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Hierarchy in ecology: its relevance to landscape ecology and geographic information systems

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The objective of this chapter is to unravel some of the complexity which obscures our understanding of the landscape and its ecology. If this objective is successful it will redefine what are the important requirements for data collection and so help structure GIS for landscape applications.

To say that landscape ecology is interdisciplinary is an understatement. While cross-discipline studies are generally seen as scientifically creative, they are also problematic. It is characteristic of such studies that there is a conceptual lag in taking new developments across discipline boundaries; geographers use old ecology, while ecologists use old geographical ideas, and so on. True to this approach, as an ecologist I report some very recent progress in ecological science and then combine it with some rather less fashionable geographical ideas from the 1930s. The result is, I hope, a much clearer picture of what ecosystems actually are. This allows a simplification of the human and biospheric interactions with ecosystems and thus a clearer perception of landscape ecology itself.

The three groups of processes identified above (the ecological, the human and the biospheric) are, in broad terms, the set of processes central to landep units—namely, the ecological complex, the anthropo-complex and the ambio-complex, respectively (see Chapter 5 in this volume). The potential to simplify at least the conceptual complexity of landscape ecology comes from the relatively recent use of hierarchy theory.

Hierarchy theory: a tool-kit for geographic information systems

Naveh and Lieberman (1983) provides a definition of landscape which captures both the variety of scale and the interdisciplinarity of landscape ecology. He says that landscapes are 'a part of the space on the Earth's surface, consisting of a complex of systems, formed by the activity of rock, water, air, plants, animals and man [which] forms a recognisable entity'. Hierarchy theory allows the decomposition of these 'complexes' into strongly and weakly interacting components. Indeed, one of the central tenets of hierarchy theory (Simon, 1973) is that objects at one level in the hierarchy are nearly independent of objects at levels below and above it and so are weakly connected in those directions, while connections at the same level are much stronger.

To apply hierarchy theory to landscape problems, some simple conceptual tools are needed. One tool has already been noted, that is the quasi-independence of objects at different hierarchical levels. However, to use this idea a second tool is needed; objects have to be clearly defined and indeed clearly separated from non-objects such as aggregates. Rowe (1961) shows that objects are organized as containing structurally connected parts, while aggregates occupy a common area, but have no structural organization. Thus, although a forest may appear as a solid object when viewed from a distance, Rowe contends it is an aggregate of objects (the plants), but is not an object itself. In comparison, the biological hierarchy of cell–organ–oganism–ecosystem is a hierarchy of objects where each object contains structurally related parts; thus the organ is composed of cells, the organism made up of organs and, as is shown later, the ecosystem is composed of organisms.

The choice of scale of observation is important in landscape ecology (see, for example, Chapter 8 in this volume). Questions of scale are also highly relevant to the distinction between aggregates and objects noted above. Objects do have intrinsic scale, if only within broad limits, whereas aggregates do not. Thus a forest can be of any size greater than a certain basic size, the individual objects (the trees) are of a characteristic size, given particular external environmental constraints and internal biological constraints.

As well as the awareness that a change in scale changes the number and extent of what is observed, it also affects the types of phenomena that can be observed. A significant change in scale is therefore associated with hierarchies of phenomena. This is perhaps most clearly seen in biological systems where observation using microscopes reveals subcellular organization, then cells and then, by direct observation, organs, bodies and so on, while observation from space is required to see the biosphere.

Hierarchies of scale, by which we mean scale of observation, present different issues because scale can be changed in a continuous manner. This leads to the final tool introduced here which concerns the importance of distinguishing types of hierarchy. It is important to do this to ensure that different types are not mixed. Thus a single hierarchy should not contain aggregates and integrated objects. Distinguishing different types of hierarchy allows the interpretation of what the hierarchies mean.

What is an ecosystem?

Landscape ecologists could be forgiven for thinking that textbook definitions of 'ecosystem' could be imported for use in the analysis of landscape phenomena. However, as shown below, the concept of an ecosystem is currently under re-evaluation within the science of ecology. This debate can be examined by looking at a traditional definition of 'ecology', its problems and the proposed solutions.

