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On the transferability of concepts and its significance for landscape ecology

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Abstract

The evolution of landscape ecology has been characterized by the definition of many principles and concepts, and by the development of metrics to quantify them. It is shown that metrics developed for landscape fragmentation are related to the equations to measure gravitational forces or diversity, which suggests the transferability of the concepts involved. This observation could lead to a better understanding of the metrics and towards a more rational development and use of landscape metrics.

Introduction

The term «landscape ecology» was used for the first time by Troll (1939) to indicate a research at the intersection of ecology and geography; landscape ecology is consequently often defined as the study of ecological phenomena in their spatial context (Antrop 2001). As a consequence of its emergence as a proper branch of science in the last quarter of the twentieth century (Forman 1995a), its evolution since has been characterized by the development of many (new) concepts and principles, which remain up to today subject to debate, improvement or completion by new ones (Forman 1995a, Forman 1995b, Wu & Hobbs 2002). Fragmentation is one of the most striking examples of a concept that has been strongly developed in landscape ecology, for which have been defined many metrics, and which has been discussed up to today with regard to its quantification, to its ecological impact on ecosystem function or biodiversity, or even to its definition (D'Eon 2002, Bogaert 2003, Ewers et al. 2006).

The discipline of landscape ecology singularizes itself by three methodological approaches. Firstly, spatial scale is inextricably bound to landscape ecology. Landscape ecologists consider the observation of an ecological process or pattern, or the outcome of an analysis of these patterns and processes, dependent on the extent of the study and on the degree of precision or spatial resolution used, the latter two parameters being the two components of spatial scale (Wiens 1989, Forman 1995b). Landscape ecology focuses in particular the supra-ecosystem level (Forman 1995b, Bogaert & Mahamane 2005), which corresponds generally to study areas from several hectares to many squared kilometers, and the appropriate resolution to be applied is accepted to increase with the extent of the landscape (Burel and Baudry 2003). Secondly, a strong relationship between ecological patterns and processes is assumed in which process outcomes are determined by their spatial context, and in which spatial pattern is assumed to be a footprint of ecological processes (Urban et al. 1987, Turner 1989, Coulson et al. 1999).

Studying spatial pattern is therefore accepted to lead to a better understanding of the ecological processes in the landscape. Thirdly, landscape ecology developed the ambition to deepen the descriptive analyses of ecological patterns and processes as often observed in life sciences by means of a quantitative approach (Levin 1992, Groom and Schumaker 1993), which has led to the widespread use of geographic information systems and remote sensing data in landscape ecology, and to the development of a large number of pattern metrics. This superabundance of metrics and the problems related to their use are widely accepted and debated in the landscape ecology community (Bogaert et al. 2002, Bogaert & Hong 2004).

From an epistemological point of view, it is crucial to understand how and why new concepts have been defined while landscape ecology evolved, and how landscape metrics have been identified to quantify these concepts. A possible pathway to achieve this objective is to seek for corresponding concepts in other scientific disciplines, and to investigate how they are analyzed quantitatively. In this contribution, this analysis is exemplified for the concept of landscape fragmentation, since we noticed that metrics used nowadays in landscape ecology to quantify the degree of habitat dispersion have been used elsewhere for other scientific concepts, such as gravitation and diversity.

Fragmentation and the transfer of concepts between disciplines

Gravitation and proximity of patches

In physics, the law of universal gravitation states that all objects in the universe attract each other (Kane & Sternheim 1983, Livesey 1992). For two uniform spheres, or for two objects of any shape that are so small compared to their separation that they may be considered as point particles, the aforementioned law has a simple form. If two spheres or particles have gravitational masses m_1 and m_2 and their centers are separated by a distance d, the forces between the two spheres have a magnitude

$$F = G\frac{m_1 m_2}{d^2} \qquad (1)$$

and G is called the gravitational constant equal to G=6.67×10^{-11} Nm^{2}kg^{-2}. Since the magnitude of the gravitational force varies as $1/d^2$, equation (1) is also referred to as an inverse square law (Kane & Sternheim 1983). Equation (1) can be rearranged into

$$F = G'\frac{m_2}{d^2} \qquad (2)$$

with G' a constant without any direct physical interpretation, regrouping two elements of equation (1), *i.e.*

$$G' = Gm_1 \qquad (3)$$

It is appealing to investigate the correspondence between physical objects and landscape patches, and to test whether the law of universal gravitation has been used, maybe unconsciously, to develop a landscape metric for fragmentation. The characteristic of a landscape patch that corresponds to the gravitational mass of a physical object is its area. As for physical objects, the distance between patches can easily be calculated, *e.g.* by means of a geographic information system.

