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Some general principles of landscape and regional ecology

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Abstract

A dozen general principles of landscape and regional ecology are delineated to stimulate their evaluation, refinement, and usage. Brief background material and a few references provide entrées into the subjects. The principles are presented in four groups: landscapes and regions; patches and corridors; mosaics; and applications. Most appear useful in solving a wide range of environmental and societal land-use issues.

Introduction

The objective of this article is to outline certain general principles in the ecology of land mosaics. I expect that such a list will stimulate discussion, refinement, replacement, additions, hypotheses, research, and further understanding. It should also help elucidate foundations that underpin a wide range of applications. Landscape and regional ecology provides spatial solutions useful in addressing all of society's land-use objectives.

The term, landscape ecology, appeared a half century ago (Troll 1939, 1968; Schreiber 1990). However, as a field with a body of theory and applications, it has coalesced and mushroomed in the past decade.

Previous lists of principles have been presented or suggested. Risser *et al.* (1984), with members of the 1983 Allerton Park Workshop, focused on areas that unite ecology and landscape perspectives: (1) spatial pattern and ecological process; (2) spatial and temporal scales; (3) heterogeneity effect on fluxes and disturbance; (4) changing patterns; and (5) a framework for natural resource management. Forman and Godron (1986) identified emerging general principles that highlighted how different the field was from ecosystem ecology, biogeography, and physical geography: (1) landscape structure and function; (2) biotic diversity; (3) species flow; (4) nutrient redistribution; (5) energy flow; (6) landscape change; and (7) landscape stability. Risser (1987) pinpointed both major areas and challenges, in describing the state of the field: (1) heterogeneity and disturbance; (2) structure and function; (3) stability and change; (4) nutrient redistribution; and (5) hierarchical organization. Turner (1989) usefully summarized progress in most of the preceding areas. The principles listed in the present article reflect developments in several of the preceding areas, as well as newer conceptual areas and syntheses.

Broad principles do not develop overnight. Generally they have roots in 'first principles' or background theory, and also are supported by a reasonable amount of empirical evidence. First principles, such as evolution and laws of thermodynamics, are fine-scale or reductionist statements of human knowledge that are highly robust. Where large complex objects render experimentation difficult, *e.g.*, in geology, astronomy, and physics, great advances are made by linking observable phenomena to existing first principles.

This approach should play an important role in understanding landscapes and regions. Thus mass flow principles, gravity and rheotaxis, central place theory, counter current principle, and form and function principles all contribute to the ecology of land mosaics. Some of the preceding are actually second- or intermediate-level principles based on background fine-scale theory. Models, such as fractal, percolation, network, and graph theory, are simplifications of complex systems to enhance understanding. They may or may not be empirically supported and robust, but they often provide highly useful insight that may lead to principles and applications.

The attributes or tests of a principle represent a time-honored and endless discussion. Six attributes seem especially relevant to me. A general principle: (1) integrates diverse areas of knowledge; (2) addresses significant questions; (3) has broad applicability, though exceptions usually exist; (4) has predictive ability; (5) is founded in theory, which in turn has considerable supporting evidence; and (6) has some direct supporting evidence. All of the general principles presented satisfy all or most of these tests.

Some of the principles are familiar to all in the field, while others result from newer syntheses. None of the general principles presented is a ‘law’, such as for conservation of matter, where no exceptions are expected. However, I suggest that each principle correctly holds for the bulk of the cases involved, *e.g.*, more than 95% of the time. Although parts of all the principles stated are falsifiable, this is a minor consideration compared with providing enhanced understanding, which often includes many additional important and pioneering advances. Furthermore, though the core of landscape and regional ecology is science, the field explicitly embraces and integrates other slices of knowledge.

The principles stated below are conceptual and often include relative terms, such as large or small, fine- or coarse-grain, and distinct or gradual boundary. In applying a principle to a particular study or environmental issue, one makes the terms operational, usually by stating assumptions and assigning scales for quantitative measurement. In addition, mathematical descriptions of the principles can be developed, which may be useful in identifying hypotheses to be tested.

The dozen principles are organized into four categories: landscapes and regions; patches and corridors; mosaics; and applications. The worldwide literature and evidence for the principles is analyzed in depth by Forman (1995). In the following list a brief elaboration and a few references for each principle provide some perspective and an entrée into the literature.

