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Are potential natural vegetation maps a meaningful alternative to neutral landscape models?

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Abstract. In this paper, we present a short overview of neutral landscape models traditionally adopted in the landscape ecological literature to differentiate landscape patterns that are the result of simple random processes from patterns that are generated from more complex ecological processes. Then, we present another family of models based on Tüxen's definition of potential natural vegetation that play an important role, especially in Europe, for landscape planning and management. While neutral landscape models by their very nature do not take into account vegetation dynamics, nor abiotic constraints to vegetation distribution, the concept of potential natural vegetation includes the effects of vegetation dynamics in a spatially explicit manner. Therefore, we believe that distribution maps of potential natural vegetation may represent an ecological meaningful alternative to neutral landscape models for evaluating the effects of landscape structure on ecological processes.

Keywords: Landscape structure; Spatial model; Vegetation dynamics.

Abbreviations: NLM = Neutral landscape model; PNV = Potential natural vegetation; PSV = Potential site-adapted vegetation; RNV = Reconstructed natural vegetation.

Introduction

Landscape ecology can be described as the study of the reciprocal interactions between the spatial heterogeneity of ecosystem mosaics and ecological processes (Keitt 2000). The spatial variation of ecosystem mosaics is generally represented by categorical (i.e. thematic) maps that quantify this variability by identifying patches that are relatively homogeneous and that exhibit a relatively abrupt transition to adjacent areas (Gustafson 1998). As a result, there are now hundreds of indices to quantify various aspects of landscape patterns from grid-based categorical maps as a surrogate of landscape mosaics and correlate them with ecological processes (MacGarigal & Marks 1995; Riitters et al. 1995). Once landscape patterns have been quantified, their effects on ecological functions can be explained if the expected pattern in the absence of specific processes is known. This pattern has been called a 'neutral landscape model' (NLM) in the tradition of neutral or null models in ecology (Caswell 1976; Harvey et al. 1983).

Neutral landscape models were introduced in landscape ecology in order to differentiate patterns that are the result of simple random processes from patterns that arise from more complex ecological processes (Gardner et al. 1987). More recently, the development of NLMs has evolved to include additional constraints on the patterns generated (Gardner & O'Neill 1991; Milne 1992). In this paper, we provide a short overview of NLMs traditionally adopted in the landscape ecological literature along with their major shortcomings. Then, we present another family of models based on the concept of potential natural vegetation (PNV) that has been developed principally in Europe for vegetation mapping purposes in cultural landscapes. Finally, we suggest that PNV distribution models have a number of properties that may render them desirable as reference term for comparison with actual vegetation patterns.

Neutral landscape models

The neutral landscape modelling approach is of primary importance for the rigorous analysis of the influence of landscape mosaics on ecological processes. Since in ecological research at the landscape scale, replication obviously cannot be considered, landscape ecologists must rely upon simulations based on computer-generated NLMs to test hypotheses on the expected relationship between a given ecological process and landscape spatial heterogeneity.

The first NLMs were simple binary random maps developed by Gardner et al. (1987) from percolation theory (Stauffer & Aharony 1991) to describe the behaviour of a single species or form of disturbance. The generated habitat distributions are neutral to the effects of topography, natural disturbances and human impact that generally shape real landscapes, providing a reference for evaluating the influence of landscape heterogeneity on ecological processes and *vice versa* (With & King 1997). A useful generalization of simple two-state random percolation models termed polychromatic or multicomponent percolation (Deutscher et al. 1983; Family & Vicsek 1992) is to consider an *n*-state model representing a two-dimensional spatial distribution of habitats with a specific spatial contagion for each pair of habitats (Gardner & O'Neill 1991; With & Crist 1995). Following the development of fractal methods in landscape ecological research (Milne 1992), a new generation of NLMs were fractal landscapes (O'Neill et al. 1992; Lavorel et al. 1993; Keitt & Johnson 1995) generated either by hierarchical random curdling, in which habitat is randomly distributed within nested map layers to mimic real landscape patterns (for mathematical details, see Mandelbrot 1983), or by the midpoint displacement algorithm, where the neutral landscapes obtained exhibit continuous environmental variability. See Fig. 1 for an example. All maps of Fig. 1 were produced using the public domain software RULE (Gardner 1999) freely available on the Web site of Dr. Robert Gardner, http://www.al.umces.edu/faculty/bobgardner.html

Recently, With & King (1997) and Keitt (2000) proposed to apply spectral methods based on Fourier or wavelet transforms to develop a common mathematical framework that represents all proposed NLMs.

However, despite the vast number of suggested NLMs, much of their use to date has been theoretical. For instance, while NLMs are an adequate reference term for comparisons with real landscapes, for example to falsify the null hypothesis that real landscapes are random assemblages of different habitats (Schumaker 1996), it has yet to be convincingly illustrated whether such models can be effectively used to discriminate overall landscape heterogeneity from heterogeneity relevant to critical ecological processes (i.e. between 'useful' and 'residual' variation, as suggested by Juhász-Nagy 1984).

