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ARE POTENTIAL NATURAL VEGETATION MAPS MEANINGFUL ALTERNATIVES TO COMPUTER GENERATED NEUTRAL LANDSCAPE MODELS?

C. Ricotta

Department of Plant Biology, University of Rome "La Sapienza", Piazzale Aldo Moro 5, 00185 Rome, Italy.
E-mail: cricotta@axrma.uniroma1.it.

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Abstract: This paper provides a short critical overview of computer generated neutral landscape models traditionally adopted in landscape ecology literature. Then, another family of models based on Tüxen's concept of potential natural vegetation is presented. The suggestion is put forward that potential natural vegetation maps have a number of properties which may render them desirable as an ecological meaningful baseline for the evaluation of the effects of landscape structure on ecological processes.

Introduction

In the last two decades, under the increasing influence of global change issues, ecological research has progressively shifted from ecosystem to landscape scale (O'Neill et al. 1988). Consequently, in landscape-level ecological research, it has become necessary to detect and quantify aspects in the spatial heterogeneity of ecosystem mosaics that can be correlated with broad-scale ecological processes (Turner 1990). Landscape ecology explicitly recognizes that there are strong links between landscape heterogeneity and ecological function (for a review, see Forman and Godron 1986, Forman 1995, and references therein).

Understanding the influence of spatial heterogeneity on the ecological processes of landscape mosaics requires a way to quantify landscape variability in space and time through a set of indices that capture meaningful ecological aspects of landscape pattern (Turner 1990, Milne 1992, Gustafson 1998). Within this framework, remotely sensed data and geographical information systems (GIS) have become increasingly widespread. As a result, there are now hundreds of indices to quantify various aspects of landscape patterns from grid-based categorical maps (e.g., O'Neill et al. 1988, McGarigal and Marks 1995, Riitters et al. 1995).

Once landscape patterns have been quantified, their effects on ecological functions can only be explained if the expected pattern in the absence of specific processes is known (Gardner et al. 1987, Gardner and O'Neill 1991, Milne 1992, O'Neill et al. 1992).This type of expected pattern has been termed a neutral landscape model (NLM) in the tradition of neutral or null models in ecology (Caswell 1976, Harvey et al. 1983, Gotelli and Graves 1996, With and King 1997). In this paper, I provide a short overview of NLMs traditionally adopted in landscape ecology literature. Then, I present another family of neutral models based on the concept of potential natural vegetation (PNV) which has been developed principally in central Europe for vegetation mapping purposes in cultural landscapes. Finally, I suggest that PNV maps have a number of properties which may render them desirable as neutral models for comparison with actual real vegetation (ARV) patterns.

Computer generated neutral landscape models

The neutral landscape modeling approach is of primary importance for the rigorous analysis of the influence of landscape mosaics on ecological processes. However, since in ecological research at the landscape scale, replication obviously cannot be considered, landscape ecologists must rely upon simulations based on computer-generated NLMs (CGNLMs) to test hypotheses on the expected relationship between a given ecological process and landscape spatial heterogeneity. CGNLMs provide "a statistical benchmark for comparisons with real landscapes, a comparison facilitated by the grid-based structure common to both CGNLMs and raster-based GIS data sets" (With and King 1997).

The first CGNLMs were simple binary random maps developed by Gardner et al. (1987) from percolation theory (Stauffer and Aharony 1991, Sahimi 1994) to describe the behavior of a single species or form of disturbance. The generated habitat distributions are neutral to the effects of topography, natural disturbances and human impact which generally shape real landscapes, providing a reference for evaluating the influence of landscape heterogeneity on ecological processes and vice versa (With and King 1997).