Perhaps the most influential definition of 'ecosystem' developed this century has been that of Lindeman (1942) given as part of the introduction to his famous

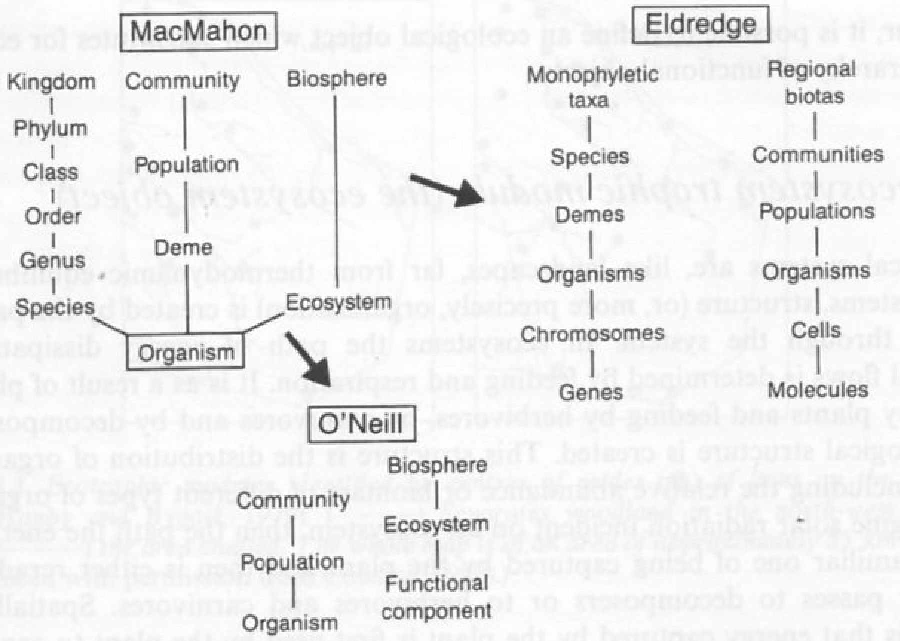


Figure 6.1. Some recent approaches to classifying the components of biological organization.

paper on trophic levels. Lindeman takes the position that:

> the ecosystem can be formally defined as the system composed of physical–chemical–biological processes active within a space time unit of any magnitude, i.e. the biotic community and its environment.

The two main features of this definition, that the ecosystem is composed of biotic and abiotic parts, and that the ecosystem has no intrinsic scale, have both become the accepted wisdom of our time. However, this view that ecosystems are, in a sense, everything and present at any scale, has led many ecologists to question the reality of the ecosystem concept. O'Neill *et al.* (1986) observe that 'the ecosystem as an independent discrete entity looks less and less tenable', while Ghiselin (1987) points to this kind of limitation at the root of ecological science, stating that 'ecologists are most unsure about the nature of their fundamental units and about what such units do'.

It is this search for basic ecological units (components) that has led many ecologists to construct hierarchies of biological phenomena in search of plausible candidates (see Figure 6.1). This is plainly a varied set of hierarchies, with each based on different types of relationship. The taxonomic hierarchies of species to kingdoms are linked by the history of evolutionary descent and are not, at each or any of the levels, functioning objects today (Grene, 1987). The hierarchies of community–population–deme and biosphere–ecosystem–organism are different in many ways (Cousins, 1988), principally because the community hierarchy is one of concepts rather than physical objects. Thus the deme (a local breeding population with high mutual gene flow), a population (a collection of demes) and a community of populations of many species all have boundaries which are subjectively chosen by the observer. The biosphere (later called the 'Earth-biosphere') and individual are, within certain limits, objectively defined functional objects which are independent of the observer and can 'do' things in the sense called for by Ghiselin (1987). Although the key concept of the ecosystem is again a subjectively determined aggregate with boundaries given by an observer, it is possible to define an ecological object which substitutes for ecosystem in a hierarchy of functional objects.

