reserves as well as managed landscapes (e.g. (13-15)).

Ecosystems are subject to natural and human-induced disturbances at various spatial and temporal scales (5, 16). Recent work has shown that humans tend to manage frequent and sometimes intermediately frequent disturbances, without perceiving the slow and rare ones (17). This is also the case in present design of most nature reserves and parks. In the long term, it will be difficult to exclude large disturbances. Hence, an exclusive focus on static reserves as the main tool for biodiversity conservation will lead to failure of the very idea of nature reserves. To be useful, reserves should not be isolated and static, but be regarded as parts of dynamic landscapes. The long term goal should be to create resilient landscapes of high biodiversity that make reorganization after disturbances possible in the future.

The importance of recognizing natural disturbance regimes in reserve design was emphasized already by Pickett and Thompson (3). They argued that reserves should be designed based on 'minimum dynamic area', defined as "the smallest area with a natural disturbance regime which maintains internal recolonization sources" (our emphasis). However, for several reasons this criterion is difficult to apply in real situations. Firstly, in many areas of the world, such as Europe and the US Mid-West, the remaining patches of natural ecosystems are so small, scattered and surrounded by intensively managed land that minimum dynamic area within one reserve or reserve network is impossible to achieve. Secondly, recent work on natural disturbance regimes shows that large-scale rare events in ecosystems have been given too little attention (e.g. (16)). Hence, minimum dynamic areas depend on the time scale of interest. Thirdly, the projected global climatic changes make any reliance on internal recolonization questionable.

For the long-term sustainability of ecosystems and the services they generate, the preservation of biodiversity as insurance is often viewed as essential (11, 18). This means that a sustainable ecosystem - a system that remains functional - contains functional

groups that each have a large number of substitutable insurance species that may seem to be unimportant for the present structure and function of the system (18-20). We term this network of species, their dynamic interactions between each other and the environment, and the combination of structures that make reorganization after disturbance possible, the "ecological memory" of the system (21). One component of the ecological memory is the "biological legacies" discussed by, e.g., Turner et al. (23) and Franklin and MacMahon (24). The ecological memory is a key component of ecological resilience, i.e. the capacity of the system to absorb disturbances, reorganize and maintain adaptive capacity (25).

Different areas of the world have different history and hence different amounts of ecological memory available. For example, Europe has a much longer history of intense human exploitation of its ecosystems than comparable areas in North America. In most European forests the amount of biological legacies is small and declining because of centuries of intense forestry, while forestry still utilizes primary forest in many parts of North America. There is a long history of large mammal grazing by wild and domestic species in Europe, both in natural grasslands and in forests. In the US, many areas have for millennia lacked such grazers. There are also differences in property rights and institutions governing land use, not only between the US, Europe and many countries in the third world, but also within Europe. The historical use of the land has affected how nature reserves and national parks have been designed and where they have been located.

Our ideas on how to preserve biodiversity and create resilient landscapes are particularly relevant for maintaining diversity and building resilience in intensively managed landscapes in which only small scattered areas are preserved. They resolve many of the conflicts between the fine-filter (species) and coarse-filter (ecosystem) approaches to conservation discussed by Schwartz (26). They are also relevant for planning land use in areas which are under immediate threat from population expansion and economic development to become intensively managed, for example, in Eastern

Europe and many parts of the tropics, and for ecosystem restoration in areas where resilience is substantially lost.

Theory for dynamic reserves

The classical view of a single equilibrium in nature has until recently dominated conservation and management efforts, especially in government agencies but also in natural resource management research. It has been reflected in, for example, rules such as fixed sustainable yields, and popular notions such as the balance of nature. It has led to what has been referred to as the pathology of natural resource management (27). Such management tends to apply strategies that aim at preventing or excluding disturbances. Since disturbances usually are intrinsic parts of ecosystems, it will rarely be possible to exclude them. Some, such as fire and flooding, may accumulate to larger temporal and spatial scales (27, 28) and thereby causing large-scale impacts (see below for examples). Others happen anyway, for example, wind storms and pathogens. Recent ecological understanding of ecosystem dynamics across scales, and how to relate to such dynamics, is critical for successful management of nature reserves and their biological diversity.

