Landscape ecology as a theoretical basis for nature conservation,,,

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Abstract

Conservation of representative biotopes, single species populations or biodiversity usually embraces two or more biotopes, and is often affected by surrounding croplands. The conclusions from landscape ecological studies can, therefore, offer important contributions to conservation, especially at early levels of landscape change or habitat fragmentation. Indicator and keystone species are useful for monitoring and managing fragmented biotopes, respectively. Communities as well as single species are affected by the juxtaposition of successional and climax biotopes, which influence climatic equability, seasonality, productivity and dispersal. Low levels of fragmentation may result in ill-functioning communities, and greater fragmentation may result in species losses and ultimately in the loss of whole communities. Fragmented habitats retain species with high reproductive and dispersal rates and generalized habitat selection. New combinations of interacting species will lead to trivialization of earlier habitat-specific interactions. Validation of these concepts was made with data from a Swedish research program on fragmented biotopes in production landscapes. General reserve selection and methods of management for preserving climax communities, single specialized species and high biodiversity are suggested.

Approaches to nature conservation

Nature conservation is a comprehensive aspect of land management, embracing ecology, economics, perception and value judgment. There are many ideas on what to conserve in nature (e.g., Usher 1986). Three main approaches to conservation are: a. Conservation (or just preservation) of representative biotopes (pieces of land with particular types of nature), including natural communities and ecological processes. b. Conservation of endangered plant or animal species populations, usually includ-ing their habitats. c. Conservation or establishment of high biodiversity areas for recreation or pedagogic purposes.

Conservation efforts seldom cover large homogeneous areas and, in the long run, tend to preserve structures but not processes. Either heterogeneous areas, with two or more intermingled biotopes (e.g., in large national parks), or small homogeneous biotopes (e.g., habitats of endangered species) surrounded by agricultural or forestry land are conserved. Reserves are actually patches linked to a surrounding matrix (Janzen 1983). Thus, con-

sideration of landscape functions is needed in all these approaches to nature conservation.

In this paper we examine whether the concepts of landscape ecology are important in conservation. We analyse the importance of reserve size and the type and extent of the surrounding matrix. The effects of landscape composition on communities and populations in the reserves are deduced. Our conclusions are compared with the results from a recent research program on fragmentation consequences.

Approaches to landscape ecology

Although landscape ecology is a fairly recently developed discipline, traditionally it has emphasized human-perceived biotopes as patches or matrices in heterogeneous landscapes (Forman & Godron 1986). Another more recent approach is to consider the landscape from the point of view of separate species. Thus, boundaries, corridors and patch sizes are perceived differently by various species such as mice and men. Comprehensive studies can disclose how landscapes are perceived and scales are experienced by separate species. Greater problems arise when considering the ways interacting species, or whole communities, integrate landscapes (Wiens 1989).

The conservation of separate species might exploit species-specific perceptions and use of a landscape, if such species populations were only dependent on the structures of a species-specific habitat or landscape. However, many species are predators dependent on prey, which moves and utilizes other habitats. Competition or predation may also cause other species to use habitats differently from humans, e.g., avoiding edges or adding extra edges as hunting areas. As a result, analyses relying on animal perceptions may get too complicated for managing species that are dependent on a surrounding community or for managing whole communities. Furthermore, technical and economic considerations usually dictate that traditional landscape components be managed. Animal perceptions, if actually discovered, may be expressed in human terms, such as forest patch + 10 m of the surrounding fields. However, if these species-

specific perceptions differ profoundly from ours and are important for species conservation, then very complicated landscape analyses may be necessary. Future conservation and management have to be based on compromises between organism- and human-perceived landscapes and scales, unless very large areas can be preserved. Conservationists have hardly begun analysing this dilemma.

This problem becomes still more important when considering the usefulness of indicator species, *i.e.* species characteristic of a certain biotope and used for monitoring its present quality. An indicator species perceives and exploits a specific habitat that usually does not completely match the human-perceived biotope or covers a larger landscape area. This is one concern about the use of indicator species in general (Landres *et al.* 1988), but it may be alleviated by selecting a 'management guild' (Wilcove 1989), where the contours of the habitat images of several separate species will cover the biotope or landscape area as well as possible.

