Patches and Structural Components For A Landscape Ecology

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Landscapes as ecological units with structure and function are composed primarily of patches in a matrix. Patches differ fundamentally in origin and dynamics, while size, shape, and spatial configuration are also important. Line corridors, strip corridors, stream corridors, networks, and habitations are major integrative structural characteristics of landscapes. *(Accepted for publication 29 May 1981)*

Landscapes surround us, yet curiously it is hard to find people with the same concept of a landscape. Artists and humanists commonly portray the landscape as what the eye can perceive and sometimes limit the idea to natural landforms or communities. Such a landscape generally includes a high degree of spatial heterogeneity. In geographical literature, the landscape plays a central role, with most definitions focusing on the dynamic relationship between two characteristics—natural landforms or physiographic regions and human cultural groups (Grossman 1977, Mikesell 1968, Sauer 1963). In this article we ask whether the landscape is a recognizable and useful unit in ecology, with a distinctive structure and function that can be analyzed, as is done for organisms or ecosystems. What are the structural components of a landscape and their characteristics? Are there interesting, indeed critical, ecological questions facing us that may be solved using a landscape approach?

Walking in a small area of an agricultural landscape, one might encounter a corn field, a bean field, an abandoned old field, an upland oak stand, and a lowland elm-ash-sycamore woods adjacent to one another. If one studied this cluster of five specific communities or stands, one would find fluxes of energy, mineral nutrients, and species between adjacent stands, indicating considerable interaction among stands of the cluster. If one moved several kilometers away within the landscape, one would find a similar cluster of stands with similar interactions. Moving on, one would find this cluster repeated until entering a different geomorphological area, or an area subjected to different natural or human disturbances. Here, a different cluster of interacting stands would be evident as one entered, for example, a landscape of ridges and valleys, a suburban landscape, or a sandy forested landscape. Such observations are at the heart of the landscape concept, which we describe as follows.

A landscape is a kilometers-wide area where a cluster of interacting stands or ecosystems is repeated in similar form. The landscape is formed by two mechanisms operating together within its boundary—specific geomorphological processes and specific disturbances of the component stands.

Landscapes vary considerably in areal extent, and a localized area of a few meters or hundreds of meters across is at a finer level of scale than a landscape. Because of the area's geomorphology, the complex of landforms and parent materials present is relatively constant over a landscape. Each stand has a characteristic disturbance regime (the sum of the frequencies, intensities, and types of individual disturbances). A cluster of stands or a "stand cluster," therefore, has a disturbance regime cluster, which in turn is fairly constant throughout the landscape. Disturbances include both natural events and human activities such as fire, hurricanes, agricultural practices, or forest cutting.

Between the stands of a cluster are transition zones or ecotones, which may vary from being abrupt to gradual and wide. In less disturbed landscapes, gradual community gradients may be common or uncommon, depending upon how sharp environmental changes are with distance. However, with greater disturbance, especially by human activity, a landscape mosaic of ecosystem patches with distinct boundaries comes into sharper focus.

We suggest that *landscape*[1] is a distinct, measurable unit with several interesting ecological characteristics. Within the landscape is a recognizable and repeated cluster of ecosystems and disturbance regimes. The boundary between landscapes (which differ in geomorphology and disturbance) is relatively distinct, particularly in vegetation structure. Ecologically, landscape structure is measured by the distribution of energy, mineral nutrients and species in relation to the numbers, kinds, and configurations of the component ecosystems. Landscape dynamics is the flux of energy, mineral nutrients, and species among the component ecosystems, and consequent changes in those systems.

The key landscape structure questions today center on the importance of numbers, kinds, and configurations of ecosystems. Randomness is rare within a landscape. The overwhelming number of

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[1] Related concepts: A *region* is bounded by a complex of physiographic, economic, social and cultural characteristics (Dickinson 1970, Isard 1975). A *stand* (or a localized community) is the group of organisms at a specific locality, and is homogeneous enough to be considered a unit (Greig-Smith 1964, Daubenmire 1968). The *ecosystem* concept—organisms and their encompassing abiotic environment—may be applied at any level of spatial scale (Odum 1971). However, in practice one looks for relative homogeneity so as to characterize an ecosystem with a limited number of measurements (Woodwell and Whittaker 1968, Forman 1979a, Bormann and Likens 1980). Though one may apply the ecosystem concept to a heterogeneous region or landscape, in this article we limit its use to stands within a landscape.

species exhibits an aggregated or clustered distribution of individuals (Chessel 1978, Greig-Smith 1964, Kershaw 1973), and even in random and regular species distributions, some aggregations of individuals normally are present in a surrounding area of lower density (Godron 1966, 1971). This basic aggregation pattern of individuals of a species underlies the patchiness of vegetation and animal communities so commonly seen in nature.