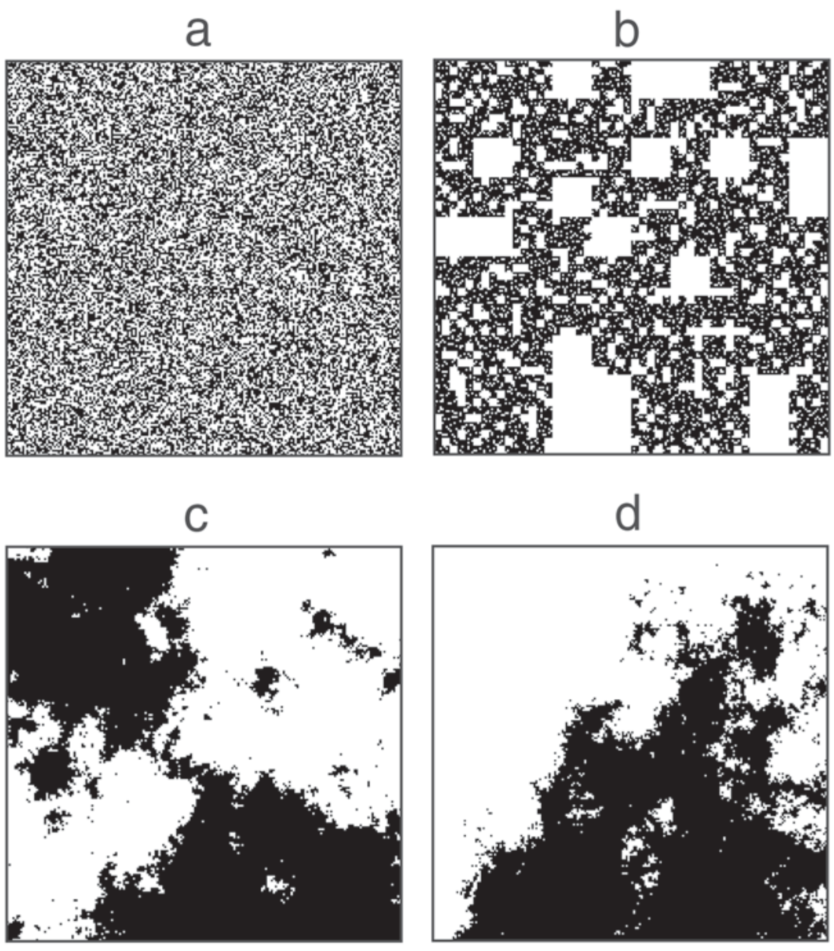

Fig. 1. Different binary NLMs produced by **a.** simple random distribution; **b.** fractal hierarchical random curdling at three different levels; **c.** fractal midpoint displacement; **d.** fractal midpoint displacement along a gradient. Each map contains the same proportion ($p = 0.48$) of shaded pixels. The proportions of shaded pixels for the three levels of the fractal hierarchical random map are $p_1 = 0.8$; $p_2 = 0.75$; $p_3 = 0.8$ ($p_1 \times p_2 \times p_3 = 0.48$).

In addition, a well-known shortcoming of most landscape indices is that their results will depend non-linearly on the extent of the area analysed. Therefore, a landscape classification scheme is needed that provides ecologically meaningful units for quantifying different aspects of landscape mosaics and correlate them to ecological processes. Due to their artificial generating procedures, NLMs obviously cannot provide the theoretical basis for the definition of such landscape units. Conversely, in the landscape ecological literature little attention has been devoted to the possible use of PNV distribution as an ecological meaningful baseline for the evaluation of the effects of landscape structure on ecological processes.

Potential natural vegetation and related concepts

In the last decade, due to the increased concern for environmental management and biodiversity conservation, ecosystem classification has been the object of a renewed interest by the scientific community (Klijn & Udo de Haes 1994; Zonneveld 1995; Bailey 1996; Blasi et al. 2000). When compared to their surroundings, ecosystems are generally perceived as relatively homogeneous. Since this homogeneity is a function of the scale of observation, ecosystem classification can thus be conceived as a hierarchical structure, where pattern and function of each ecosystem level depend both on the potentiality of lower levels and on the constraints imposed by higher levels (O'Neill et al. 1992). Such a hierarchical framework provides the theoretical foundation to deal with many challenging scale-dependent problems of nature conservation and sustainable development (Rowe 1996; Blasi et al. 2000).