Area1 restrictions causing new ecological processes

Natural habitats or biotopes occur only as small remnants in production landscapes in many parts of the world. Often, they can be easily 'developed' and are thus expensive. Only a few remnants or small parts can be purchased or hired for national parks or nature reserves. It is possible to legislate against management that may damage species or ecological processes in such valuable natural areas, and such restrictions are often applied within "landscape protection areas". However, in most cases the protected areas are fairly isolated islands in a sea of production land. Certain biotopes can be preserved as 'archipelagoes' and others only as separate patches or 'islands'; the fragmentation may be gradual or abrupt in both time and space.

Isolation causes several problems for both the species and the communities to be protected. Recent interest in conservation biology (e.g., Soulé 1986, 1987) has centered on island biogeographic (e.g., One Large Or Several Small reserves? – the 'SLOSS' question) and population problems. Recent theoretical studies (e.g., Goodman 1987) have

demonstrated great risks for stochastic extinction of species appearing in low numbers. A large, and partly controversial, literature has developed around this theme (cf., e.g., Gilpin 1988), and it will not be analysed further here (see the SLOSS discussion by, e.g., Soulé and Simberloff 1986). However, the possibility of stochastic extinction, especially of vertebrates and other sparsely occurring animals (or plants) in habitat patches, probably due mainly to environmental variability, should be of great concern. The general SLOSS problem seems in principle unsolvable, as the extinction risk is strongly dependent on species-specific demographic and genetic conditions and levels of environmental correlation between habitat patches (Boecklen and Bell 1987, Gilpin 1988, Burley 1989). Still, it may be a pseudoproblem, as other landscape and regional conditions may be of much greater concern.

The conservation approach discussed so far covers mainly the final dynamics in diminishing populations; extinction may be truly stochastic in this phase. It has been considered the main important process in landscape planning (Balser *et al.* 1981). However, other causally more predictable processes occur at an earlier level of fragmentation and may be more important for rescuing communities and species populations that are still in a natural state. Two factors are of great concern: First, species preserved in a nature reserve (or managed for persistence) may depend also on habitats that occurred earlier in the neighborhood but have been transformed into productive land. The segregation between habitats for nesting and hunting are well known for many mammals and birds, but also smaller animals, such as insects, may need several habitats, e.g., for reproduction and hibernation (Dingle 1985, Solbreck 1985). The second factor relates to negative influences from the surroundings, e.g., in the form of competition or predation. Such effects will be most severe at the edges of the habitat fragments, and small fragments are comprised of nothing but edges (Levenson 1981).

Communities and ecological processes will be affected as much as the central species ('keystone species', being bases for whole (sub)communities), which are dependent on missing habitats or are in-fluenced by processes external to the community (Janzen 1983). Indicator species, which often are fairly rare, will not perpetuate disturbance to the same extent as common keystone species. Indicators may thus not demonstrate the importance of natural mosaics or external influences equally well for whole communities.

Generally, the more homogeneous the environment has been in both space and time the more likely the system is to have low fluctuations and low resistence to disturbance (Holling 1973). A regime of natural perturbations should lead to a high diversity of dispersal and recovery strategies. Thus, the greatest problems with fragmented habitats should be expected for those communities that developed in relatively uniform and temporally constant environments. Boreal communities may show more resilience upon fragmentation than the tropical species now rapidly vanishing, but still the species and communities of the forest interior are at great risk (Temple and Cary 1988). Species that survive habitat fragmentation are characterized by high dispersal and reproductive rates and generalized habitat selection permitting large-scale movements, and seasonally migrating species may be favodred over resident species (e.g., Väisänen *et al.* 1986).

Influences from new environments

Protected biotopes or ecosystems are usually of a climax type or comprise climax stages; production landscapes usually contain various secondary successions that are abruptly restarted after cropping at a premature state. The environment (or 'matrix') of the protected areas will, under such circumstances, consist of more productive land (primary production higher than respiration, cf. Odum 1971, Table 9-l for a general comparison of successional and climax habitats), open nutrient circulation and unpredictable changes in gross productivity. Animals adapted to such biotopes are more 'r-selected' (Pianka 1978), with high reproduction and low survival (often generalized annual species). The physical environment is more variable in open croplands as compared to climax forest. The successional croplands and forest stages show a large

Table 1 .ᐟComparison of physical and biological effects (+ signs indicate the comparatively highest level) of matrices consisting of successional ('grasslands') and climax ('forest') ecosystems.