The ecosystem trophic module (*the ecosystem object*)

Biological systems are, like landscapes, far from thermodynamic equilibrium. In such systems, structure (or, more precisely, organization) is created by the passage of energy through the system. In ecosystems the path of energy dissipation and material flows is determined by feeding and respiration. It is as a result of photosynthesis by plants and feeding by herbivores, by carnivores and by decomposers that an ecological structure is created. This structure is the distribution of organisms in space, including the relative abundance or biomass of different types of organism. If we imagine solar radiation incident on an ecosystem, then the path the energy takes is the familiar one of being captured by the plant and then is either reradiated as heat or passes to decomposers or to herbivores and carnivores. Spatially, what occurs is that energy captured by the plant is first used by the plant to concentrate what was the uniform field of solar energy into a variety of energy states including energy-dense sources such as seeds, down to energy-poor leaf drip (Cousins, 1980). These energy sources are then further concentrated, dispersed, or respired by herbivores and detrivores such that some of the energy reaches the top predator.

Figure 6.2 shows a diagram of energy flow directions where sunlight falls evenly over a number of contiguous territories of a top predator social group, perhaps a breeding pair of foxes or a pride of lions. Little of the energy incident on the whole territory reaches the top predator, but it enters the food chain which leads to the top predator as soon as energy has been captured by the green plant. Energy which falls on one side of the territory boundary goes to one predator; energy which falls across the boundary flows towards the adjacent predator group.

It is these structures which are bounded in space by territorial behaviour, bounded in time by the initiation and termination of the territorial unit, and which are made up of all the locally interacting organisms which form the food web of the top predator, which forms the largest ecological object at any one point on the Earth. Cousins (1988, 1990) has called this object the Ecosystem trophic module (ecotrophic module or ETM; 'trophic' meaning feeding).

The ETMs of a region of the Serengeti plain in Tanzania are shown in Figure 6.3. Note that the spacing of the lion prides which define the ETMs as shown is of the order of 10 km, giving an area of approximately 100 km^2 as the size of the

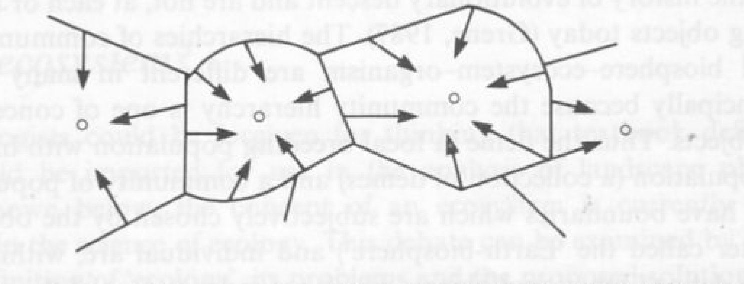


Figure 6.2. The boundaries of the ecosystem object, the ETM, formed by the overall paths of energy flow from incident solar to the social group of the top predator. (○) *Centre of range of top predator social group. Arrows indicate the direction of flow of energy.*

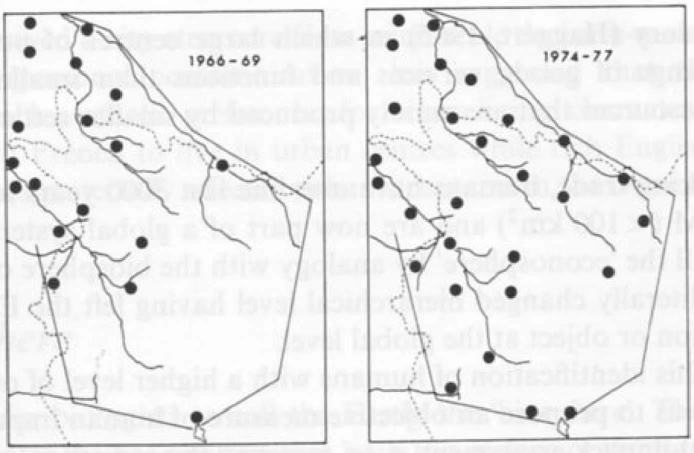


Figure 6.3. Ecotrophic modules identified by centres of prides (●) of lions on the Serengeti plains (Hanby and Bygott, 1979). (– – – –) Separates woodland in the north-west from the plains; (——) the area studied. The whole map is of an area of approximately 85 km × 60 km. (Reproduced with permission from Cousins (1990).)

ecological object. Note too that the distributions differ between the two periods shown. Hanby and Bygott (1979) suggest that this change is due to a change in the environment, namely a change in rainfall. This change in climate arises at a different hierarchical level from the behaviour of the global weather system which impacts on the ETM structure of the Serengeti.

