

Space series analysis of vegetation: processes reconsidered

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Abstract: Space series analysis is understood in a broad sense to refer to logical sequences of changes or transformations applied to vegetational entities in both topographic and conceptual spaces. This term is suggested to replace spatial processes which, although being historically clear, have a multiple meaning and may lead to confusions. A literature survey illustrates that space series analysis includes commonly used pattern recognition methods associated with the real, topographic space, but also supports generalization to data, resemblance, ordination, classification spaces and derived variables. It is suggested that space series analysis is a potential tool to evaluate any problems in vegetation studies where scale effects are influential.

Historical background: a few milestones

Spatial scales are associated with all studies of vegetation structure and, therefore, indirectly affect any research which concentrates "only" on temporal changes of and causal factors behind the structural characteristics. I can only agree with Palmer's (1988) statement that "Spatial dependence is a characteristic of nearly all vegetation surveys". Published work may be arranged along a hypothetical gradient which reflects the degree of understanding the importance of scales. At one terminal point complete neglect of spatial dependence is typical, whereas the problem of scales in vegetation analysis is deeply understood at the other end. Reports on plant pattern represent the first examples for the latter case, although history goes further back in time, (see Juhász-Nagy, this issue). Suffice to mention the pioneering studies by Greig-Smith (1952, 1983) and Kershaw (1957) who used a sequential arrangement of increasing sample plot (or "block") sizes to detect particular areas that characterize the spatial distribution of a given plant species. Of

studies at the community level, attempts to determine "minimal areas" by species/area curves (Cain & Castro 1959) deserve our attention in the present context. These two approaches were simultaneous in time and illustrate two contrasting objectives analyzed by similar tools: detection of pattern (searching for plot sizes to maximize variance or a related measure) and estimation (attempting to find a plot size large enough to express a diversity property). Pattern detection objectives at the community level, which are analogous to the univariate case, were first formulated by Juhász-Nagy (1967, 1976). His information theory methods evaluate species assemblages based on the gradual turning of absences into presences as plot size increases. He coined the term *spatial process* with events belonging to a sequence of plot sizes (and also to increasing volumes of sampling units used for plankton, Dévai et al. 1971). This concept was generalized later to any spatial changes that can be arranged into a logical sequence (Podani 1984). I suggested that a spatial (and time-static) process is in fact an

analytical tool by which one learns a lot more about the subject than when a single scale point is considered only. Often, such processes are almost inevitable, for example, when the size of clumps is to be detected. In other cases, processes yield merely some extra information on the subject, which is not apparent otherwise, especially when the changes are associated with conceptual spaces (e.g., data, resemblance or ordination spaces). Examination of the effect of species number upon the results of multivariate analyses is a case in point. Furthermore, processes in the above sense may help us to solve the dilemma of many arbitrary choices we have to make during data recording and analysis (e.g., classification sequences from single link to complete link through many intermediates). Such processes provide a potential solution in many cases to the problem summarized by Wiens (1989) as: "If we study a system at an inappropriate scale, we may not detect its actual dynamics and patterns but may instead identify patterns that are artifacts of scale."

Processes: three uses

Although a fairly precise definition was given for *time-static* spatial processes, clearly distinguished from other types of processes (Podani 1984), this terminology was not generally accepted in the past eight years. A reason is that the term process has a multiple and inconsistent use in the literature, as obvious, for example, from a recent proceedings volume devoted completely to this topic (Krahulec et al. 1990). In most cases, process is used in a *spatio-temporal* context even if the title suggests restriction to spatial analysis (e.g., Willems & Bobbink 1990). In fact, one easily associates some temporal aspect with processes, especially in ecology, since Watt's (1947) paper on pattern and processes. A complication arises from

the mathematical jargon of spatial statistics for which a spatial process is essentially a pattern generating *rule*. For example, a random point pattern is considered as a realization of a two-dimensional homogeneous Poisson point process (see e.g., Ripley 1981, Diggle 1979, Cliff & Ord 1981). That is, a spatial process may refer to at least three different things which are often interrelated: a spatio(-temporal) ecological process develops a plant pattern in the real topographical space; this pattern can be modeled by the spatial processes of statistics, and they can also be analyzed by spatial processes represented by increasing series of sample plots. Given these circumstances, it is obvious that the reader is easily confused whenever the term spatial process is encountered in any ecological text. Therefore, I am tempted to clarify at least part of this terminological confusion by proposing the term *space series analysis* to replace spatial processes formerly defined in relation to analytical tools.