Effects	Matrix	
	Forest	Grassland
Climatic equability	+	-
Seasonality	-	+
Permanence	+	-
Gross productivity		+
Shelter	+	-
Predation	-	+
Niche generality	-	+
Mobility	-	+

seasonality due to cropping and restructuring (Table 1). Other combinations of climax/successional stages at reserve borders are possible, especially in afforestation regions, but globally they are less common.

Close arrangements of reserves and matrix will result in a changed physical environment in the border of the reserve, usually expressed as greater temperature variability and exposure. Similarly, dispersal inward by allochtonous and generalized species will be greater than movements of indigeneous species (especially the specialized ones) through the matrix to distant biotopes of similar kind. Predation rates will generally be greater in the matrix, due to a higher overall productivity in that environment (Angelstam 1986), and, as a consequence, also at the edges. However, it may increase abruptly at the matrix seasonal turnover, and predators may then invade the reserve; there will be a shift in community composition, at least at the edges or in the whole of small reserves. Movement patterns of climax species also will change when small patches are surrounded by foreign habitats; such species may use the landscape after fragmentation in a coarse-grained fashion (including several habitats within their ranges) rather than in the fine-grained fashion under more natural conditions. This may affect the social behavior and reproduction of such species.

The matrix may vary in composition of biotopes and productivity. Very intense agriculture will provide little surplus for wildlife and influence reserves less than extensive agriculture and forestry, where

a lot of surplus production is utilized by generalized species. The relative human exploitation of matrix production should be assessed.

Keystone species are characterized by being especially well adapted to one or more biotopes of a reserve and by showing long-term persistence there. Changes brought about by matrix influences may affect populations of such species more or less severely and will be easily passed on to dependent species. Keystone species may be at the bottom or top of food webs depending on the type of community regulation (Pimm 1982); those at the bottom (plants) are very common but usually sensitive to changes in climate, light or soil processes, and those at the top (predators) are rare and easily affected by landscape alteration as they often use several habitats. As a consequence of numerical or qualitative changes in populations of keystone species, communities will be transformed, and there is a high probability that certain species, e.g., specialized predators or pollinators, will be lost. Communities are probably affected functionally at a lower extent of habitat fragmentation than are species numbers. Complete communities, however, will be lost only at a high level of fragmentation, especially if generalized consumers are important components of these communities and species can be replaced with little change in function (Fig. 1).

Types of emergent populations and communities

Several types of more or less spatially structured populations may occur under original circumstances. The simplest, but not necessarily the most common type, consists of a homogeneous population with a spatially continuous surplus of offspring. This is the common population envisioned in textbooks. Another configuration may include local sources and sinks (Pulliam 1988), which are either spatially constant or variable. A special case of metapopulation, described by Levins (1969) and often used for developing new models in conservation biology, consists of similar-sized local populations with a dynamic balance between immigration and extinction, and thus with long-term persistence. In exploited or transformed landscapes there
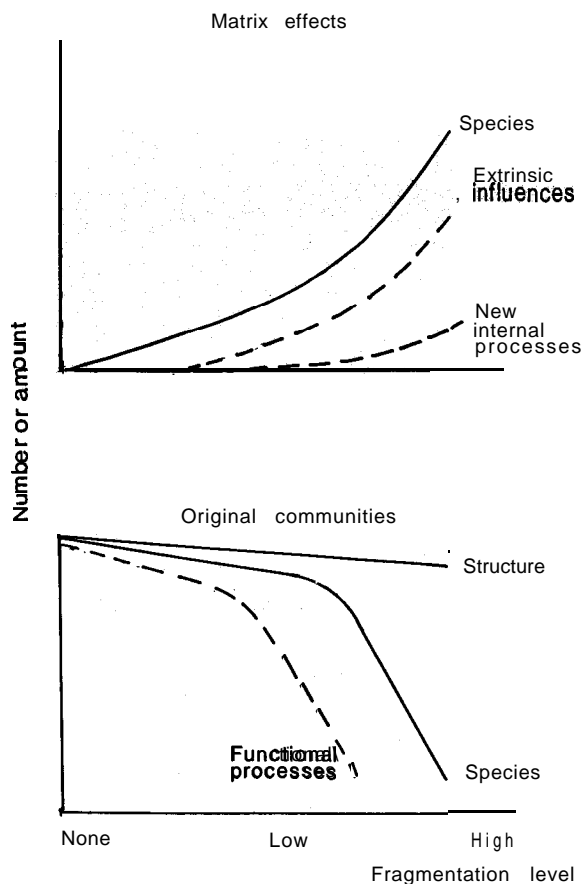
Matrix effects