Landscapes and regions

1. Landscape and region

A mix of local ecosystem or land use types is repeated over the land forming a landscape, which is the basic element in a region at the next broader scale composed of a non-repetitive, high-contrast, coarse-grained pattern of landscapes.

The landscape and region are two scales, both at the ‘human scale’. They are land mosaics. Mosaics are evident at all scales from submicroscopic to the planet and universe. All mosaics are composed of spatial elements. Those at the landscape scale are commonly called landscape elements, and those at the regional scale are landscapes (Forman and Godron 1986; Forman 1995). Just as full understanding of a liver or a town requires information from both broader and finer scales, understanding a landscape requires information on the broader region and on the finer-scale local ecosystems.

The boundary between landscapes is easily determined by recording the landscape elements present along transects or in randomly or regularly distributed plots. For example, a line of plots across an agricultural landscape might contain cornfields, beanfields, hedgerows, farmsteads, farm roads, woodlots, paved tarmac roads, stream corridors, and some rarer ecosystems or land uses. Each plot contains most of these types, although the percentages of individual elements may vary considerably from plot to plot. Eventually the line encounters the first of a sequence of plots with quite a different composition of spatial elements, say, residential neighborhoods, schools, ballfields, shopping areas, streets, cemeteries, small parks, and some rarer types. This is a suburban landscape.

Relative to the diameter of ecosystem and land use patches, boundaries separating patches are usually but not always abrupt, due to patterns of substrate patchiness, natural disturbance, and human activity. Relative to the diameter of landscapes (*i.e.*, kilometers, 10's or 100's of kilometers), boundaries separating them are similarly distinct, as commonly seen in images of regions from space. This is mainly due to geomorphology and human activity. Ecological conditions differ in the center and edge of a landscape (Angelstam 1992; Martinsson *et al.* 1993; Liu *et al.* 1994). The boundary between landscapes is evident from the contrasting composition of spatial elements in the plots, and can be precisely delineated at this scale using various statistical analyses (Mueller-Dombois and Ellenberg 1974; Greig-Smith 1983; Forman and Godron 1986). The least distinct boundaries are where land uses, such as residential areas, are somewhat independent of geomorphology.

A region is a broad geographical area with a common macroclimate and sphere of human activity and interest (Koppen 1931; Isard 1975; Foin 1976; Burke *et al.* 1991). It is tied together relatively tightly by transportation, communication, and culture, as in the idea of regionalism, but often is extremely diverse ecologically.

The typically distinct boundary of landscapes, plus the sharp difference in appearance or predominant land uses of adjacent landscapes, provide a high contrast pattern to a region. Moreover, regions tend to have a coarse-grained pattern, because most of their area is usually composed of large landscapes. The repetitive nature of spatial elements within a landscape means that, for example, certain agricultural or forested landscapes in different regions may appear quite similar to one another. In contrast, no repeated pattern of landscapes characterizes a region, so each region tends to be spatially quite distinctive.

2. Patch-corridor-matrix

The arrangement or structural pattern of patches, corridors, and a matrix that constitute a landscape is a major determinant of functional flows and movements through the landscape, and of changes in its pattern and process over time.

Every point in a landscape is either within a patch, a corridor, or a background matrix, and this holds in any land mosaic, including forested, dry, cultivated, and suburban. This simple model provides a handle for analysis and comparison, plus the potential for detecting general patterns and principles (Lovejoy *et al.* 1984; Harris 1984; Fahrig and Merriam 1985; Forman and Godron 1986; Kozova *et al.* 1986; Saunders *et al.* 1987; Hansen and di Castri 1992).

This is also effectively a spatial language with familiar dictionary terms, which enhances communication among several disciplines and decision makers (Forman 1979; Baudry and Burel 1984; Froment and Wildmann 1987; Schreiber 1988; Harms and Opdam 1990; Ruzicka and Miklos 1990; Haber 1990). For instance, patches vary from large to small, elongated to round, and convoluted to smooth. Corridors vary from wide to narrow, high to low connectivity, and meandering to straight. And a matrix is extensive to limited, continuous to perforated, and aggregated to dispersed.