The ecosystem renewal cycle

The heuristic model of ecosystem dynamics of Holling (e.g. (2, 29)) has evolved from field observations of dynamic processes in large-scale ecosystems. We refer to this model as the "ecosystem renewal cycle" (Fig. 1). The essence of this theory is that ecosystems are complex dynamic systems, in which functionally different states or multiple stability domains exist (e.g. (20, 30)), and that instabilities can move a system from one stability domain to another (a "flip") (e.g. (30, 31)). For example, many shallow lakes seem to have two stability domains, one with clear water and the other dominated by microalgae and a low water quality (30). Ecological resilience in this context is the magnitude of disturbance that can be absorbed by the ecosystem before the variables and processes that control its behavior changes, and moves it into another stability domain (4, 25).

Disturbances are part of ecosystem dynamics

The concept of the ecosystem renewal cycle implies that simply setting aside land as a nature reserve with the purpose to maintain it as it is without allowing for disturbance, will not secure the protection of biodiversity within the reserve. Such reserves, if they are too small to incorporate natural disturbance regimes (3), are social constructs disconnected from ecosystem dynamics. There are a number of well-known examples of this phenomenon, from high-diversity grasslands and meadows in Northern Europe, which were set aside by biologists without allowing for the grazing or haymaking necessary for their persistence (e.g. (32)), to Yellowstone National Park, where the suppression of small-scale fires led to an ecosystem that was more vulnerable to large-scale fire, when it finally struck (28).

Disturbances as pulses

Most ecosystems are subject to several disturbance regimes at different temporal and spatial scales. Natural disturbances usually are <u>pulse</u> disturbances with a characteristic magnitude and frequency, but human activities tend to transform pulse disturbances into <u>press</u> or chronic disturbances. For example, unrestricted grazing by ungulates tends to move across the landscape in a pulsed manner, while live-stock fenced by humans create continuous grazing and do not allow for recovery of the vegetation (20). Hence, the frequency and magnitude of the disturbance is altered. Moving from pulse to press disturbances reduces resilience (2). The significance of large and infrequent disturbances for ecosystem management is now increasingly recognized (16, 17, 33).

Reserves are open systems

Reserves are open systems and will be affected by land use change outside their boundaries, a fact recognized already by Janzen (34). Changes outside the protected area may alter the capacity of reserves to reorganize after disturbance.

Ideally, reserves should cover large parts of the landscape (e.g. (3)). However, since this is clearly impossible in a human-dominated world, reserves should be adjusted to natural landscape

dynamics. During some periods of the ecosystem renewal cycle, many reserves could be subject to sustainable resource use (sustainable being defined as maintaining the capacity for local reorganization in the landscape). Management of non-protected areas also needs to be adjusted to the dynamics of natural landscapes to conserve biodiversity in the long run.

The role of ecological memory

For a nature reserve to function in the longer term, there has to be a buffer to disturbance in the landscape that conserves the capacity to reorganize and recover from perturbations; there has to be ecological resilience. We refer to this capacity of buffering and renewal, generally depending on areas in the vicinity of the area affected by disturbance, as spatial resilience (35, 36). For example, for a forest ecosystem to reorganize (the alpha phase of Fig. 1) after a fire (the release phase of Fig. 1), there have to be nearby areas in the landscape not hit by the fire (still in the exploitation and conservation phases of Fig. 1). These areas contain the ecological memory contributing to ecological resilience and avoiding irreversible shifts between stability domains.

In practice, the ecological memory has several components (Fig. 2). One is internal or within-patch memory, which consists of the biological structures that serve as foci for regeneration and allow species to colonize, for example tree stumps and logs after a fire. It also includes those species that survive within the disturbed area (19, 24, 37). This part of the ecological memory has been extensively discussed in the recent literature on 'biological legacies' (e.g. (17, 23, 24)).