(Graph labeled "Matrix effects" with y-axis "Number or amount", curves labeled "Species", "Extrinsic influences", "New internal processes")

(Graph labeled "Original communities" with curves labeled "Structure", "Functional processes", "Species"; x-axis "Fragmentation level" with marks "None", "Low", "High")

Fig. *1*. Tentative picture of the changes in community composition of reserves at increasing fragmentation levels. Structure (e.g., stem density) and species numbers have been separated (continuous lines) from processes (species interactions regarding e.g., predation, herbivory and pollination, broken lines).

Table 2. Spatial population structures at habitat fragmentation. Presence and absence, according to fairly well documented observations, are marked with + and − while ? denotes general uncertainty. Convincing evidence for island equilibria has only been provided for oceanic islands.

Structure	Fragmentation level			Reference
	None	Low	High	
Uniform	?	−	−	Any textbook
Source-sink	+	+	+	Pulliam (1988)
'Mainland'-island	−	+	−	Hanski (1991)
Metapopulation			?	Levins (1969)
Island equilibria	−	−	+ ?	MacArthur and Wilson (1968)

lose both the sensitive species and communities relying upon such species, as will a sink that is part of a heterogeneous but originally balanced population. 'Mainland'-island populations (Hanski 1991) may develop at low levels of fragmentation, leaving a few large fragments ('mainlands'). Originally fairly homogeneous and extensive populations, especially of climax species, may develop into internal sources and edge sinks at heavy fragmentation due to the various disturbances at the borders. Principally, when reserves are established, mortality in a population due to fragmentation should not be permitted to increase above a level where it can be compensated by immigration. This immigration will depend on areas of similar biotopes, the distances to them and their connectivity, possibly in the form of habitat corridors (Merriam 1988, Baudry and Merriam 1988). The latter factor will be strongly affected by matrix composition and functioning.

Community composition will depend on the interaction strength; if some base or keystone species disappears locally due to habitat change, or becomes distant and rare, then specialized consumers, pollinators etc. depending on this species will also decrease in numbers and more generalized species may increase proportionally. Such truncated communities will be trivialized, in the sense that habitat-specific processes disappear and matrix-generated extrinsic effects may be added to the most generalized intrinsic processes.

may be a selection for species with an original metapopulation structure, although such species seem rare. An evolutionary development towards metapopulation behaviour may appear in originally mobile species, but has yet to be demonstrated. It is questionable if this specific model is representative for many natural populations. Finally, the whole local population may be a sink, being supported wholly from outside. This may be especially common in very mobile species such as insects or birds (Table 2).

It is obviously of great importance to know what kind of metapopulation exists in an area before parts of it are transformed into a reserve. A local sink will change very soon upon fragmentation and

Fig. 2. One experimental study area in the Swedish research program on 'Remnant biotopes in production landscapes'. Differently-sized patches of a virgin coniferous forest is left on a large clearcut. (Photo: 0. Jennersten).

Validation of concepts

Mathematical models have not been developed that are capable of accurately predicting the effects of fragmentation (*cf.* also Hall 1988), especially as matrix effects are difficult to distinguish and quantify. Instead, validation of some of the ideeas presented has been performed as empirical tests on representative populations or communities in a Swedish research program on 'Remnant biotopes in production landscapes' (Ericson *et al.* 1988). The following, partly unpublished, examples constitute a few of the findings (Fig. 2).

Climatic equability

To study the effects of fragmentation on plants, small fragments from 1/16 to 1 ha of virgin taiga forest were left in the center of a large clearcut, and these were compared with undisturbed forest (Esseen *et al.* 1991). Most of the trees in the smaller fragments (less than 1/2 ha) soon blew down, and the field layer communities were destroyed in these sites by the stems and branches of the trees covering the field vegetation. Likewise, lichens sensitive to desiccation disappear from the edges of both small and large forest fragments on large clearcuts (Esseen 1983).