In simplest terms, patches are communities or species assemblages surrounded by a matrix with a dissimilar community structure or composition. The matrix exhibits several characteristics itself, such as the degree of heterogeneity and connectivity, but in this article we focus on patches and the other structural components, corridors, networks and habitations. We further limit the analysis to patches at a single level of scale, the landscape, though most of the resulting patterns appear to apply to all levels of scale.

PATCH ORIGINS

Causal Mechanisms

Five causal mechanisms predominate and the five types of patches produced differ strikingly in their dynamics and stability (Forman 1979b). A *spot disturbance patch* results from disturbance of a small area in the matrix (Figure 1). For example, patches are produced by a small fire in a grassland, a large blowdown in a forest, overgrazing by a local exploding population of rodents, or local spraying of a generalized insecticide. Other examples are given by Heinselman (1973), Levin and Paine (1974), Pickett and Thompson (1978), and Forman and Boerner (1981). Following the disturbance, succession proceeds until the patch disappears by becoming like the matrix; that is, population changes and immigrations and extinctions of species take place until the relative abundances of the species are similar to those of the surrounding matrix. In unusual cases, especially where the intensity of disturbance is severe or the matrix is undergoing rapid change, succession may lead to a semi-stable patch that differs significantly from the matrix. The spot disturbance patch typically has high population changes and species immigration causes its ultimate disappearance.

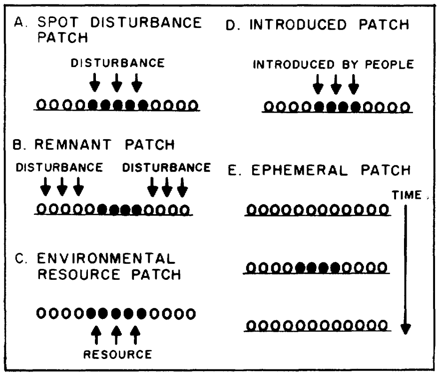

Figure 1. Patch origins. Species dynamics within a patch and turnover of the patch itself differ substantially according to the mechanisms causing a patch. ○ ○ ○ = matrix; ● ● ● = patch; disturbance = a sudden severe environmental change.

A *remnant patch* is caused by widespread disturbance surrounding a small area, the inverse of the spot disturbance mechanism. This patch is a remnant of the previous community embedded in a matrix that has been disturbed. Examples of remnant patches are woodlots in an agricultural area, a shrub-covered island produced by flooding a valley, a breeding warbler community on a south-facing slope that survived a rare freeze, or a pocket of herbivores that escaped the invasion of an aggressive non-native species. Further examples are described by Galli et al. (1976), Gottfried (1979), Helliwell (1976), Pollard et al. (1974), Seignobos (1978), and Southwood (1961). If the disturbance in the matrix is temporary, succession will proceed until the matrix converges with the patch in species similarity. Here again the patch disappears. If this convergence is rapid, the patch may change relatively little in species composition. However, if the disturbance of the matrix is chronic, inhibiting the normal successional rate and direction, the patch will remain. In this case, a net loss of species may take place (Diamond 1972, Willis 1974). This hypothesized net loss would be rapid at first, finally dropping to zero, a response referred to as a relaxation period. The species lost are those requiring a habitat larger than the remnant patch or those sensitive to a modified microenvironment within a patch.

Hence, remnant patches vary from short-lived, as produced by a single natural or human disturbance, to long-lived, resulting from chronic human disturbance. In the same way, spot disturbance patches may be short- or long-lived. In remnant patches caused by chronic disturbance, the net loss of species during a relaxation period results in the patch remaining, but with a species composition differing from the original patch.