Form or structure, *i.e.*, what we see today, was produced by flows yesterday (Watt 1947; Forman and Godron 1986). Yet a linkage or feedback between structure and function is evident. Not only do flows create structure, but structure determines flows and movements. Finally, movement and flows also change the land mosaic over time, much like turning a kaleidoscope to produce different patterns.

Patches and corridors

3. Large natural-vegetation patches

These are the only structures in a landscape that protect aquifers and interconnected stream networks, sustain viable populations of most interior *species, provide core habitat and escape cover for most large-home-range vertebrates, and permit near-natural disturbance regimes.*

Large natural-vegetation patches serve many major ecological roles and provide many benefits in a landscape, including those highlighted above (Forman **1995).** Consequently a landscape without large patches is eviscerated, picked to the bone. A landscape with only large patches of natural vegetation misses few values. On the other hand, small natural-vegetation patches serve as stepping stones for species dispersal or recolonization, protect scattered rare species or small habitats, provide heterogeneity in the matrix, and habitat for an occasional small-patch-restricted species. In effect, small patches provide different benefits than large patches, and should be thought of as a supplement to, but not a replacement for, large patches.

We may hypothesize that an optimum landscape has large patches of natural vegetation, supplemented with small patches scattered throughout the matrix. Alternatively, most of the small-patch functions can be provided by small corridors in the matrix.

4. *Patch shape*

***To** accomplish several key functions, an ecologically optimum patch shape usually has a large core with some curvilinear boundaries and narrow lobes, and depends on orientation angle relative to surrounding flows.*

A compact or rounded form is effective in conserving internal resources, by minimizing the exposed perimeter to outside effects (Harris and Kangas **1979).** But patches affect, and are affected by, manifold ecological processes in a landscape (Forman **1995).** Interactions with adjacent ecosystems, *e.g.*, for multihabitat species or to escape from predators, are enhanced by curvilinear boundaries. Interactions with more distant portions of the landscape are enhanced with narrow lobes, *e.g.*, to increase recolonization rate following local extinction in the patch, or for species to disperse to other patches.

The orientation of the long axis of a patch relative to flows in the landscape, *i.e.*, the orientation angle, is a key to several ecological phenomena (Forman and Godron **1986;** Turner **1987;** Skidmore **1987;** Brandle *et al.* **1988;** Gutzwiller and Anderson **1992).** These include wind and water flows, which sculpt patch shapes, produce distinct areas of turbulence, and cause soil erosion. The orientation of wooded patches has also been linked to the probability of their use by migrating birds (Gutzwiller and Anderson **1987, 1992).**

5. *Interactions among ecosystems*

All ecosystems in a landscape are interrelated, with movement **or** *flow rate of objects dropping sharply with distance, but more gradually* **for** *species interactions between ecosystems* **of** *the same type.*

A first 'law' of geography states that everything is interrelated, but near objects are more related than distant objects. Examples of interactions among nearby ecosystems or land uses are numerous and familiar (Swingland and Greenwood **1983;** Saunders *et al.* **1987;** Senft *et al.* **1987;** Shaver *et al.* **1991;** Saunders and Hobbs **1991;** Noss **1993).**

From ecosystem science we learn that energy and mineral nutrients flow from one object to another within, or between, ecosystems. From behavioral science, because certain habitats are more suitable than others for a species, many locomotion-driven movements are directional, toward patches of the same type. Combining these principles with the geography law provides this spatial-flow principle (Forman **1987, 1995),** useful for example, in estimating which ecosystems of the mosaic to focus on in planning and management.

6. *Metapopulation dynamics*

For subpopulations on separate patches, the local extinction rate decreases with greater habitat quality **or** *patch size, and recolonization increases with corridors, stepping stones, a suitable matrix habitat,* **or** *short inter-patch distance.*

A metapopulation is a population consisting of spatially-separate subpopulations that are connected by the dispersal of individuals (Wilson **1975;** Fritz **1979;** Merriam **1988;** Opdam **1991;** Hanski **1991).** Metapopulation dynamics is of special importance, because subpopulations may drop to zero (local extinctions), especially in small isolated patches. If each subpopulation dropped to zero, this would mean extinction of the whole metapopulation. However, because individuals sometimes move between subpopulations, two results occur. First, the local extinction rate (the number of species disappearing from a patch per unit time) is lowered. Second, when local extinction does take place, recolonization of individuals may reestablish a new subpopulation at the site. Consequently, with extinctions followed by colonizations the metapopulation as a whole persists. The local (subpopulation) scale may be highly unstable, while the broad (metapopulation) scale exhibits more stability.