Matrix productivity – predation

Experimental grouse nests and nest boxes in forest fragments were robbed by matrix-derived predators, mainly corvids and small mustelids. These predators occur mainly in productive agricultural land and on vole-rich clearcuts, respectively (Angelstam 1986, 1991, Andrén and Angelstam 1988). The predation rates were clearly higher at the edges

of the forests than in their centers, thus demonstrating the matrix influence.

Matrix productivity – herbivory

Studies in central and western Europe have shown wood mice *(Apodemus sylvaticus)* invade forest groves from croplands, especially at plowing (Green 1979, Gurnell 1985). Swedish wood mice do not seem equally prone to move to forests but may change ranges to include forest islands in autumn-winter (Loman, unpubl.). More importantly, the consumption of seeds by mice is considerably higher in small woodlots than in extensive forests. Thus, mice, at least partly matrix-based, may affect plant regeneration and community structure in forest environments.

Matrix productivity and climax shelter

The tree-hole nests of the black woodpecker are used by a multitude of other birds and mammals for nesting and shelter; the black woodpecker (*Dryocopus martius)* is thus a keystone species for hole-nesting animals in boreal forests. However, when such nests occurred at forest edges, they were monopolized by jackdaws *(Corvus monedula),* which are otherwise wholly dependent on the agricultural landscape. Thus, competition from these matrix-supported species strongly interferred with the breeding of typical forest species (Nilsson and Ericson 1991).

Keystone species and sinks

Small patches of traditional agricultural areas, with flower-rich meadows, in a matrix of modern intensively-used agricultural land demonstrated a lack of pollinators, both hymenopterans and lepidopterans, in relation to more extensive traditional agricultural land (Jennersten 1988). The occurrence of certain plant species especially rich in nectar strongly influenced the seed-setting of the remaining species. When these keystone plants had disappeared, then both pollinator fauna and seed-setting was decimated.

Natural mosaics and landscape use

Insect herbivory on blueberry *(Vaccinium myrtillus)* leaves and stems was greater in dark wet forests in northern Sweden than in the lighter drier main coniferous forests, probably due to a lower content of carbon-based phenolics (antiherbivore substances) and a higher content of nitrogen in the vegetation of the dark forests, with a lower level of carbon assimilation (Sjöberg and Ericson 1991). The high number of insects in the wet forest patches caused flycatchers to forage preferably in this type of forest even if they nested in the main forest type. Similarly, grouse *(Tetrao urogallus)* hens led their clutches to such wet dark forests in order to find enough insects during the first stage of feeding by the young, when they are very dependent on animal food. Thus, destruction of the wet forests, as often occurs when forests are drained, will have major consequences in other and more extensive parts of the boreal forests.

Natural patchy distributions and dispersal powers

Epixylic moss species in boreal forests are characterized by very different dispersal strategies (Soderström 1987). Furthermore, originally their populations showed very different stability, partly due to different habitat affinities and the longevity and renewal rate of their substrate of rotting tree logs. When combined, these features lead to four different distribution patterns of the moss species (Soderström 1987, Hanski 1991), core (large populations with good dispersal), satellite (small populations with poor dispersal), urban (large populations with poor dispersal) and rural species (small populations with good dispersal). Species with low dispersal rates (as in two of the four categories above) are not able to survive after fragmentation with large matrix interstices (Hansson *et al.* 1991).

Preadapted metapopulations

The original metapopulation structure of pool frogs (*Rana lessonae*) was based on small lakes surrounded by coniferous forest. These patchy lake populations seem to show a dynamic balance between immigration and extinction (Sjögren 1991), one of the few examples of populations obeying the Levins (1969) model (Gilpin and Hanski 1991).