The other important part of the ecological memory is the external memory, which provides sources of and support areas for species colonizing disturbed patches (Fig. 2). Metapopulation biology and landscape ecology have highlighted the importance of spatial configuration for single-species persistence and management in fragmented landscapes (e.g. (38)), and Polis et al. (39) emphasized the role of surrounding habitats for ecological processes. Extensive work in biogeography (40, 41) has shown that variation in immigration and dispersal is important for species composition. Furthermore, recent studies have shown many plant species to be dispersal-limited (e.g. (42)). The concept of 'biological legacies' has not sufficiently considered these processes at the regional or between-patch level. The debate between those emphasizing colonization from external sources and those arguing that

biological legacies within disturbed patches are important has old roots, for example, in studies of the recolonisation of Krakatau (Backer vs. Docters van Leeuwen, cited in Thornton (43)). We find no conflict between the two components of the ecological memory, and depending on disturbance intensity and landscape composition their relative importance may vary.

Distinguishing between the internal and external memory is useful because it highlights the different ecological processes involved in within-patch and between-patch dynamics (Fig. 2). Within patches, the major processes can be viewed as "assembly rules" (e.g. (44)), e.g., facilitation of regeneration, competition and trophic interactions, that determine which species proliferate after a disturbance. However, to colonize, species have to disperse from patches in the surrounding landscape. In the latter case, processes affecting immigration, such as distance from source areas, the availability of dispersal agents, or structures attracting dispersal agents, become crucial for the way that reorganization of a patch proceeds (see below for an example of seed dispersers). These "dispersal filters" act mainly on the landscape level, and determine the availability of species after a disturbance. Another part of the external memory, not directly involved in dispersal and immigration but still determining the fate of disturbed areas, is organisms dynamically linking support and disturbed areas, e.g., herbivores and predators that have a large scale of their movements.

Natural and managed landscape dynamics

In landscapes with little human impact, the dynamics of the renewal cycles in different patches will usually be partly unsynchronized in time and space, leading to a mosaic of patches and successional stages. Many species depend on particular stages in the renewal cycles, and have evolved dispersal rates and other traits that are appropriate to persist in the natural mosaic landscape. In these landscapes, humans usually participate in and utilize natural processes and system dynamics, rather than imposing disturbances and synchronizing large-scale ecosystem dynamics (45, 46).

On the other hand, in modern intensively managed landscapes, differences between patches have been actively reduced (e.g. (47)). This has led to large areas having similar temporal dynamics, often favouring early-successional stages with their particular species. Thus the time to complete an ecosystem renewal cycle is considerably shortened. In temperate forests, the maximum age of trees is

around 300 years or more in natural stands, whereas it is less than 100 years in many managed forests (48). The disappearance of the natural mosaics results in the loss of species that do not have the capacity for long-range dispersal between suitable patches (38, 49), while many opportunistic species, such as pests, are favoured by the homogenization of the landscape (47). Intensively managed ecosystems thus tend to be depauperate and require high amounts of external energy inputs to be sustained.

Theoretical and empirical studies have shown that diversity usually increases with landscape heterogeneity (e.g. (38, 50, 51)). It is well established that species diversity has declined in modern managed agricultural and forest landscapes (e.g. (52, 53)). The lower diversity and more synchronized ecosystem dynamics in managed and fragmented landscapes are likely to lead to a lower capacity to recover naturally after disturbances, such as pest attacks or extreme climatic events (e.g. (47, 54, 55)).

The mismatch between reserves and disturbance regimes

An important consequence of these findings is that there is usually a mismatch between the size and temporal extent of many present-day nature reserves and natural ecosystem dynamics (Fig. 3). For example, in Sweden, median reserve size is approximately 0.2 km^2 (8). On a global level, the majority of the protected areas larger than 1 km^2 are nevertheless smaller than 100 km^2, and the size distribution is heavily skewed towards smaller areas (6). Many small-scaled disturbances, e.g., moderate trampling in grasslands and treefall gaps, can be absorbed at this scale by the component ecosystems, and do not threaten the integrity of the reserve. However, large-scale disturbances, such as cyclones or large fires in small reserves, will destroy reserves that are smaller than the combined area of the disturbance and the necessary ecological memory for reorganization. If the areas surrounding such a reserve do not contain sufficient spatial resilience in the form of (external) ecological memory to restore the ecosystems that were to be preserved, the reserve will fail its objective.