Space series analysis: a definition and an overview of relevant literature

Space series analysis involves the examination of a sequence of well-defined and strictly ordered changes or transformations in the real topographic space and any conceptual spaces that are associated with vegetation surveys (Fig. 1). These changes occur in a given point of time or when temporal aspects are neglected or irrelevant in the study.

Two basic types of series are used in space series analysis. The *primary series* is defined more or less arbitrarily by the investigator according to the objectives of the study. Examples for primary series are transformations such as the increase in plot size, elongation of plots, increasing the number of

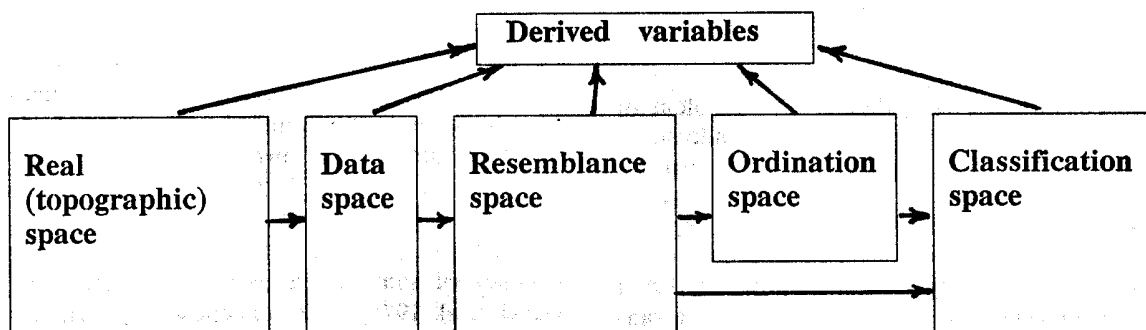


Figure 1. Conceptual spaces and main directions of information flow in spatial vegetation analysis.

sampling units, changing the number of species considered, varying exponents in data transformation and resemblance functions, and changing spatial criteria in clustering and ordination, etc.

The *dependent series* is the sequence of changes generated by the primary series; they describe some behavior of the analyzed object in the function of the primary changes. The dependent changes occur either in the same space as the primary series, or in any subsequent conceptual space associated with the given step of the methodological pathway. (An example of such a sequence of spaces is: real → data → resemblance → ordination). Often, the relationship of the primary and dependent series is illustrated in a Cartesian coordinate system (block size vs variance/mean ratio, plot size vs number of species, distance vs correlation, etc.). Further statistical analyses and related graphical tools are required to visualize the relationships in more complex situations (plot size vs classifications, data transformation vs ordinations). The results do not have to show "peaked" effects to be interpretable; the general objective of space series analysis is to show spatial trends and scale dependence.

Space series analysis is used as a broad collective term which includes many traditional pattern detecting methods of ecology, geostatistical procedures, spectral analysis, fractal analysis, sample size optimization and many more. Some of the techniques are those of time series analysis adopted and extended to spatial data (Ripley 1981). The diversity of the topic is illustrated by the subsequent overview summarizing a complete literature search upon some main forums of vegetation ecology (Coenoses=C, Journal of Vegetation Science=JVS, and Vegetatio=V) and a partial examination of many other relevant journals and books for the period of 1983-1991. Earlier work is reviewed in Podani (1984). This list, although far from being exhaustive, pretty well illustrates the wide variety of possibilities, the importance and rapid development of space series analysis in vegetation surveys. Emphasis is placed on applications rather than on theoretical foundations of particular methods. Relevant work is grouped according to the spaces of the primary and dependent series, abbreviated by P and D, respectively. To save space, these items do not occur in the list of references; only abbreviated bibliographic information is presented. The authors are listed in alphabetic order within each subject.