An *environmental resource patch* reflects the normal heterogeneous distribution of resources in the environments and results from the environmental resources of a relatively permanent and discrete area which differ from the surrounding area. Unlike the other patches, the environmental resource patch is not dependent on disturbance. Concentrations of amphibians and reptiles in a desert oasis, patches of heaths on an exposed mountain ridge, acid-tolerant mosses in a glacier-caused bog, and pollinators in a moist alpine gully are examples. Other examples are described by Brown (1971), MacArthur and Wilson (1967), Simberloff (1976), Smith (1974), Stiles (1979), and Willis (1974). Since the cause of the environmental resource patch is relatively permanent, the patch is permanent, and species changes simply reflect those normal in the interaction between a small community in dynamic equilibrium with a surrounding matrix community.

An *introduced patch* is dominated by an aggregation of individuals introduced into a matrix by people. Pine and eucalyptus plantations (*Pinus, Eucalyptus*), golf courses, fields of wheat and corn (*Triticum, Zea*), or a large feeding station that attracts vertebrate species to a small area are examples. Introduced patches remain as long as the human disturbance regime maintains them. Thereafter, species from the matrix colonize, and like the spot disturbance patch, the patch disappears as it converges with the matrix.

An *ephemeral patch* is a transient aggregation of species caused by normal short-lived fluctuations in resource levels, that is, levels of biotic or abiotic environmental change that are frequent enough and of a low enough intensity that species have adapted to them. Especially rare or severe environmental changes are considered disturbances, which in turn cause spot disturbance and remnant patches. Examples of ephemeral patches are mammals feeding at dawn around a large savanna mudhole, a localized bloom of annuals in the desert, or a large shrubby area in field-to-forest succession. However, the rapid-turnover ephemeral patch appears more prominent at finer levels of scale than the landscape.

In summary, patch is a spatial concept focused on a small area. Both the causal mechanisms of patches and the resulting dynamics of patches differ greatly. As with most biological patterns, some overlaps exist among the five basic patch origins. For example, a severe chronic disturbance in the matrix might so change the matrix that convergence with a remnant patch community is prevented, and the remnant patch develops into an environmental resource patch.

Other Characteristics

A multitude of possible community types, named primarily by physiognomy or predominant species, may characterize patches in a landscape. The number of such different community types is a key structural characteristic of landscapes, not only for mapping, but to provide an index of the range of biotic richness, productivity, and nutrient and water fluxes in a landscape.

In addition, each ecosystem component is normally patchy in the landscape. For example, superimposing maps of soil types, tree communities, and herbivorous mammal communities for a landscape may show several places where boundaries coincide and many places where they do not. The degree of congruity in space among the units of different components is useful in mapping, land use planning, and analyses of landscape structure (Forman 1979b, McHarg 1969).

PATCH SIZE

Productivity, nutrient and water flux, and species dynamics are all affected by the size of landscape patches. Island biogeographic theory developed from studying archipelagoes in a matrix of water lends insight into the relationship between species and area. The number of species, S, (= species diversity) on an island was related directly to three factors in order: the island area, its isolation, and its age (MacArthur and Wilson 1967). The basic island area effect, though, is mainly due to habitat diversity; in most cases, larger islands simply have more habitats which, therefore, support more species. However, there is also an area effect: When the habitat diversity of large and small islands or patches does not differ, more species are typically found on the former (Forman et al. 1976, Simberloff 1976). Finally, one of the major factors determining diversity on an island or patch is the history and present regime of disturbance (Carlquist 1974, Pickett and Thompson 1978). Summarizing the patterns for islands, species diversity is a function of certain island characteristics listed in the suggested order of overall importance:[2]

$$S = \mathrm{f}(\text{habitat diversity} \pm \text{disturbance} + \text{area} - \text{isolation} + \text{age})$$

Patches in the landscape, however, differ significantly from islands surrounded by water (Forman 1979b). Above, we analyzed patch origins and here note that average turnover rates (the appearance and disappearance) of landscape patches may be high, whereas islands are essentially permanent. Similarly, the sharpness of the patch boundary varies greatly in the landscape (Whittaker 1973), and gradual gradients may be more conducive to the movement of species between patch and matrix. The heterogeneity of the landscape matrix is often high, which implies a large source of species in the matrix and strong directional effects of the matrix on different sides of the patch. The landscape matrix may be used as a rest stop for many species moving between patches, particularly in the limited area of a landscape compared with extensive oceanic archipelagoes. Here the importance of isolation, a central characteristic of island biogeographic theory, is lessened.