Extinction rate and colonization rate must be related both to patch attributes and the surrounding pattern (Opdam **1991).** Extinction rate tends to be high in small patches and in low-quality patches. Extinction rate also increases with higher environmental variability (den Boer **1981;** Karr **1982),** such that a population widely fluctuating in size is more prone to extinction. Recolonization is enhanced by spatial patterns such as corridors, networks, a row of stepping stones, and a cluster of small patches. Some evidence exists that recolonization correlates with the area of woodland surrounding a patch (van Noorden **1986),** and with the average distance to other patches occupied by the species (Verboom *et al.* **1991;** Opdam **1991).**

Mosaics

7. *Landscape resistance*

The arrangement of spatial elements, especially barriers, conduits, and highly-heterogeneous areas, determines the resistance to flow or movement of species, energy, material, and disturbance over a landscape.

Landscape resistance is described as the effect of spatial pattern impeding the rate of flow of objects, such as species and materials. For example, boundaries separating spatial elements are locations where objects usually slow down (or in some cases accelerate) (Swingland and Greenwood **1983;** Forman and Godron **1986;** Brandle *et al.* **1988;** Forman and Moore **1992).** Hence, boundary-crossing frequency, *i.e.*, the number of boundaries per unit length of route, appears to be a useful measure of resistance.

In several landscape areas studied in The Netherlands, resistance to species movement increases as the percent of area deforested increases (Harms and Opdam **1990;** Knaapen *et al.* **1992).** In built areas (more or less continuous lots containing buildings) butterfly movement is most inhibited, and movement of forest birds least inhibited. However, in rural areas bird movement is most inhibited, and large mammals least affected. Highway and river/canal corridors are serious barriers to bird movement, and least inhibitory to large mammals.

Certain landscape elements are more suitable, and others less suitable, to movements and flows (Forman **1995).** In addition, corridors can act to channel or enhance flow, or act as barriers or filters inhibiting spread. Finally, highly-heterogeneous areas have a high probability of containing unsuitable elements, thus requiring a high boundary-crossing frequency and/or a convoluted route. Therefore, we expect heterogeneous fine-grained areas to have a high resistance.

8. *Grain size*

***A** coarse-grained landscape containing fine-grained areas is optimum to provide for large-patch ecological benefits, multihabitat species including humans, and a breadth of environmental resources and conditions.*

The grain size of a landscape mosaic is measured as the average diameter or area of all patches present (Forman and Godron **1986;** Norton and Lord **1990;** Wiens **1990;** Angelstam **1992;** Wiens *et al.* **1993;** Forman **1995).** A coarse-grained landscape with only large patches may provide large natural-vegetation patches for aquifer protection and specialist interior species, large built areas for industrial specialization, and so forth. Coarse grain is moderately monotonous, that is, although landscape diversity is high (being in a farmland is very different than in a city), site diversity is low (moving from one site or point to the adjacent point in almost all cases involves no change in land use). Except near boundaries, movement is costly (considerable distance required) for multihabitat species, *i.e.*, those that use two or more habitats.

In contrast, a fine-grained landscape has predominantly generalist species, since specialists requiring a large patch of one land use cannot survive. A fine-grained landscape is monotonous (every portion is about the same), although site diversity is high (each adjacent point is a different land use). Species that survive need only move short distances.

Some variables such as air and water quality tend to be low in a fine-grained landscape, because pollution sources may be widely distributed throughout the land. Indeed, the overall resource base is truncated and narrower, due to the absence of specialized resources in large patches.

A medium-grained landscape misses the large-patch benefits and offers no other advantages. In short, all of the preceding benefits, and few shortcomings, are provided by a coarse-grained landscape that contains some fine-grained areas.

9. Landscape change

Land is transformed by several spatial processes overlapping in order, including perforation, fragmentation and attrition, which increase habitat loss and isolation, but otherwise cause very different effects on spatial pattern and ecological process.