While the small spatial extent of most reserves and national parks is obvious, and has long been discussed in the literature (e.g. (26, 56)), the limited temporal extent of most reserves has not been commonly recognized. Many small reserves may not yet have encountered the disturbances that could disrupt their dynamics and connections to the rest of the landscape. In Sweden, the oldest national parks

are not even 100 years old, and apart from those in mountain areas they are much too small to contain all the stages in the renewal cycle (8). In Scandinavian forests, there is a shortage of medium-aged (100-200 years) forest stands that can replace the present old-growth reserves when these enter the release phase (Fig. 4). Hence, an even greater fragmentation of old-growth forests can be expected in the foreseeable future. This leads to a "resilience gap", i.e. a decrease in landscape resilience that in the long term will be detrimental to biodiversity and lead to increased uncertainty concerning the delivery of essential ecosystem services.

Case studies on ecosystem dynamics, disturbances and resilience

In this section, we discuss some examples of the dynamic nature of marine and terrestrial ecosystems, and how these reorganise after disturbances. Our key points are that disturbances are a part of ecosystem development, and that all reserves sooner or later will be subjected to disturbances. Therefore, the ecological memory of these systems, situated inside or outside the disturbed area, is of crucial importance for recovery.

Example 1. Coral reefs

Coral reefs are among the least protected of all natural ecosystems (57). The protected areas in coral reefs that have been constructed to date protect biodiversity, fisheries and recreational values (58). Reserves have been successful in several areas, leading to increased abundances of both targeted and non-targeted fish, inside as well as outside the protected areas (59, but see 60). However, with few exceptions such reserves have not addressed the problem of disturbances and long-term management of coral reef ecosystems.

The disturbance regimes and human impacts on coral reefs have been reviewed in (35) (Table 1). Today's reefs have experienced various disturbances ranging from small scale grazing, modest siltation and salinity fluctuations, to larger and more infrequent events such as outbreaks of the coral predator Crown-of-Thorns starfish, diseases and hurricanes (Table 1; Fig. 3). Some disturbances, such as grazing by herbivores, are so essential for ecosystem functioning that the real threat is the loss of the

disturbance, often leading to overgrowth by algae (e.g. (31)). Many corals are long-lived and therefore infrequent disturbance events are likely to occur during their lifetimes (61).

Present reefs are not only affected by natural disturbances but also those induced by humans. Human impacts include emitted substances such as oilspill, heavy metals and pesticides, and also actions that alter natural disturbance patterns (35). When already exposed to human-induced press disturbances reef systems show poor recovery after natural disturbance pulses (62), often resulting in alternative stable states of coral communities (30, 31, 33).

The ability to reorganise after disturbance is determined by surviving individuals (residuals), their spatial distribution, functions of mobile link organisms between reefs (36), the import of larvae from outside the area (all together constituting the ecological memory), and the time before the next disturbance. Coral reefs are open systems connected to surrounding ecosystems, i.e., other coral reefs, the terrestrial, riparian (mangrove) and sea grass systems, and the open ocean (63, 64). The openness depends on the location of the reefs, on the presence of mobile link organisms and the prevailing currents transporting plankton, nutrients and juveniles.

The Great Barrier Reef Marine Park (GBRMP), established in 1975, attempts to take natural disturbance regimes into account (65). A matrix of zones with different levels of protection has been developed to buffer against large-scale disturbances. In these zones different use categories are allowed, e.g. research, fishing and tourism. Protection of areas may also be limited to periods of particular interest, e.g. the breeding season (66). About 4% of the whole GBRMP area and 16% of the reefs are protected areas embedded within the multiple use areas. Much attention has been paid to the local ecological knowledge possessed by aborigines, fishermen and tourist operators (65).

Example 2: Forest dynamics

The ecosystem renewal cycle in forests gives rise to a coarse mosaic of patches in different stages of a forest cycle (67), initiated by disturbance and comprising a series of structural phases; commonly recognized are the (a) gap (in our terms reorganization), (b) building (exploitation), (c) mature (conservation), and eventually (d) degenerative (release) phases (68, 69). The build-up of ecological memory in the form of biological legacies and species in the mosaic landscape usually takes several

forest generations during which the soil is formed and nutrient pools and decomposer organisms are accumulated. Although it is common to characterize forest types by particular disturbance regimes, most forests are affected by various disturbances acting at different temporal and spatial scales (Fig. 3; 70-73). Organisms in natural forests have over evolutionary time adapted to the characteristic disturbance regimes of these forests. Boreal taiga forests and Mediterranean forests (74) are often disturbed by large-scale fires, while temperate deciduous forests, e.g., beech in Central Europe, mainly are affected by small-scale windthrows. Human activities have drastically changed the frequency, intensity and spatial extent of fires for centuries (75). In boreal forests, fires have been suppressed, whereas fire frequency has increased in many tropical areas (76).