Finally, it is important to address the question of the scale of observation in the context of the ETM. Choosing a scale of observation is always a subjective judgement based on the type of problem that is being analysed. The recognition of the ETM does not change this, as the chosen scale will include one, less than one, or more than one ETM. The size of the ETM is just one more factor to add to those governing the choice of the observation scale.

The human dimension

The human dimension is particularly important to landscape ecology. The definition of an ecosystem as a bounded ecological object, the ETM, raises the important question of where humans fit into such a structure. Are humans top predators, or do human social systems represent an entirely new level of energy flow and organization? Certainly human social groups with weapons have primitively acted as top predators and may still do so today in hunter–gatherer societies. Subsequent human groups differ from the top predator group by one very important activity, they engage in trade. Thus, whereas in the ETM the energy and materials are organized within the spatial unit circumscribed by the ETM boundary (Figure 6.2), trading humans exchange energy and materials *between* ETMs, thereby creating a new and larger entity or organization.

Geographers have long studied the spatial structures generated as a result of trade. An example of one such structure is the hierarchy of market settlements from village, local town, regional towns to cities. Christaller (see Haggett, 1965) proposed a seven-tier hierarchy of settlement from hamlet to world city in which there are an increasing range of specialist functions undertaken at each larger scale. This is the central place theory (Haggett, 1965) in which large centres of population have a much greater range of goods, services and functions than smaller centres. Large cities consume resources that are mainly produced by smaller settlements and farms (see Figure 6.4).

By undertaking trade, humans have over the last 3000 years left the ecological scale of the ETM (<100 km^2) and are now part of a global system of world trade which we can call the 'econosphere' by analogy with the biosphere concept. Humans appear to have literally changed hierarchical level having left the ETM and created a new organization or object at the global level.

Ironically, this identification of humans with a higher level of organization than the ETM allows us to propose an objective measure of human impact. This method of environmental-impact assessment is to measure the reduction in the size of the impacted ETM compared with the preimpacted state and, ultimately, with the ETM area of the top-predator characteristic of that part of the Earth.

As one indication of the impact of human activity on ecosystems, Figure 6.5 shows the average number of species of bird found within a 20-mile radius of the centre of London and a transformation of that information showing the average species body weight of those species. For the methods used, see the Appendix. Although these data are for all bird species rather than a count of the number or size of the ETMs, they do show a net decline in body size towards the centre commensurate with a decline in energy availability to territorial birds in cities caused by limited green space and other factors such as pollution (Cousins, 1982). These maps may also be considered as a representation of an intersection of human and natural systems.

Finally, it is important to emphasize that trading or economic activities are framed within human-value systems which reinforce or override economic activities and the spatial patterns created by trade. Allen *et al.* (1984) have modelled these

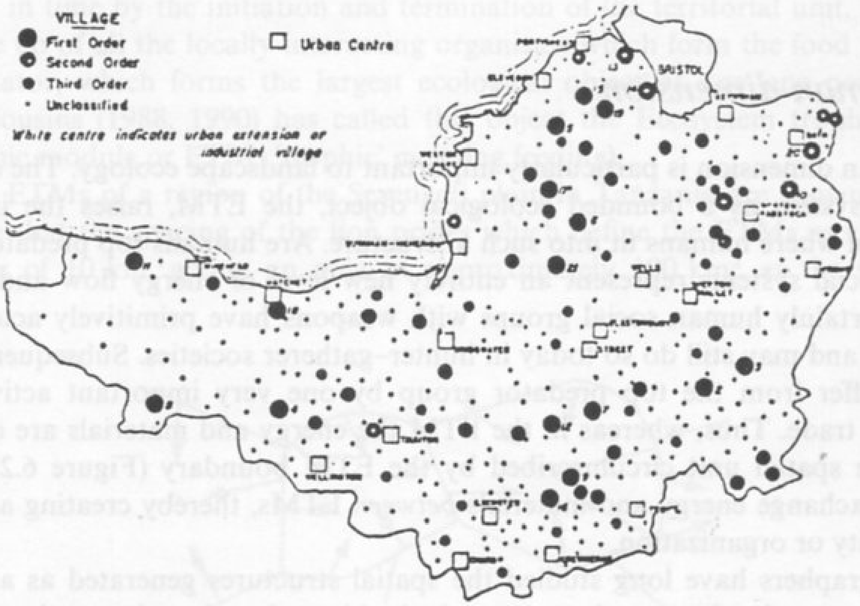


Figure 6.4. A hierarchy of settlements in Somerset, south-western England. The classification of villages is based on a continuum with breaks at 5, 10 and 20 shops. Urban centres are distinguished from villages and the city of Bristol.
(Reproduced with permission from Haggett (1965).)