Within a landscape, the "species rain" appears to be high, that is, most species reach most patches within their life cycle. Therefore, when species extinctions take place in patches, rapid recolonization is facilitated and the effect of isolation minimized. While this species rain is suggested to be high for a community, as measured by species diversity, a relatively small proportion of individual species has a limited dispersability within the landscape. Isolation in the landscape may be critical for these individual species, many of which are uncommon. Thus, in conservation not only must the basic community pattern be considered, but also the specific populations (Diamond and May 1976, Forman et al. 1976, Pickett and Thompson 1978, Simberloff 1976, Terborgh 1976). Summarizing the species diversity patterns for landscape patches we suggest:

$$S = \mathrm{f}(\text{habitat diversity} \pm \text{disturbance} + \text{area} + \text{age} + \text{matrix heterogeneity} - \text{isolation} - \text{boundary discreteness})$$

Landscape patch area has been shown to correlate strongly with species diversity (Galli et al. 1976, Gottfried 1979, Moore and Hooper 1975, Peterken 1974, Robbins 1980, Whitcomb 1977), but rarely has area been considered separate from habitat diversity. When patch area alone is evaluated, we find it to be an important determinant of species diversity, and that species groups (such as trees, seed-eating birds and insectivorous birds) respond differently to patch area (Elfstrom 1976, Forman et al. 1976).

PATCH EDGE AND SHAPE

The microenvironment in the center of a tiny patch of woods differs strikingly from the center of an extensive woods. This results largely from penetration of air from the surrounding matrix throughout the tiny woods, whereas this air penetrates only a limited distance into the edge of the extensive forest. The outer band of a patch, which has an environment significantly different from the interior of the patch, is known as the *patch edge*. This produces an *edge effect,* that is, a difference in species composition and abundance in the edge. For example, differences between the edge and interior of deciduous forests in North America and Europe have been documented for a host of meteorological factors, vegetational characteristics (Jakucs 1972, Wales 1967, 1972), and animal communities (Galli et al. 1976, Johnston 1947, Leopold 1933, Patton 1975). Soil and fire characteristics probably also differ.

Several factors affect the width of the patch edge. The angle of the sun plays a major role, with edges facing equatorward typically wider than those facing poleward (Wales 1972), and those in temperate areas wider than in tropical areas. Wind also exerts a major influence, with the prevailing wind direction during the active or growth period having a wider edge than other sides. The degree of species difference between the patch and matrix is significant, too.

The patch edge appears to vary in width from a few meters to a few tens of meters in patches at the landscape level. Different groups of organisms respond differently to the environmentally determined edge width. For example, in woodlots, avian and tree communities appear to differ from the interior only in the outer portion of a forest edge, while herbs and mosses appear sensitive to essentially the entire edge width.

Patch shape as a variable is important in several ways, such as a target for dispersal or home range suitability; here we consider patch shape in the context of the edge concept. A large isodiametric patch is mostly interior, with a band of edge in the outer portion of the patch. A

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[2] + = positively related to diversity; − = negatively related; ± = usually negatively, but sometimes positively, related. Units are not considered in this encapsulation.

rectangular patch of the same size has proportionally less patch interior and more patch edge. Finally, a narrow strip patch of the same size may be all edge. Since community and population characteristics differ between the interior and the edge, comparing these characteristics with the interior to edge ratio of patches may be useful in evaluating the importance of patch shape in a landscape.

Whitmore (1975) noted that plant species composition and community structure varied according to the shape of openings in tropical rain forests. Stiles (1979) found sharp differences in wasp nesting density in the New Jersey Pine Barrens according to the width of the habitat. In Idaho rockslides, small mammal density correlated best with the length of the rockslide perimeter (Bunnel and Johnson 1974). Unpublished data (Forman and Clay) on mushroom diversity in old New Jersey two-hectare oak woodlots indicate a halving of species diversity and a threshold response in proceeding from isodiametric through rectangular to strip patches. Patch width or shape, therefore, appears to be a major ecological variable in the landscape.