Other disturbances in forests are biotic. Large-scale attacks by insects such as the spruce budworm may occur with 50-100-year intervals (2). Large herbivores have had large impacts on forests (e.g. (49, 73, 77)). In Europe, many forests have been grazed by domestic animals, but American forests were to a large extent allowed to develop without large herbivores after the last glacial, when human invaders extinguished most large mammals. The effects of large herbivores range from the small-scale effects on individual trees and creation of small glades, to the long-term and large-scale opening up of the forests, creating an open woodland with little resemblance to today's managed forest landscapes (49).

The gap/reorganization phase is of crucial importance in determining the floristic composition of the entire forest cycle (e.g. (67)). The pattern of reorganization among plants is often dependent on modes of dispersal and the presence or absence of dispersers. In tropical rain forests vertebrate frugivores are often the main seed vectors (78). In a lowland rain forest in Samoa disturbed by cyclones and fires, seedlings of species dispersed by birds or flying foxes were most abundant in the most severely disturbed area, but this was not the case in less disturbed areas (79). Remnant trees may attract seed-dispersers such as fruit-eating birds and bats (37, 80-82). Vertebrate frugivores can be viewed as keystones in the reorganization phase. In their absence succession would follow a different trajectory dominated by wind- and passively dispersed plants, and the risk of invasion of wind-dispersed exotic species may increase.

In both natural and managed forest landscapes it is essential that ecological memory is maintained. For example, the mycorrizal fungi necessary for regrowth after disturbances or clearcuts in

western USA require deciduous shrubs and trees as temporary host and "seedling" plants to be maintained (83). Preserving old trees when harvesting can favour the development of an old-growth mycorrizal community (84).

In Scandinavia, forest reserves constitute about 1 % of the forest area below the alpine zone (8, 53), and there are much too few large old stands (>100 years) that could become part of larger reserve systems. Dividing forest landscapes into large areas of intensively managed production forests and the remainder left as pristine reserves will not preserve biodiversity. The alternative is to manage most forest land for both production and biodiversity, combined with an expanded reserve system (48, 85). Indeed, as a response to markets demanding sustainable forestry, different practical forest management regimes promoting biodiversity are presently being developed throughout the world. A common view is that mimicking the disturbance regimes found in natural forest landscapes can provide management guidelines (Table 2; 71, 73, 85, 86). Incorporating natural ecosystem dynamics into large-scale management of landscapes for both biodiversity conservation and production of ecosystem services and ecosystem goods, such as timber, pulpwood, vodka and game, also seems more efficient than more traditional management plans (85).

Example 3. Disturbance regimes in mountain regions in Scandinavia

In the Scandinavian alpine and subalpine regions, dominated by heaths and mountain birch forests, the first national parks were established in the beginning of the century. In these low-diversity ecosystems, the vegetation is relatively little influenced by human activities. Local resource users have for a long time been integrated components of these ecosystems, through reindeer grazing, hunting and fishing.

Among the major disturbances are grazing by rodents, reindeer and moth caterpillars (*Epirrita autumnata*) (87-90). These occur as pulses with different frequencies and spatial scales (Table 3). Rodents are usually cyclic (e.g. (87)) and play a role in the maintenance and dynamics of dwarf shrubs and mosses (88). Reindeer,

controlling the abundance of lichens, traditionally grazed in a pulsed manner both between years on single sites and regionally on a longer time scale as reindeer populations waxed and waned on a 30-50 year cycle (89). Fire occurs irregularly, and affects dwarf shrub composition, favouring *Vaccinium* at the expense of *Empetrum* (91).

During at least the last 500-1000 years, these areas have been used and managed by the nomadic Sami people. Their semi-domestic reindeer herds migrated between summer grazing lands close to the Atlantic coast in Norway and winter grazing lands east of the mountains in the extensive lichen areas of the boreal forest.