In Gustafson & Parker (1994), a proximity index (*PX*) is presented, inspired by biogeography theory, which quantifies the spatial context of a habitat patch in relation to its neighbors. It distinguishes sparse distributions of small habitat patches from clusters of large patches and could therefore be considered as an index of fragmentation, since fragmentation leads to dispersion and patch isolation (Bogaert et al. 2000). The index is most suited to evaluate high contrast landscapes where the habitat of interest is distinct from the surrounding matrix (Gustafson & Parker 1994). A *PX* value is calculated for each patch by identifying every other patch whose edge lies at least partially within a specified zone (called proximity buffer) of the patch being indexed:

$$PX = \sum_i \frac{a_i}{d_i} \qquad (4)$$

with a_i the area of the i-th patch situated at distance d_i of the patch being indexed. It should be noted that *PX* is not unit less, and is expressed in length units. A correspondence between equations (2) and (4) can be observed. The main difference is that equation (2) is developed for two objects and equation (4) for all patches inside the buffer zone. Simplification of equation (4) for two patches with areas a_1 and a_2, of which one is indexed (say, the one with area a_1) and which are separated by a distance d, gives

$$PX = \frac{a_2}{d} \qquad (5)$$

which links *PX* to equation (2), given that the distance involved is not squared. To understand this relationship between both concepts, it can be stated that, when the gravitational forces decrease with increasing distance between the physical objects and decreasing gravitational masses of the objects at study, the proximity metric will generate lower values for small patches that are separated by large distances, which indicates in its turn a higher degree of fragmentation.

Otherwise formulated, one could conclude that small objects ($m_1 \rightarrow 0$ and $m_2 \rightarrow 0$) situated far away from each other ($d \rightarrow \infty$) are characterized by negligible attractive forces; analogously, landscape patches separated by a large distance from a small patch, could be considered as (completely) isolated and hence characteristic for highly fragmented landscapes. The attentive reader could object that equation (3) considers m_1 as a constant. It should be noted that the area of the patch being indexed is also not used to calculate *PX*.

Diversity, richness, entropy and fragmentation

Landscape pattern is accepted to be an integration of landscape composition (number of patch types and their proportional area) and landscape configuration (the spatial arrangement of the patch types). Both components are generally quantified by separate metrics. Diversity metrics are appropriate metrics to quantify the composition of a system, since they quantify the partition of elements over a number of categories. In life sciences, these elements are often individuals (animals or plants) and the categories the corresponding species; every element is assumed to belong to one single category. In landscape ecology, the elements correspond to the elementary units of area that compose a patch type and the categories to the patch types themselves. A landscape is then considered more diverse or heterogeneous when many patch types are present and when no dominant type can be identified. Landscape homogeneity will be observed for landscapes with few different land covers and/or with one or several patch types dominating the landscape. Because two features are quantified simultaneously in the diversity concept, *i.e.* "richness" or the number of categories and "evenness" or the relative differences between the number of elements per category, two types of metrics have been developed: those quantifying only richness or evenness, and those quantifying both concepts at the same time.

The most simple metric to quantify richness is the number of categories (*S*). Because its upper limit is dependent on the number of elements (*N*) in a sample, S is often expressed as a function of *N*. The Menhinick richness index (R_{Mn}) is an example of such a metric (Magurran 2004), *i.e.*

$$R_{Mn} = \frac{S}{\sqrt{N}} \tag{6}$$

The richness of the sample will be considered high when the elements are distributed over a large number of categories, *i.e.* $R_{Mn} \approx \sqrt{S}$. On the other hand, concentration of the elements in a few categories will indicate a low degree of richness ($R_{Mn} \approx 0$). In landscape ecology, its interpretation will be equivalent; high values will indicate the presence of many different land covers in the landscape without a clear landscape matrix dominating all other classes. When a richness metric is used inside a patch type, instead of at the landscape level, it will quantify the partition of the patch type area over the patches composing this type and it will not quantify the composition of the patch type but its configuration. Used in this way, the presence of many patches in the patch type will lead to a high value for richness. However, the presence of many patches in a patch type also indicates a high degree of fragmentation of this type. Fragmentation will be low when one single patch is present, *i.e.* in case of concentration of the patch type area; it is considered high when many patches with a minimal area compose the patch type.