Several special cases of shape bear mention. Ring zones are belts of vegetation, commonly within a particular altitudinal range, which extend around a mountain, and contain a "hole" with different vegetation at a different altitude (Hedberg 1955, MacArthur and Wilson 1967). The interior to edge ratio indicates that ring zones are more similar to strip patches than isodiametric patches. Linear patches and dendritic patterns contain special characteristics and are considered below.

The peninsula, where a narrow portion projects from a large patch, is a common shape, and species diversity commonly decreases progressively toward the tip. The reason for this pattern in major continental peninsulas of North America is hypothesized to be species extinction on the peninsula during the Pleistocene and subsequent gradual recolonization from the continent (Simpson 1964, Taylor and Regal 1978). An alternative explanation based on the edge effect, that the peninsular edge has a climate strongly modified by the surrounding water leaving little if any interior environment, is well known to farmers who must grow different crops on peninsulas (e.g., Squier 1877). Apparently the peninsular effect has not been studied at the landscape patch level.

PATCH NUMBERS AND CONFIGURATION

So far we have focused on the characteristics of individual patches. Patches, however, generally do not exist singly, but vary in numbers and in their configuration and juxtaposition to one another. Patches exhibiting any of the above described patch characteristics may, of course, vary from zero to many in a landscape. In understanding a landscape, determining the number of patches in each of at least four categories appears essential. How many patches are there of each of the patch origins? How many of each community type are there for each of the patch origins? In each category thus formed, what is the size distribution of the patches? And what is the distribution of patch shapes in each of these?

Determining the numbers in each of these four categories is not difficult in some landscapes. A subsample can then be selected for measurement of the species, energy, or nutrient component of interest, and by simple multiplication the status of the component in the patches of a landscape can be estimated with a measure of variability. However, this estimation is inadequate, because the spatial configuration among the patches has been ignored. For example, a landscape with ten evenly-distributed large patches differs fundamentally in most ecological fluxes from a landscape with the ten patches clustered at one end.

Various spatial configurations (Figure 2) can be examined using standard statistical techniques (Chessel 1978, Daget 1979, Godron 1971, Kershaw 1973) applied to the distribution of patches in each of the categories just described. The patches of a category may be random, regular, or aggregated; or positive or negative associations among patches of different categories may be present. This provides insight into both the cause of the patches and the potential for interpatch interaction. For example, common nonrandom patterns of patches are seen in limestone karst topography, in dendritic stream basins, along roads and property lines, or encircling towns. Finally, the actual distance between patches is an important measure of potential patch interactions.

CORRIDORS

There are four types of corridors in landscapes: *Line corridors,* such as paths, roads, hedgerows, property boundaries, drainage ditches, and irrigation channels, are narrow and typically have only species characteristic of patch edges. *Strip corridors* are wider bands containing a patch interior environment in which interior species may migrate or live. *Stream corridors,* which border water courses and vary in width according to the size of the stream, control water and mineral nutrient runoff, minimizing flooding, siltation, and soil fertility loss. *Networks* are formed by intersecting or anastomosing corridors and therefore contain loops. Some overlap among the four basic types exists, such as edge species moving in all four, or a wide stream corridor also functioning as a strip corridor for movement of patch interior species.

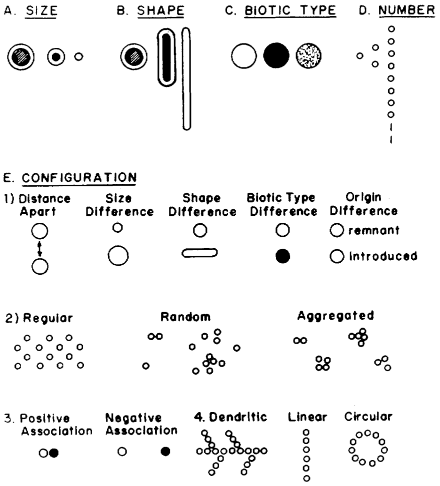

Figure 2. Patch characteristics in a landscape.

Line corridors are particularly characteristic of landscapes dominated by human disturbance. They originate in the same ways as patches, e.g., remnant tree lines left between fields from an earlier forest, paths as spot disturbance lines, and introduced lines as shrub and tree plantings for defense, enclosing livestock or decreasing wind (Kellogg 1934, Rotzien 1963, Seignobos 1978, Van Eimern et al. 1964).