In phytosociology (Braun-Blanquet 1928; Westhoff & van der Maarel 1973) a standard methodology has been developed for a nested vegetation classification that is widely adopted in most European countries for landscape description based on vegetation composition (see Blasi et al. 2000 and references therein). Within this context, as an outcome of the long-lasting debate on the existence of 'climax' vegetation, Tüxen (1956) introduced the concept of potential natural vegetation to express the biotic potential of a region with regard to all site factors relevant for vegetation development. According to Westhoff & van der Maarel (1973), the PNV is "the vegetation that would finally develop in a given habitat if all human influences on the site and its immediate surroundings would stop at once and if the terminal stage would be reached at once". Since the knowledge of PNV plays an important role in landscape planning and management especially in Europe (Chytrý 1998), Tüxen's definition has been successively refined by Kowarik (1987) who put emphasis on the influence of irreversible anthropogenic changes (e.g. landscape changes due to mining activity or the introduction and naturalization of exotic species) on PNV assessment.

To avoid the effects of long-term climatic changes and environmental modifications during plant succession, Tüxen imagined that the terminal potential stage should be reached 'at once' (Zerbe 1998). However, it remains unclear how to exclude the factor time from the PNV definition. For instance, while some authors (Kowarik 1987; Härdtle 1995) rely on the original definition with the successional time excluded, Leuschner (1997) proposed the concept of potential site-adapted vegetation (PSV). PSV is the vegetation that would finally develop taking into account all "succession-related changes in soil and nutrient stocks, and in this sense, differs from the PNV. By accounting for succession processes, PSV would represent an extension of the original PNV concept for those sites where soil regeneration is an important process in the context of landscape planning and forest management". Similarly, focusing on climatic changes, Stumpel & Kalkhoven (1978) suggested to couple "the attainment of a (provisional) final stage to a development period of 50 to 150 yr because there will likely occur no climatic changes within that period". Obviously, any PNV definition is hypothetical. Therefore, PNV-maps are generally constructed at map scales < 1:25000. At larger map scales, due to the highly hypothetical character of PNV, problems arise in drawing boundaries between the hypothetical vegetation units (Chytrý 1998). In addition, particularly in cultural landscapes where human impact is strongly marked, PNV characterization is often problematic. In such cases, scattered remnants of natural or semi-natural vegetation are used as a reference to define PNV (Wildi & Krüsi 1992).

To overcome the major shortcomings of PNV mapping in artificial habitats various PNV-related concepts have been proposed. Neuhäusl (1963) introduced the concept of reconstructed natural vegetation (RNV). Reconstruction vegetation mapping is based on "the extrapolation of mapping units of the primary vegetation to the original natural habitat conditions" (Moravec 1998). Therefore, RNV and PNV are almost identical on sites where the abiotic natural habitat conditions remain practically unchanged, while major differences occur where the habitat conditions were irreversibly changed by man (Moravec 1998). In addition, Chytrý (1998) proposed the concept of potential replacement vegetation (PRV) as an alternative to PNV. "Potential replacement vegetation is an abstract and hypothetical vegetation, which is in balance with climatic and soil factors currently affecting a given habitat, with environmental factors influencing the habitat from outside such as air pollution, and with an abstract anthropogenic influence (management) of a given type, frequency and intensity. For every habitat, there is a series of possible PRV-types corresponding to the different anthropogenic influences, e.g. grazing, mowing, trampling or growing cereals" (Chytrý 1998). PRV maps are especially useful at map scales > 1:25000 where replacement vegetation is in the focus of attention of managers and land-use planners, and may therefore be considered a large-scale surrogate of PNV maps.

Are PNV maps a meaningful alternative to NLMs?

Due to their spatially explicit nature, PNV maps may be effectively used as a valid alternative to NLMs. While none of the NLMs used to date in ecological work takes somehow into account neither vegetation dynamics, nor any abiotic constraint on actual vegetation distribution, any of the above-mentioned PNV-related definitions incorporates the concept of plant succession in a spatially explicit manner. This major difference among NLMs and PNV maps may render the latter ones desirable as reference terms for comparison with actual vegetation patterns. Nevertheless, substituting PNV maps for NLMs should not be accepted without criticism. First, the PNV concept is close to Clements' (1916) Association-Unit model and Odum's (1969) Superorganism, which are both based on a linear deterministic interpretation of vegetation succession. In contrast, in more recent papers, succession dynamics has been modeled as a discrete-time Markov chain perturbed by 'white noise' with an early phase of linear determinism and long-term chaotic behaviour (Hastings et al. 1993; Stone & Ezrati 1996; Anand & Orlóci 1997). Interestingly, despite the fact that succession processes emerge from the model as partially individualistic and not exactly repeatable, the PNV hypothesis is supported in that, starting at different points, succession trajectories converge into a strange attractor of finite dimension in phase space (Anand & Orlóci 1997). Second, as previously stated, PNV is a hypothetical model. Therefore, subjective expert knowledge of the relationships between actual vegetation types, environmental factors and vegetation dynamics is crucial for defining PNV mapping units (Ricotta et al. 2000). Nonetheless, although far from perfection, we believe that the comparison between actual vegetation patterns and PNV distribution represents a promising approach to assess the effects of disturbance on vegetation patterns and diversity.

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