Habitat fragmentation is but a phase in a broader sequence of spatial processes transforming land by natural or human causes from one type to another. Other spatial processes in landscape change or transformation are equally prominent and ecologically significant (van der Zande *et al.* **1980;** Harris **1984;** Pickett and White **1985;** Wilcove *et al.* **1986;** Peterken and Allison **1989;** Saunders and Hobbs **1991;** Forman and Collinge **1995;** Forman **1995).** In fact, some ecologically-interesting land transformations have no fragmentation at all.

Perforation is the process of making holes in an object such as a habitat or land type (*e.g.*, dispersed houses or fires in a forest). Dissection is the carving up or subdividing of an area using equal-width lines (*e.g.*, by roads or powerlines). Fragmentation is the breaking of an object into pieces (that are often widely and unevenly separated). Shrinkage is the decrease in size of objects, and attrition is their disappearance.

These five spatial processes overlap through the period of land transformation. They also are usually ordered in their importance, with perforation and dissection both peaking in relative importance at the outset. Fragmentation and shrinkage predominate in the middle phases, and attrition peaks near the end.

These spatial processes all increase habitat loss and isolation. However, average patch size decreases in the first four processes, and typically increases upon attrition, because small patches are most likely to disappear. Connectivity across an area in continuous corridors or matrix typically decreases with dissection and fragmentation. The total boundary length between original and new land types increases in the first three processes, and decreases with shrinkage and attrition. In short, each spatial process has a highly distinctive effect on spatial pattern, and consequently on ecological processes, in a changing landscape.

10. Mosaic sequence

Land is transformed from more- to less-suitable habitat in a small number of basic mosaic sequences, the ecologically best being in progressive parallel strips from an edge, though modifications of this pattern lead to an 'ecologically optimum' sequence.

Diverse mechanisms from logging and suburbanization to wildfire and desertification transform land from one type to another. Each land transformation is effectively a mosaic sequence, *i.e.*, a series of spatial patterns over time (Franklin and Forman **1987;** Forman **1995).** Five sequences are widespread. **(1)** Edge: a new-land-type spreads unidirectionally in more or less parallel strips from an edge. (2) Corridor: a new corridor bisects the initial-land-type at the outset, and expands outward on opposite sides. (3) Nucleus: spread from a single nucleus within the landscape proceeds radially, and leaves a shrinking ring of the initial-land-type. (4) Nuclei: growth from a few nuclei produces new-land-type areas expanding radially toward one another. (5) Dispersed: widely dispersing new patches rapidly eliminates large patches of the initial-land-type, produces a temporary network of the initial-land-type, and prevents the emergence of large patches of the new-land-type until near the end.

Mosaic sequences can be analyzed for many changing spatial attributes, such as patch size and boundary length (Richter 1984; Wiens *et al.* 1986; O'Neill *et al.* 1988; Turner 1989; Odum and Turner 1990; Forman 1995). The five sequences can then be compared based on a wide range of ecological characteristics known to correlate with the spatial attributes (Forman and Godron 1986; Ambuel and Temple 1983; Franklin and Forman 1987; Brandle *et al.* 1988; Noss 1993). Here we assume the initial-land-type is more ecologically suitable than the new type. Then the mosaic sequences are compared to determine which retains the ecologically best arrangement of initial-land-type for the longest period.

Based on the ecological characteristics correlated with the spatial attributes, the 'edge' mosaic sequence is considered ecologically the best of the five transformation sequences. It has no perforation, dissection, or fragmentation. It is best for the large-patch attributes, and good for connectivity. Yet, shortcomings of the 'edge' sequence include no 'risk spreading', a progressive narrowing of the remnant initial-type until it is only a strip, and an extensive area of new-land-type without small patches and corridors.

A theoretical mosaic sequence (labelled with a 'jaws and chunks' metaphor) overcomes these shortcomings (Forman 1995; Forman and Collinge 1995). Draw an isolated square landscape of initial-land-type, where L-shaped or wide-open 'jaws' of new-land-type will progressively move from upper to left to lower right. Early in land transformation the jaws appear to grip a huge 'chunk' of initial-land-type, and 'bits' of initial-land-type (small patches and corridors) are scattered over the jaws themselves. In the mid-transformation phase, the thickening jaws covered with scattered bits hold a few large separated chunks. In the late transformation phase the huge jaws covered with bits hold a single large chunk. At the end the bits disappear. This may represent an 'ecologically optimum' land transformation.