The plant and animal species of line corridors generally also characterize patch edges (Pollard et al. 1974). These corridors provide habitat and breeding sites for species requiring the surrounding matrix environment for protection or feeding. Introduced nonnative species are common in line corridors, especially the disturbance-caused corridors.

The microstructure of the line provides insight into its potential functions (Les Bocages 1976, Lewis 1969, Pollard and Relton 1970, Pollard et al. 1974, Southwood 1961). Hence, a path line contains mainly disturbance-resistant species and has compacted soil, often with attendant erosion along the line. In contrast, the hedgerow line of shrubs or trees, which is higher than the matrix, cuts wind velocity, shades the adjacent matrix, and has a high evapotranspiration rate. Irrigation channels, and often roads and hedgerows, include adjoining ditches and embankments with considerable microhabitat diversity where amphibians, reptiles, and moisture-tolerant plants are often favored. Changes in line corridors through time are little known. M. D. Hooper, however, found a linear correlation between hedgerow age and shrub species diversity in managed British hedgerows, with an average one species gained per century (Les Bocages 1976, Pollard et al. 1974).

General characteristics of the wider strip corridors are reasonably well known, despite a paucity of direct studies. The corridor must provide protective cover for species from natural predators, domestic animals, and human effects lining each side of the corridor. The outer portions of the strip corridor have the edge effect, while the central portion contains the interior environment required for many patch interior species (Anderson et al. 1977, Johnson et al. 1979). For this reason, the width of a strip corridor is critical, since the interior environment must be present and sufficiently wide itself to be used by interior species.

In contrast to the line and strip corridors, the stream corridor is normally a dendritic pattern formed by intersecting narrow fingers upstream which gradually widen downstream. The stream corridor is the most widespread corridor type, and the concept has developed from considerations of water and mineral nutrient flows. This corridor strongly affects the erosion rate of the stream banks and adjoining upland and the absorption rate of water from precipitation and runoff. These, in turn, control siltation and flood levels in downstream ecosystems. The stream corridor is optimum when it doubles as a strip corridor for the migration of interior species. Since many species cannot survive the occasional floods of the stream lowland or the wet soils of the lowland and adjoining banks, the corridor must include a strip of interior environment on well-drained soil atop the stream bank.

A corridor should be continuous for maximum effectiveness (Getz et al. 1978, Schreiber and Graves 1977). In landscapes with ample human activity, one type of corridor, such as a road, commonly crosses another type, such as a hedgerow. The degree to which such crossings are effective barriers to the migration of different species needs study.

The corridor may exist as an isolated unit or it may interconnect patches in the landscape. In patches, species become extirpated for many reasons. Following loss of a species in a patch, a connected corridor facilitates rapid reestablishment of certain species in the patch. A strip corridor that links small patches may enrich those patches with species that otherwise could not survive in small isolated patches, because many species have minimum patch size requirements for survival (Galli et al. 1976, Robbins 1980, Terborgh 1976). Additionally, corridors facilitate gene flow across the landscape.

Networks are particularly widespread in landscapes bearing the heavy imprint of human activity. Anastomosing line corridors generally form networks, though occasionally networks may be composed of strip corridors. Familiar examples are the interconnected hedgerows or "bocage" and the networks of roads and railroads. A few networks reflect natural conditions, such as the polygon soils of arctic tundra areas or the reticulate trails of large mammals in east African savannas.

As isolated units, single corridors are considered to enhance the movement of species. However, as a series of interconnected links and loops, a network provides a more efficient migratory system, since alternative pathways are present. This structure is important for animal foraging efficiency, predator avoidance, and minimizing the barrier or isolating effect of a local disturbance or break in a corridor link. The frequency of intersections of corridors and the degree to which such intersections are expanded nodes or patches may play an important role in migration efficiency. Some networks, such as paths and roads, are especially effective for movement of people and domestic animals. We hypothesize networks to be important migration routes for native species, but as yet, the evidence is meager (Pollard et al. 1974).

In short, networks are prominent features of most landscapes today. Their functional importance rests not only in movement along the links, but in their impact on the matrix and patches in the surrounding landscape.