Major changes in the disturbance regimes have occurred during the last 20-30 years. Large-scale regulation of rivers for hydro-electric power led to large decreases in fertile grazing lands in valleys. Forest management uses large-scale clearcuttings. There have been changes in Sami culture and reindeer management through mechanization, permanent settlement, and the radioactive fallout from the Chernobyl accident in 1986. The natural migration routes of reindeer between Sweden and Norway over the mountains have been cut off by fences, concentrating grazing to certain areas, with the Swedish reindeer staying in the high mountains during summer, and the Norwegian ones in the high mountains and high plateaus during winter.

Although the causes of these changes are still debated, there is a growing consensus that reindeer numbers probably are too high and grazing too concentrated to certain places for the sustainable use of the mountains. Especially inside fences, the vegetation is not allowed to recover between grazing pulses (92-95). It is likely that a breakdown of the sustainable use of the mountain areas is occurring because of socioeconomic changes as well as management institutions not being matched to the natural scales of the disturbance regimes. Setting aside large static reserves excluding the land use of indigenous people would hardly ameliorate this situation. However, if we recognize the dynamic nature of the mountain ecosystems and the rights of the Sami and other local residents to use these areas for their subsistence, another approach is more likely to be successful. This includes the removal of fences that hinder the natural

migration routes, and a dynamic reserve or set-aside system aimed at restoring the semi-natural dynamics of mountain ecosystems, with their pulsed disturbances.

Synthesis - a new approach to biodiversity management: Building resilient landscapes

These examples illustrate our main points: Ecosystems are subject to pulse disturbances at various spatial and temporal scales. Reorganization requires ecological memory which is found both inside and outside the area of disturbance. Changes in disturbance regimes can have large-scale ecological and socioeconomic consequences. Hence, disturbance regimes and ecological memory need to be incorporated in ecosystem and biodiversity management.

The recent papers on large infrequent disturbances (16, 23, 33, 72) seem to assume that there is always a set of species and functional groups available for ecosystem reorganisation. Given the present human transformations of the planet and the ensuing loss of diversity, this cannot be taken for granted. Reserves have earlier been treated as if they will not be disturbed, or will quickly recover from disturbances. To us, this implies that reserves have to be large and with a substantial internal ecological memory that ensures rapid reorganization (Fig. 5a). However, as reserves become increasingly smaller, the internal memory sooner or later becomes insufficient for rapid reorganization, and they become more and more dependent on patches in the surrounding landscape, i.e. the external memory (Fig. 5b). In a highly fragmented and intensively managed landscape (Fig. 5c), the external memory will be degraded, more distant and reduced, most likely leading to a much longer time period for reorganization. This represents a reduced resilience which increases the probability that ecological surprises may occur. For example, after a disturbance reserves in areas with little ecological memory could develop into something completely different in terms of plant and animal composition. Static reserves require an existing diverse internal and external ecological memory that is not available in the intensively managed landscapes that cover most of the world. Thus, simply setting aside such reserves will be insufficient for maintaining biodiversity and ecosystem functioning in the landscape.

Additional approaches to static reserves smaller than minimum dynamic areas (3) are required. As a first step in this direction, we propose the development of several new types of <u>dynamic reserves</u> to

be used in sustainable management and biodiversity conservation at the landscape level. The purpose

with dynamic reserves is to maintain enough diversity within and among functional groups to secure

buffering capacity and sustainable use of natural resources. In this way, human activities are not

separated from biodiversity conservation.

There are several different views on the role of reserves for biodiversity conservation and

sustainable land use. At one extreme is a view that has put excessive focus on static reserves and has led

to a discussion focussed on the size and connectivity of static entities (e.g. (96)). It has put humans

outside ecosystems, and divided ecosystems into those that should be conserved and those that can be

used or exploited to their full (short-term) capacity (Fig. 6a). This view implies that protected areas are

not needed for production landscapes dominated by humans ("1" in Fig. 6a).

A second less extreme view of static reserves recognizes that protected areas may function as

seed or source areas creating disperser pressure to production landscapes (Fig. 6a, indicated by "2") and

hence be useful for production of ecosystem services in production landscapes. According to this view,

reserves preserve biodiversity and function as insurance for the rest of the landscapes surrounding them.