Landscapes for reserves

There are obviously very different landscape requirements between the original or native fauna and flora of climax biotopes of a region and those species inhabiting croplands or occurring almost everywhere due to their generalized habits. However, certain generalized species may be native inhabitants of a region, usually occurring in successional stages. For native species (*cf.* Harris 1989 for a discussion of this concept) in landscapes originally structured by natural disturbances (e.g., windfalls or fires), as the boreal forest, there is a need for 'minimum dynamic areas' (Picket and White 1985), with successional and climax stages juxtapositioned to mimic virgin states. Natural disturbance waves are easily counteracted by heavily fragmented landscapes (Forman 1987, Turner *et al.* 1989). Furthermore, there are often shifting loci of disturbance in natural landscapes (Hobbs *et al.* 1987). Thus, spatial components of a reserve should be permitted to change locations with time and regenerate spontaneously. However, the regeneration processes may be perverted by excessive numbers of easily-dispersed generalist species in extensively managed landscapes.

Climax species may need wide habitat corridors (Harris 1984, Harris and Galagher 1989) through the matrix to improve movements between fragments, as such organisms often show low dispersal rates (Hansson 1991). Such corridors or stepping stones will stabilize the social organization, and, thus, reproduction and survival of mobile habitat-dependent species. Unless such precautions are taken, there will be losses of naturally wide-ranging interior climax species or possible erosion of the genetic diversity of these species (Harris 1989). Isolated climax reserves in oceans of cropland instead will get an increased abundance of generalized or weedy species. Edges should be minimized both to avoid an increase in these latter species and to prevent 'habitat traps'. Edges, as well known in game management, are often attractive due to superior food (e.g., Kroodsma 1982, Hansson 1983) but are, at the same time, places of excessive predation and competition (Angelstam 1986, Harris 1988).

Natural dynamic processes may occur only in landscapes where climax patches are either large or numerous, where other (successional) habitats are designated to develop freely towards climax stages and all stages are allowed to be influenced, and even set back, by disturbance agents. Typical landscapes, e.g., juxtapositioned riparian and upland forests, boreal spruce-pine forests and fire successions or mires with 'island' fire refugia, should be preserved (Noss 1987). Many present landscapes containing valuable (climax) components need to be restructured with extensive production areas separated from reserves by successional buffers. This also should be done where there is unavoidable encroachment into large climax areas (Harris 1984).

Protection of single species, or viable populations, should be based on similar principles. Landscape elements of importance for the particular species, e. .*g,* as source areas and perhaps not perceived as a landscape component by humans, should be distinguished and managed within the range of the existing or potential populations.

If we want the highest possible biodiversity, then climax and very productive successional stages should be juxtapositioned, e.g., deciduous forests and swamps. Fairly large climax areas are needed and the successional stages have to be managed. Such a landscape will not be very representative of pristine conditions but may provide a multitude of species for recreational and pedagogical purposes.

In summary, climax habitats may be preserved by having at least two large areas combined with stepping stones, which will resist wholesale disturbances by, e.g., fire or disease. Specialized species need a few large surplus areas. High general biodiversity can be brought about artificially.

Table 3. Comparison of relevant articles in 1987-89 in the journals Conservation Biology and Landscape Ecology, both founded in 1987, regarding landscape approaches. The proportions (%) of these articles which consider common species and landscapes and general theory differ clearly between journals, with stronger emphasis on rare species, reserves and empiricism, including hypothesis testing, in Conservation Biology.

	Journal			
	Conservation biology		Landscape ecology	
Topic	n	%	n	%
Common (vs rare) species	51	51	17	88
Common landscapes (vs reserves)	57	79	58	100
Theory (vs empiricism)	60	12	58	50

Conclusions

The present survey once again stresses the importance of large reserves. However, strong consideration should be given to the areas interacting in their original state; small dispersed patches with important community components (e.g., wetlands in forests) may be as important as large expanses of homogeneous habitat (e.g., pure forests). Thus, selection or restoration of reserves must be based on a profound knowledge of the spatial population dynamics of keystone or indicator species and of species or resources deciding community integrity, including habitat-specific processes. Such analyses should be performed before establishment of reserves and must be preceeded by a careful analysis to determine what constitutes the most specific natural values of the biotopes or landscapes.

Conservation biology has focused its interest on extinction processes in very sparse populations; landscape ecology has the opportunity to provide a basic understanding of the ecological functioning of such populations and communities in both natural and derived environments. The number of published articles (Table 3) indicates that a work on common landscapes and common species is under way. We have some concern about the amount of theorizing in landscape ecology and, we believe, there is great need for field tests of both basic concepts and derived hypotheses.

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