processes and derived a city structure from microscale decision-making. As a further example, Allen (personal communication) has suggested that the difference in English and French aesthetic preferences for urban living, characterized as a greater preference of rich French to live in urban centres while rich English tend to prefer rural outposts, has materially affected urban structures in the two countries.

Earth biosphere

It is traditional for biologists to call the Earth, the 'biosphere'. The one word 'biosphere' encapsulates the proposition that both the surface of the Earth and its atmosphere have been radically altered by the presence of life (Rambler *et al.*, 1989). Where the term 'biosphere' is weaker is that it obscures the processes of the deeper geology, and so volcanism, for example, is left out of the equation of the biologists' atmosphere. The term 'biosphere' also obscures the recent development of the econosphere, recent that is in terms of biological and planetary history.

I shall use the term 'Earth biosphere' as a stimulus to a clearer understanding of the structure which is created by energy flows involving the Earth. We are not interested in these in detail, but only in the kind of phenomena concerned in order to find where 'landscape' fits into such a scheme.

In Figure 6.1 the hierarchy, organism–ecosystem–biosphere is replaced here by a hierarchy of organized objects, **Organism–ETM–Earth**, where the organization is achieved by flows of energy and materials. The question of interest for landscape ecology is whether there are other discrete organized objects which constitute component parts of the Earth and which are not the ETM.

Primarily, hierarchy theory allows for the creation of a new level of organization out of the interaction of a number of different parts. In the case of the body there were components of different kinds, for example organs of different types. For the Earth biosphere we may identify a series of components which together interact to form the new unit. These include, the ETM, sea and atmosphere circulation patterns, surface-water runoff, plate tectonics, and volcanism. The Earth is then part of a planetary system with gains from and loses to space.

The energy required to maintain the observed structure of the Earth comes from two principal sources, the cooling of the Earth's core and the heating up of the Earth from space by solar energy. Although we are almost exclusively interested in the structures created by solar-energy transfer, the outgassing of volcanoes adds new material to the atmosphere and can also affect the energy balance due to volcanic dust altering the Earth's albedo. To this list of the Earth's components we must also add structures created by human trade, which are treated here as contiguous city hinterlands.

With regard to the landscape without human intervention, there are two main implications of Earth-biosphere level phenomena. We need to look for structures created by energy dissipation at a scale larger than or of the same order as the ETM. We therefore see air and water movement as the structuring forces driven by temperature gradients created by differences in surface reflectance (albedo) and by evaporative cooling. Alterations in albedo, in greenhouse gas composition of the atmosphere, or other sources of climate changes, results in different rainfall levels and in different drainage amounts or patterns. On land, therefore, the landscape unit of observation is the river basin and the organizing principle is water flow from