Both these views tend to emphasize a <u>conflict</u> between conservation and land use. They have

neglected the fact that smaller reserves hit by large disturbances will not be able to reorganize unless

there is ecological memory available <u>outside</u> the disturbed area, i.e., in the production landscapes. The

presence of this memory depends on how the landscape outside reserves is managed. This leads to a

third view that in managed landscapes there is a strong need for insurance reserves that secure

resilience by preserving biodiversity in those managed landscapes (Fig. 6b, indicated by "3").

The new types of temporally and spatially dynamic reserves that we propose should be placed

both in human-dominated production landscapes and in more pristine ecosystems. Many of them will

have a limited temporal extent, and be part of management of whole landscapes rather than of single

socioeconomic units such as farms or woodlots. It may be easier for land-owners to accept a temporary

limitation on their use of their land, rather than the dead hand of a static reserve.

"Ecological fallows" would be areas set aside for natural or low-intensity managed succession

immediately after a disturbance (release) event. As time goes by some management and resource

utilization can be allowed, and finally the reserve may not be needed. For example, after clearcuttings or

forest fires fairly large proportions of the affected area could be left as ecological fallows for natural

regeneration and succession. Selective logging of the growing and mature mixed forest by modified

logging techniques could later be allowed.

"Ephemeral reserves" aimed at preserving species in the early succession or exploitation phases

that otherwise may be threatened by large-scale intensive management, would be even shorter in

duration. Land-owners should clearly see when they are finished within the time of their management

plans.

In "mid-succession reserves" the necessary management, in contrast to static reserves, can be

allowed to cease or change in parts of the landscape, if there are other nearby areas providing

continuity. This type would be appropriate for habitats such as grazed grasslands. Another type of

"dynamic successional reserve" can be set aside early in the exploitation phase. Succession is allowed to

continue unmanaged until the area is hit by a disturbance (release), whereafter other types of

management can be allowed, given that other areas in the landscape provide temporal continuity.

Imperative to all these new types of reserves is that they <u>must</u> be part of management at the

landscape level, that is, on a spatial scale of 10-100 km^2 or more, although the size of the actual

reserves can be much smaller. Hence, they will impose restrictions on land use of single landowners,

such as farmers or forest and fishery rights owners. In the European tradition, restricted use has usually

been achieved by establishing reserves, but in other traditional landscape management systems sacred

groves, customary marine tenure areas, and watershed management such as in ancient Hawaii, are

examples of institutions with the same function (45). A major question currently under debate is how

management on the landscape level, such as forest certification schemes, can be implemented where

there are many small landowners and where strong property rights are the rule, such as in many parts of

Europe (97).

Sustainable use of the services ecosystems provide is unlikely without improved understanding

of ecosystem dynamics. Management practices and institutions need to be matched to the structure and

dynamics of ecosystems (10). This requires capacity of social systems to monitor change and to build

institutions (formal and informal norms and rules) that make it possible to respond to feed-back signals

of the environment (10, 45). In a similar way to "ecological memory", an "institutional memory" , i.e.

an accumulation of experiences concerning management practices and rules-in-use, is important for

maintaining the linked ecological-social system during periods of change or crisis (98).

Conclusions

We argue that there is a need for a paradigm shift toward dynamic reserves in the design and management of nature reserves. This is necessary if the goal of long-term biodiversity conservation and socioeconomic sustainability in a changing world is to be achieved. We do <u>not</u> suggest that the present-day static reserves should be terminated. Our main point is that many reserves need not be static entities, but be part of large-scale dynamic and adaptive landscape management. This will require new incentive structures that coordinate a diversity of stakeholders, including those of agriculture, aquaculture, forestry, fisheries, water management, urban development and nature conservation.

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Table 1. Natural disturbances in coral reefs at different spatial and temporal scales (Adopted from 61).