A useful generalization of simple two-state random percolation models termed polychromatic or multicomponent percolation (Deutscher et al. 1983, Family and 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 and O'Neill 1991, With and Crist 1995, With et al. 1997). Following the development of fractal methods in landscape ecological research (Mandelbrot 1983, Milne 1992, Scheuring and Riedi 1994), a new generation of CGNLMs were fractal landscapes (O'Neill et al. 1992, Palmer 1992, Lavorel et al. 1993, Keitt and Johnson 1995, Moloney and Levin 1996, With et al. 1997) generated either by hierarchical random curdling or by the midpoint displacement algorithm (Figure 1). Other CGNLMs consist in regular point patterns (Adler and Nuernberger 1994), checkboard and sinusoidal habitat distributions (Milne 1992) and gradient percolation maps (Keitt and Johnson 1995, Milne et al. 1996). Furthermore, With and King (1997) proposed to apply spectral methods based on Fourier or wavelet transforms to develop a generalized concept for CGNLMs.

However, despite the vast number of proposed CGNLMs, much of their use to date has been theoretical while their practical application has yet to be convincingly illustrated (Schumaker 1996). While CGNLMs represent a meaningful "statistical benchmark for comparisons with real landscapes", for example to falsify the null hypothesis that real landscapes are not random assemblages of different habitats, the value of such models as a baseline to differentiate among the landscape heterogeneity that can be mapped and measured and the heterogeneity that is relevant to critical ecological processes may be biased by their artificial generating procedures. Conversely, in the landscape ecological literature little attention has been devoted to the possible use of potential natural vegetation distribution as an ecological meaningful baseline for the evaluation of the effects of landscape structure on ecological processes.

Potential natural vegetation and related concepts

As an outcome of the long-lasting debate about 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 and 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 (e.g., Chytry 1998 and references therein), Tüxen's definition has been successively refined by Kowarik (1987) to 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 the terminal potential stage as reached "at once" (Zerbe 1998). However, it remains unclear how to exclude the time factor from the PNV definition. For instance, while some authors (e.g., 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 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 and Kalkhoven (1978) suggested to couple "the attainment of a (provisional) final stage to a development period of 50 to 150 years because there will likely occur no climatic changes within that period". Notice that from the above definitions it follows that any PNV is hypothetical, and its characterization and spatial distribution is therefore often difficult and controversial, especially in cultural landscapes where human impact is more pronounced (Brzeziecki et al. 1993). PNV mapping is traditionally based on taking scattered remnants of ARV with natural and semi-natural character occurring in present-day landscapes as a reference object for PNV. Then, the potential distribution of these remnants is extrapolated to sites of similar habitat where no natural (primary) vegetation exists anymore (Moravec 1998, Zerbe 1998).

PNV-maps are generally constructed at scales <1:25.000. At larger scales, due to the highly hypothetical character of PNV, problems arise in drawing boundaries between the hypothetical vegetation units (Dierschke 1994, Chytry 1998). For these reasons, numerous authors (e.g., Neuhäusl 1984, Kowarik 1987, Härdtle 1995) proposed to avoid PNV mapping in highly artificial man-made habitats where the actual anthropogenic habitat conditions do not correspond to any natural vegetation. However, it is generally not satisfactory to leave blank spots on PNV maps, especially when the maps have been constructed for landscape planning and management purposes.

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, Chytry (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" (Chytry 1998). PRV maps are especially useful at scales >1:25 000 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 meaningful alternatives to CGNLMs?

Due to the spatially explicit nature of PNV, I think that PNV maps may be effectively used as a valid alternative to CGNLMs. While none of the above mentioned CGNLMs takes somehow into account vegetation dynamics, any of the above mentioned PNV-related definitions implicitly or explicitly incorporates the concept of plant succession. This major difference among CGNLMs and PNV maps may render the latter ones desirable as null models for comparison with ARV patterns.