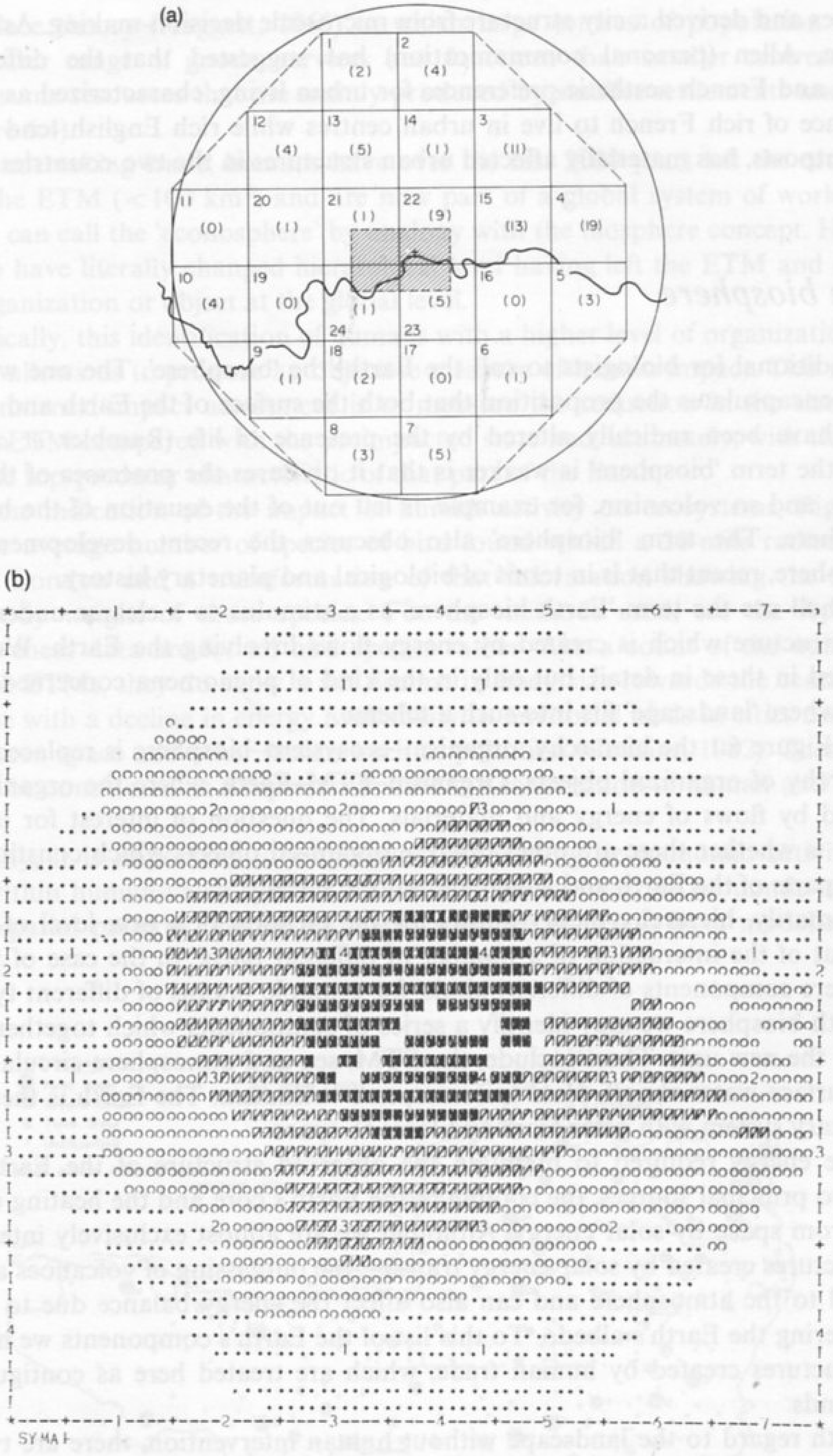
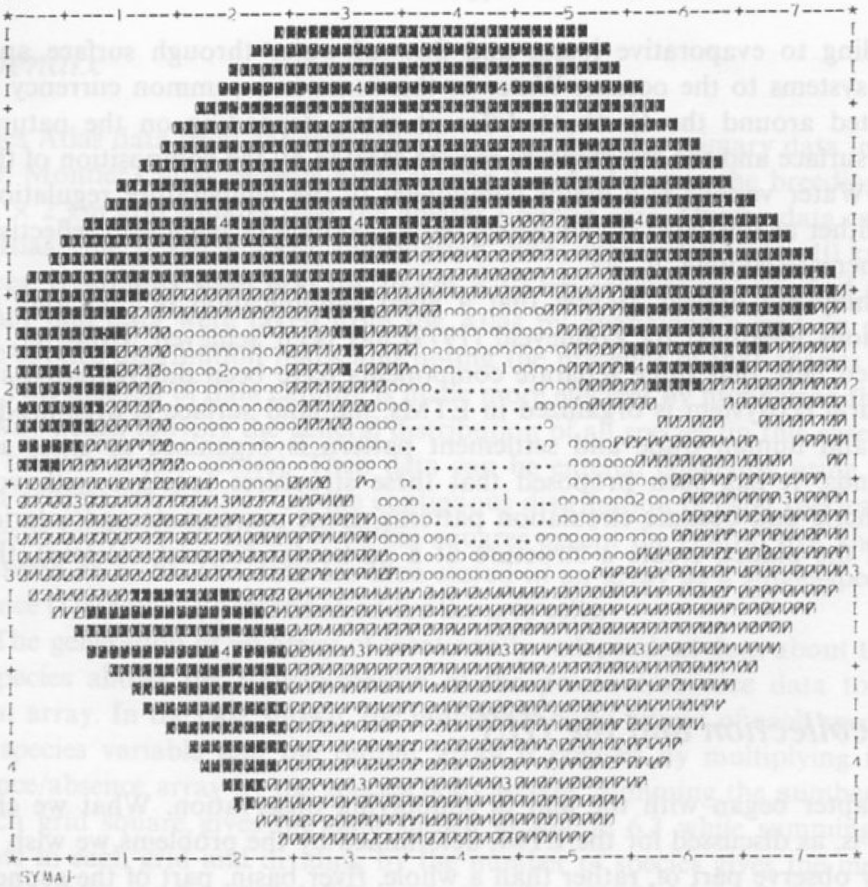