This concept equivalence is underlined by the existence of a robust and simple metric for fragmentation (Monmonier 1974), denoted *FI*, which quantifies the number of patches (n_p) as a function of the total area of the patch type, expressed as the total number of pixels (a_t), *i.e.*:

$$FI = \frac{n_p - 1}{a_t - 1} \tag{7}$$

The correspondence between equation (6) and (7) is obvious and evidences the resemblance between richness and fragmentation. Its ecological interpretation, however, is opposite. While the high richness of a vegetation is accepted to be beneficial and a positive property of the system, a high fragmentation of a natural land cover is associated with inferior habitat conditions and a lower species diversity inside the habitats. Nevertheless, it remains remarkable that two independently developed concepts refer to the same property, *i.e.* the partition of elements over categories. It should be noted that this correspondence not only applies for richness and fragmentation, but also holds for diversity (sensu the integration of richness and evenness) itself (Bogaert et al. 2005). Jaeger (2000) proposed a series of metrics to measure fragmentation, based on a central concept named "coherence" (*C*), expressing the relative area of every patch in a patch type, *i.e.*

$$C = \sum_i \left(\frac{a_i}{a_t} \right)^2 \tag{8}$$

with a_i the area of the *i*-th patch and a_t the total area of the patch type at study. Higher values of coherence indicate the presence of large patches in the patch type, hence a low degree of fragmentation. Equation (8) is identical to the Simpson index (Simpson 1949), *i.e.*

$$D = \sum_i p_i^2 \tag{9}$$

with p_i the proportion of category *i*; equation (9) is a special form of the Renyi entropy index (Renyi 1961) developed in the framework of the mathematical theory of communication. It has found many applications in the biological sciences to quantify sample diversity. The correspondence between equations (8) and (9) confirms that fragmentation and diversity are also to be considered as equivalent concepts, nevertheless should be interpreted differently. A profound discussion of the use of entropy metrics as an indicator of anthropogenic effects on landscapes with links to the thermodynamic aspects of pattern change can be found in Bogaert et al. (2005).

Concluding remarks

In this contribution, it has been shown that a central concept of landscape ecology, namely fragmentation, corresponds to concepts developed in other scientific disciplines. Using the law of universal gravitation (Kane & Sternheim 1983, Livesey 1992) and the proximity index (Gustafson & Parker 1994), a correspondence between the attractive forces characterizing two physical objects and the degree of fragmentation of a patch as measured by the proximity of other patches (Gustafson & Parker 1994), has been found. By means of the Menhinick richness metric (Magurran 2004) and the Monmonier fragmentation metric (Monmonier 1974), it has been shown that the richness of a sample can be considered as equivalent to the degree of fragmentation of a patch type. For diversity, which includes richness and evenness and which is directly related to the entropy concept, a same observation has been made. These findings can be applied to disentangle the problem of pattern quantification in landscape ecology. Many patterns are too complex to be described by means of one single metric (Dale et al. 1994). Application of a large number of metrics to cover this complexity has also been shown problematic, due to difficulties in interpretation, index redundancy, unwarranted conceptual flaws in pattern analysis, inherent limitations of indices, and improper use of indices (Bogaert et al. 2002, Bogaert & Hong 2004, Li & Wu 2004). Besides a reduction of the number of metrics based upon a decomposition of pattern, as proposed by Bogaert & Mahamane (2005), it could be suggested to choose pattern features for which equivalent metrics have already been developed in other disciplines. Existing interpretation of the corresponding concepts can complement or orientate their interpretation in landscape ecology. Metrics that have been tested elsewhere are more reliable than new metrics. In this way, a cross-disciplinary study of metrics and concepts could contribute to a more coherent and consistent theory of landscape ecology.

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