HABITATIONS

A final major structural characteristic of many landscapes is human habitation, including the house with its associated yard, courtyard, farm buildings and immediate surroundings. Habitations, of course, are disturbance-caused, partially or totally eliminating the natural ecosystem at that spot. The continued existence of the habitation depends on maintaining a chronic disturbance level.

The primary ecological structure of habitations is based on the types of organisms that have replaced the naturally occurring ones. Foremost are people, who provide the continued disturbance regime to maintain the habitation area. Most of the plants, in turn, are introduced by people. Some may be native species, but humans exhibit a propensity for surrounding themselves with a diverse and exotic species assemblage. People also generally introduce domestic, rather than native animals into homes, and both animal and plant pests are inadvertently introduced. Native species from the surrounding matrix or patches immigrate into habitation areas, but their success depends upon the level of disturbance maintained.

Distance between habitations in effect defines urban, suburban, town, village, and various rural areas. The greatest density and diversity of introduced species appears, on the average, in suburban areas, and indeed, in all areas with contiguous homes, the ecosystem is dominated by humans and introduced species (Schmid 1975). In rural areas with isolated homes, the entire border of the habitation interfaces with patches, networks, corridors or the matrix, so that interaction with other landscape elements is at a maximum. This interaction is the primary ecological importance of habitations in rural landscapes.

DYNAMICS OF THE LANDSCAPE

Our primary objective in this article is to lend insight into the ecological structure of landscapes, particularly patches (Figure 3). Yet, the structure is ultimately of importance as it relates to function. We have touched on the dynamics of patches themselves. Here we briefly suggest some examples of fluxes between structural components of the landscape (Forman 1981), that is, interactions between patch and matrix, patch and patch of the same type, patches of different types, network and matrix, and the like.

Interactions between patch and matrix are important in both directions. Heat energy carried by wind from one to the other accelerates the evapotranspiration rate and desiccates the microenvironment for certain species. Similarly, wind carries moisture, ash, dust, and propagules back and forth. Fire and other disturbances start in one and enter the other, and many types of animals forage from one to another.

Corridors and networks facilitate movement of species from patch to patch in the landscape, but also play a major role in inhibiting migration of matrix species by subdividing the matrix into isolated units. Networks and stream corridors retard surface water and nutrient runoff, and subsequent siltation and floods in downstream ecosystems, and in a similar fashion, a network modifies the flow of air and heat energy over the landscape, which in turn alters evapotranspiration and the moisture patterns of the soil.

Finally, habitations, as species sources, provide people and nonnative plants and animals. They, in turn, harvest species, form corridors and networks, produce various disturbances, and colonize both the surrounding patches and matrix.