Figure 6.5. (a) The study zone of 24 10 km × 10 km grid squares (plus central rectangle) is shown within a radius of 32.5 km (25 miles) of St Pauls Cathedral (marked by a cross). In (b) to (d) the data are interpolated to the hatched lines. The river Thames is shown. (b) Built environment index of settlements in London. Contours 1–4 (light to dark): 3–10.9 points, 11–18.9 points, 19–26.9 points, 27–35 points. Points given for housing density; for definition of units see Cousins (1982). (c) Land bird species density/100 km^2. Contours 1–4 (light to dark): 43–51 species, 52–60 species, 61–68 species, 69–77 species. (d) Land bird average species weight/100 km^2. Contours 1–4 (light to dark): 90.5–98.5 g, 98.6–106.5 g, 106.6–114.5 g, 114.6–122.5 g.
(Reproduced with permission from Cousins (1982).)

(c)



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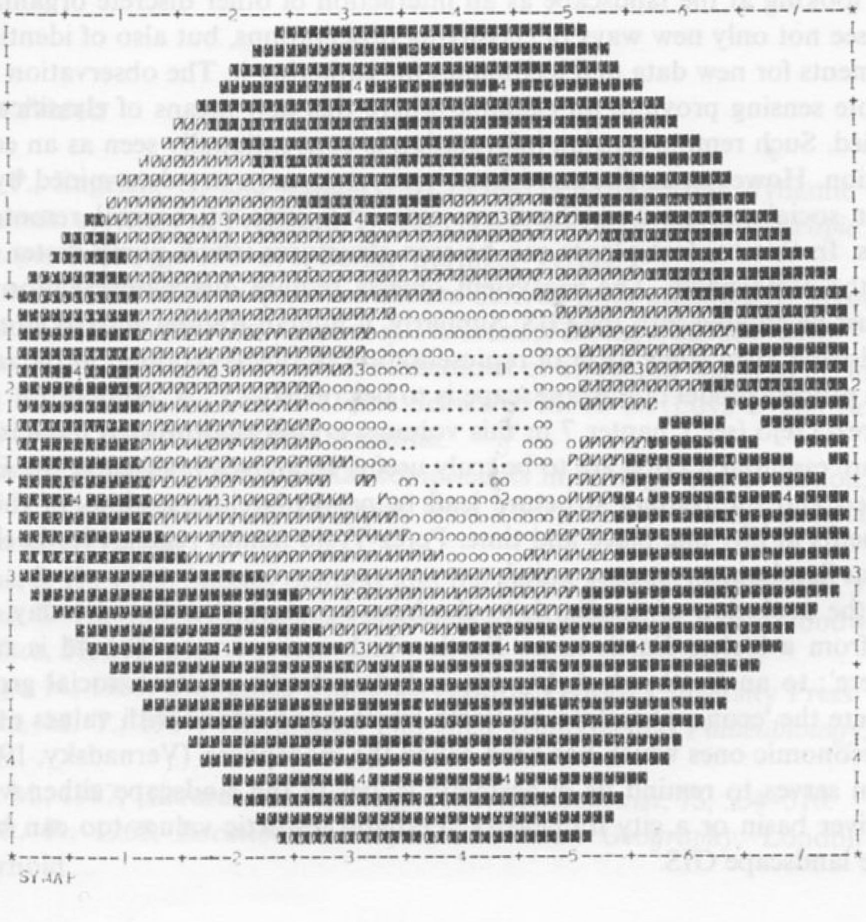