Process	Spatial extent	Frequency	Duration
Predation	1-10 cm	Weeks-months	Minutes-days
Damselfish gardening	1 m	Months-years	Days-weeks
Coral collapse (bioerosion)	1 m	Months-years	Days-weeks
Bleaching or disease of ind. corals	1 m	Months-years	Days-weeks
Storms	1-100 km	Weeks-years	Days
Cyclones	10-1000 km	Months-decades	Days
Mass bleaching	10-1000 km	Years-decades	Weeks-months
Crown-of-Thorns outbreaks	10-1000 km	Years-decades	Month-years
Epidemic disease	10-1000 km	Decades-century	Years
Sea-level or temperature change	Global	10 000-100 000 Yrs	1 000-100 000 Yrs

Table 2. Characteristics of forest disturbance regimes and proposed management strategies for

biodiversity conservation.

	Large-scale disturbance and succession	Frequent low-intensity disturbances	Small-scale gap-phase dynamics
Variation in tree age in stand	Low	Distinct cohorts	Very high
Time to reach desired condition for biodiversity conservation	From hours/days for burned stands to >150 yrs for old-growth	Several centuries for large size woody debris	About 300 years for the development of structural diversity
Management	Prescribed burning, tree retention and maintenance of tree species diversity in younger successional stages. Large reserves are needed for old-growth conservation.	Prescribed burning, increased tree retention, maintenance of several cohorts of living and dead trees	Single-tree cutting or very small clearcuts. In reserves without management

Table 3. Natural disturbance regimes in Scandinavian mountain areas.

Disturbance agent	Spatial extent	Frequency	Duration
Rodent grazing	m^2 to ha	3-10 years	1-2 years
Reindeer grazing	km^2	30-50 years	1 year
Epirrita outbreaks on birch	10-1000 km^2	30-100 years	2-3 years
Fire	m^2 to ha	irregular	days

Figure legends

Fig 1. The renewal cycle of Holling (2, 29). The first part (from exploitation to conservation) is the

classic ecosystem succession. Exploitation is dominated by opportunistic species (r-strategists)

rapidly recolonizing recently disturbed areas, and the conservation phase is characterized by slow

accumulation and storage of energy and material. Two more phases are required to more fully

capture the dynamics of ecosystems. The third is the release phase in which tightly bound energy and

material are released by some disturbance (e.g. forest fire or insect outbreaks), and the fourth is the

reorganization phase where species and processes in the system reorganize to start another lap in the

renewal cycle. At this time, ecosystems may 'flip' into new stability domains depending on which

species that are available to colonize the disturbed area.

Fig. 2. The ecological memory is the network of species, their dynamic interactions between each other and

the environment, and the combination of structures that make reorganization after disturbance possible.

Its composition is determined by the past ecological and evolutionary history of the system. The

ecological memory can be divided into the internal memory present within the disturbed area (also

termed biological legacies; 23, 24), and the external memory that provides source areas and propagules

for colonization from outside the disturbed area (components of spatial resilience; 36). Grey colour

indicates the disturbed area.

Fig. 3. The mismatch between the spatial scales of most nature reserves and natural ecosystem dynamics in

forests (upper panel) and marine environments (lower panel). Spatial and temporal scales of important

disturbance agents are shown (modified after 4). Grey areas indicate approximately 50% of the reserves

(based on data in 6 and 8 for forests, for marine reserves from 99).

Fig. 4. The age structure of forests in central Sweden (data from 53). There is a shortage of forests older

than 150 years that can become oldgrowth stands when the present oldgrowth reserves enter the

release phase, i.e. there is a <u>resilience gap</u>. Area in 10^6 ha.

Fig. 5. Reorganisation of reserves as dependent on the amounts of internal and external memory. In (a), land-use is least intense, reserves are large and rapid reorganisation is achieved through a large internal memory. In (b), land use is of medium intensity and the area of reserves is smaller, but the smaller internal memory is compensated by the external memory in the surrounding landscape. In (c), the landscape is heavily modified by human activities, reserves are small and scattered, and the diminished external memory in the surrounding fragmented landscape is not sufficient to allow reorganization.

Fig. 6. Different views (charicatures) on the function of reserves. Grey area represents reserves, white area production landscape.

(a) Static reserves separating protected areas and production landscapes. In the long run, static reserves will be subject to disturbance. Lack of ecological memory in production landscapes will postpone or prevent recovery after disturbance.

(b) Dynamic reserves and protected areas as management tools in sustainable production landscapes. The conflict between conservation and use in (a) is removed in (b) for enhancement of resilience in protected areas as well as production landscapes (see also text).