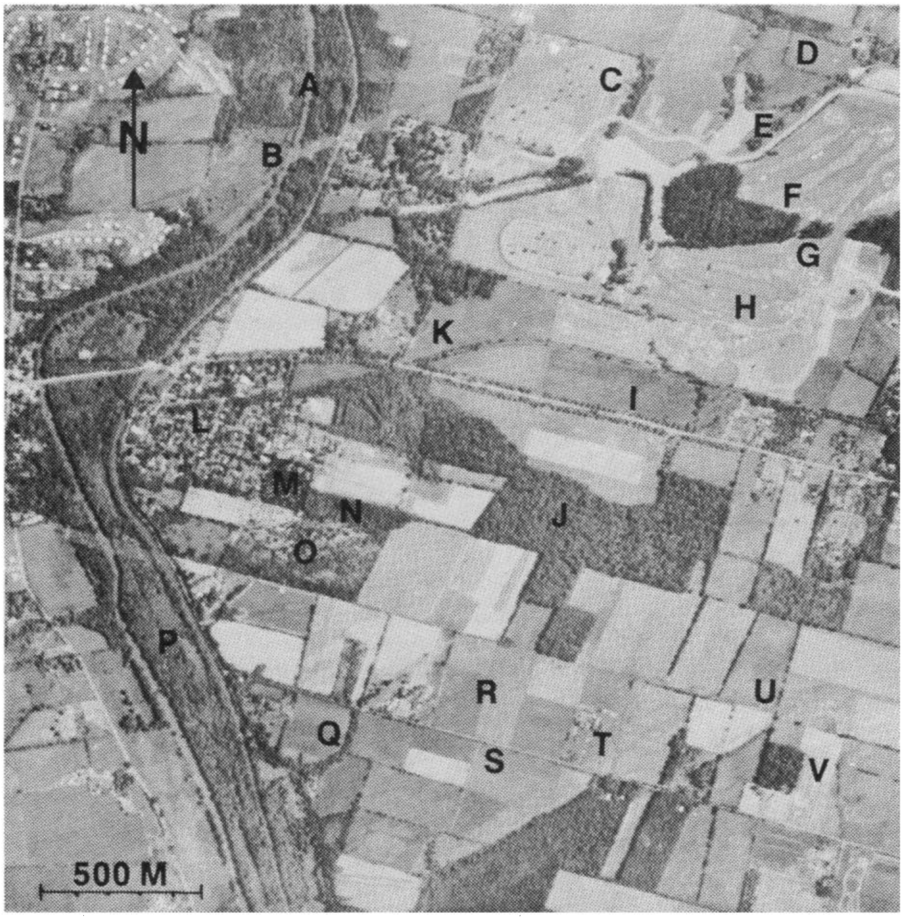

Figure 3. Portion of an agricultural landscape in New Jersey. Farming practices for corn and beans since 1701 have molded this landscape. Limited suburbanization effects are recent. The geomorphology is a level Triassic red shale, on which a well-drained silt loam of the Penn series predominates. The biotic patch types present are dominated by white, red and black oak (*Quercus alba, Q. borealis, Q. velutina*), except in stream corridors and wet spots where pin oak, red maple, ash and elm (*Q. palustris, Acer rubrum, Fraxinus, Ulmus*) predominate. Photograph taken May 29, 1970. **A.** Spot disturbance patch (small opening in forest). **B.** Strip corridor (powerline crossing stream corridor). **C.** Narrow patch with no forest interior. **D.** Strip corridor (wooded). **E.** Tiny patches with no forest interior. **F.** Peninsula. **G.** Tiny remnant patch affected by proximity to larger patch. **H.** Introduced patch (golf course). **I.** Introduced line corridor (*Platanus* planted along road). **J.** Large remnant patch (well-developed forest interior; patch edge about twice as wide to south as north). **K.** Road network. **L.** Dwellings clustered (village). **M.** Introduced patch (cemetery conifers and grass). **N.** Environmental resource patch (lowland tree species on wet spot). **O.** Temporal patch (area of shrubs and successional trees undergoing rapid change). **P.** Wide stream corridor (containing both river and canal). **Q.** Narrow stream corridor. **R.** Matrix (corn and bean fields). **S.** Line corridor (road). **T.** Habitation (area of farm buildings). **U.** Hedgerow network (connecting woods patches). **V.** Small remnant patch (contains limited area of forest interior).

CONCLUSION

The structure of a landscape is primarily a series of patches surrounded by a matrix. The origins of patches differ according to the disturbance regime in the patch, disturbance in the matrix, natural distribution of environmental resources, species introductions by people, and time. These differences in patch origin determine the species dynamics and the stability and turnover of patches themselves.

Patch area, and secondarily isolation, have traditionally been considered the major variables indicating the species diversity of a patch. We hypothesize that species diversity in a landscape patch is a function of the following patch variables in order of overall importance: habitat diversity ± disturbance + area + age + matrix heterogeneity − isolation − boundary discreteness. Patch shape as a modifier of area is important to species diversity and is mediated through the patch edge or edge effect.

The numbers of patches of each patch origin, biotic patch type, size, and shape determine in part the landscape structure. However, the spatial configuration among the patches present may be just as important as the numbers.

Corridors vary in width and function. Line corridors, particularly those resulting from human activities, are very narrow and used primarily for movement of edge species or people. Strip corridors, for effective movement of species characteristic of the interior of a patch, are wide enough to include an interior microenvironment as well as edge effect on both sides. A special case is the stream corridor, which also controls water and nutrient flows across the landscape.

Networks composed of intersecting corridors are prominent features of most landscapes. Networks provide an efficient migratory route as well as alter the flow of nutrients, water, and air across the landscape.

The concept of repetitive patterns in the structure of landscapes opens up a host of ecological questions related to both structure and function, and provides a relatively simple framework for testing them. It also provides a land management tool for helping to determine priorities in the land use. Finally, it emphasizes that no patch stands alone.

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