rain falling to evaporative losses and flow of water through surface and below surface systems to the oceans. Water in this sense is a common currency which is distributed around the Earth at different rates, depending on the nature of the ground surface and the temperature regime created by the composition of the atmosphere. Water vapour is a major component of the temperature regulation of the Earth, either as low-level clouds which reduce cooling or high-level reflective clouds which increase cooling.

It may not appear at first that a great simplification of that long series of interactions identified by Zonneveld (1979) has been achieved. However, we have concluded here that three separate components have been differentiated such that the natural ecosystem is organized in ETMs, the land surface is organized in river basins, and human trade and settlement pattern is organized as cities and their hinterlands. It has been proposed that these structures together with volcanoes, atmospheric and oceanic circulation patterns, crust movements and interior structures of the planet, create a structure at a particular hierarchical level, the Earth today.

Data collection and the GIS

This chapter began with the aim of simplifying observation. What we choose to observe is, as discussed for the ETM, determined by the problems we wish to solve. We may observe part of, rather than a whole, river basin, part of the economy of a distant city and not the whole hinterland, and so on.

By looking at the landscape as an interaction of other discrete organized units we can see not only new ways of classifying observations, but also of identifying the requirements for new data and techniques for gathering it. The observation of plants by remote sensing provides an example where this new means of classification can be applied. Such remote-sensing information is conventionally seen as an ecosystem description. However, as discussed here, ecosystem units are determined by the top predator social groups and, therefore, are not visible by normal remote-sensing methods. In this context plants can be seen structures which pump water from the soil to the atmosphere. The ecosystem objects require direct observation and the data must be entered into the GIS. Similarly, if human trading activity is central to the landscape, then some form of representation of this is required in the landscape GIS if a process model of the landscape is to be created.

Perez-Trejo (see Chapter 7 in this volume) argues that process models of landscapes are essential if GISs are to be truly useful. In a given landscape, the ETM, the watershed and the trading structure lead to particular intersections of these three components at any one place and time. Perez-Trejo names regularities in this intersection as 'landscape response units'.

In the evolution of the Earth to the form in which it is found today, we have passed from a lifeless Earth to an Earth which incorporates life and is called the 'biosphere'; to an Earth which has life including trading human social groups and called here the 'econosphere'; to an Earth which has humans with values other than purely economic ones which has been called the 'noosphere' (Vernadsky, 1945). This last term serves to remind us of aesthetic values of the landscape either within the ETM, river basin or a city framework. Perhaps aesthetic values too can be placed onto the landscape GIS.

Appendix

Species Atlas data from Montier (1977) were used as the primary data input for the study. Montier's atlas records birds seen in London during the breeding season in 2 km × 2 km grid squares over the greater London area. During data capture from the atlas, the 2 km × 2 km information was aggregated into 10 km × 10 km squares. A suitably sized grid for 10 km × 10 km squares was marked on a transparency and data were taken from the Atlas by overlaying a grid on each of the single-species distribution maps and noting the presence of that species in the grid cells. This method of data capture is made more efficient by numbering the grid cells in a way which mirrors the general distribution of all species (in this case as a spiral from outside to the centre). Then data can be entered efficiently using a program which accepts information on the contiguous distribution of each species. Thus, if a species is found in all 10 km × 10 km squares except the central five, then this can be entered as 1, 20. The data are then stored in an array as a single-species row of presence (1)/absence (0) information for the grid cells.

The generation of an array of locationally independent data about the individual species allows the transformation of the presence/absence data to create an output array. In the case shown, the individual body weight of each species is used as a species variable and the output array is created by multiplying the species presence/absence array by the species body weight. Summing the number of species in each grid square gives the data shown in Figure 6.3 while summing the body weights in each grid and dividing by the number of species gives the mean species size data shown in Figure 6.4. This technique has also been applied to the distribution of breeding birds over the UK (Cousins, 1989).

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