However, substituting PNV maps for CGNLMs should not be accepted without criticism. For instance, 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 vegetational succession. To the contrary, 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 behavior (Hastings et al. 1993,

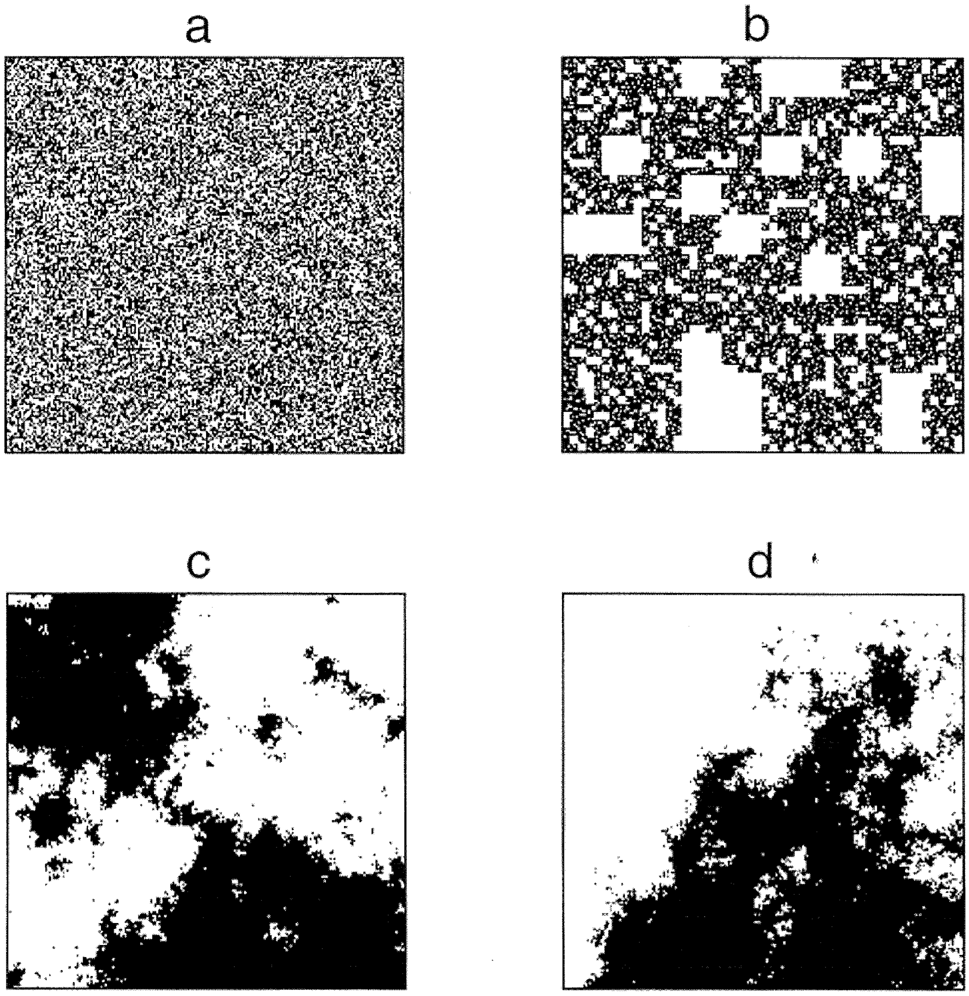

Figure 1. Four different binary CGNLMs produced by a) simple random distribution; b) fractal hierarchical random curdling at three different levels; c) fractal midpoint displacement; d) fractal midpoint displacement along a gradient. Each map contains the same proportion ($p = 0.48$) of shaded pixels.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

Orlóci et al. 1993, Stone and Ezrati 1996, Anand and Orlóci 1997). Interestingly, despite the succession process emerges from the model as partially individualistic and not exactly repeatable, the PNV hypothesis is supported in that, starting at different points, succession trajectories converge onto a strange attractor of finite dimension in phase space (Anand and Orlóci 1997).

For this reason, I think that the substitution of PNV maps for CGNLMs as a baseline for comparison with ARV patterns represents an interesting conceptual improvement for providing a general model of landscape spatial complexity and for the evaluation of the effects of landscape structure and human pressure on ecological processes.

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