Applications

11. Aggregate-with-outliers

Land containing humans is best arranged ecologically by aggregating land uses, yet maintaining small patches and corridors of nature throughout developed areas, as well as outliers of human activity spatially arranged along major boundaries.

Seven, mainly landscape-ecological attributes are incorporated into or solved by this spatial principle or model (Forman 1995; Forman and Collinge 1995): (a) large patches of natural vegetation; (b) grain size; (c) risk spreading; (d) genetic diversity; (e) boundary zone; (f) small patches of natural vegetation; and (g) corridors. An example will illustrate the principle.

Start with a coarse-grained landscape with only large patches or areas of the major land uses present, *e.g.*, natural-vegetation, agricultural, and built areas. Scatter small patches (and corridors) of natural vegetation over the agricultural and built areas to provide bits of heterogeneous nature over these developed areas, to protect dispersed rare species and small habitats, and to provide stepping stones for species movement. Add major corridors connecting the large natural-vegetation patches to facilitate movement of patch-interior species. Add small patches of agriculture near the boundaries between natural-vegetation and built areas. Also with increasing distance from the large agricultural areas, make the small farm-patches further apart from one another. Then distribute small built patches (towns, villages, houses) in exactly the same manner; near boundaries between natural-vegetation and agricultural areas, and increasingly isolated with distance from large built areas. This distribution of small patches of all types enhances the development of genetic diversity, and provides risk spreading against severe disturbance. The boundary zones between large patches, especially around junctions (convergency points) of three land-use types, are fine-grained areas within a coarse-grained landscape. These fine-grained corridor and junction areas are effective for multihabitat species.

The aggregate-with-outliers model for land planning thus has numerous ecological benefits (McHarg 1969; Forman and Godron 1986; Franklin and Forman 1987; Turner 1989; Hansen *et al.* 1992). In addition, a range of direct benefits to humans is suggested by this spatial approach. These include an exceptionally wide range of locations for urban dwellers to hermits, fine-scale areas where jobs, homes and shops are close together, efficient transportation connecting built areas, large patches for resource harvest or extraction, and high visual diversity. The principle appears applicable in any landscape, from dry to forest, and from agriculture to suburb.

12. Indispensable patterns

Top-priority patterns for protection, with no known substitute for their ecological benefits, are a few large natural-vegetation patches, wide vegetated corridors protecting water courses, connectivity for movement of key species among large patches, and small patches and corridors providing heterogeneous bits of nature throughout developed areas.

The background and references for most of these have been introduced in the preceding pages. The indispensables should be essential foundations in any land plan, since they accomplish major ecological or human objectives, and no other practical mechanism is known to accomplish them (Forman 1995; Forman and Collinge 1995). Other patterns appear to simply be efficient or optimal solutions to difficult land planning problems. As evidence accumulates, two additional patterns may be considered indispensables in the future. One is the aggregate-with-outliers pattern, which is an integration of several individual patterns. The second is a fine-scale pattern, *i.e.*, the irregular, curvy, mosaic-like, aggregated, and complex nature of nature. Its ecological benefits are surprisingly little documented, but probably cannot be otherwise replicated.

Conclusion

The objective of this article is to identify general principles largely emerging from a decade of work in landscape ecology to understand the ecology of land mosaics or large spatially-heterogeneous areas. The objective is also to stimulate evaluation, discussion, and additional work to further solidify the conceptual foundations.

Presenting a dozen principles is somewhat arbitrary; some number between ten and twenty seems appropriate today. A higher number means adding principles whose significance or applicability is narrower or more limited in scope. Alternatively it means adding ones with less supporting evidence. Other scholars in the field would articulate a different list, and the preceding list will change in the years ahead as new questions are posed and additional evidence accumulates.

Finally, these principles should be applicable for any environmental or societal land-use objective. In a probabilistic or uncertain world, principles should be applied intelligently, not blindly, to solving our land use problems. They are useful in growing wood, protecting species, locating houses, protecting soil, enhancing game, protecting water resources, providing recreation, locating roads, and creating sustainable environments. Each objective is accomplished more effectively, and for a longer time frame, using a healthy dose of landscape and regional ecology principles.

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