P: real; D: data

Plot size vs data tables: Camiz & Gergely 1990 (Abstracta Botanica 14:83). **Plot size vs frequency or frequency distributions:** Kwiatowska & Symonides 1985 (Acta Soc. Bot. Polon. 54:465), Nosek 1986 (Acta Bot. Hung. 32:97), Weir & Wilson 1987 (V. 73:81). **Plot size vs univariate estimation:** Kwiatowska & Symonides 1985 (Acta Soc. Bot. Polon. 54:465, 493). **Plot size vs density:** Nosek 1986 (Acta Bot. Hung. 32:61), Taylor & Aarssen 1989 (J. Ecol. 77:975).

Sample plot arrangement vs estimation of distributions: Mohler 1983 (V. 54:97).

P: real; D: derived variables

Plot size vs number of species (species/area) and its variance: Bartoli & Massari 1988 (C. 3:61), Bongers et al. 1985 (V. 63:13), Brown & Hopkins 1983 (Aust. J. Ecol. 8:63), Gitay et al. 1991 (JVS. 2:113), Hatton & Carpenter 1986 (V. 68:33), Hommel 1990 (V. 89:39), Leps & Stursa 1989 (V. 83:249), McGuinness 1984 (Biol. Rev. 59:423), Nosek 1986 (Acta Bot. Hung. 32:61), Palmer 1987 (V. 70:61), Rice & Westoby 1983 (V. 52:129), Shmida 1984 (Isr. J. Bot. 33:41), Shmida & Ellner 1984 (V. 58:29). **Plot size vs frequency distribution of diversity:** Kwiatowska & Symonides 1986 (Acta Soc. Bot. Polon. 55:129). **Plot (block) size vs different measures of pattern intensity (or non-randomness):** Agnew & Gitay 1990 (in Krahulec et al.: 191), Bigwood & Inouye 1988 (Ecology 69:497), Bouxin 1983 (V. 52:161), Bowman 1986 (V. 65:105), Busing 1991 (V. 92:167), Carlsson & Callaghan 1990 (J. Ecol. 78:152), Carter & Connor 1991 (JVS. 2:231), Charpentier & Chaney 1983 (V. 53:153), Chessel & Gautier 1984 (in Knapp: Sampling methods. . . , Junk, p. 61), Dale & MacIsaac 1989 (J. Ecol. 77:78), Dale & Blundon 1990 (JVS. 1:153), 1991 (JVS. 2:73), Davis et al. 1989 (V. 84:53), Franklin et al. 1985 (V. 64:29), Galiano 1983 (V. 53:129), 1985 (V. 63:121), Galiano 1986 (Oikos 46:132), Galiano et al. 1987 (J. Ecol. 75:915), Gitay & Agnew 1989 (V. 83:241), Leps 1990 (in Krahulec et al.: 71), Nosek 1986 (Acta Bot. Hung. 32:79), Read & Hill 1985 (V. 63:67), Sakai & Oden 1983 (Am. Nat. 122:489), Stewart 1986 (V. 68:115), Taylor & Halpern 1991 (JVS. 2:189), Usher 1983 (J. Ecol. 71:945). **Plot size vs measures of community pattern:** Bartha 1990 (in Krahulec et al. : 31), Bartha & Horváth 1987 (Abstracta Botanica 11:9), Camiz & Gergely 1990 (Abstracta Botanica 14:83), Juhász-Nagy & Podani 1983 (V. 51:129), Podani 1984 (Acta Bot. Hung. 30:403), 1987 (C. 2:9), Szollát & Bartha 1991 (Abstracta Botanica 15:47). **Plot size vs ordination eigenvalues:** Maslov 1990 (in Krahulec et al.: 83), Ver Hoef & Glenn-Levin 1989a,b (V. 82:59, V. 83:147). **Plot size vs variance of eigenvalues for multivariate**

estimation: Kenkel & Podani 1991 (JVS. 2:539). Plot size vs variance based on ordination scores: Galiano 1983 (V. 53:129), Gibson & Greig-Smith 1986 (V. 66:41), Sterling et al. 1984 (Oikos 42:334). Plot size vs diversity: Kwiatkowska & Symonides 1986 (V. 68:99), Pablo et al. 1982 (V. 50:113). Plot size vs beta diversity (gradient length): Okland et al. 1990 (V. 87:187). Plot size vs number of species with given pattern: Kwiatkowska & Symonides 1985 (Acta Soc. Bot. Polon. 54:477).

Distance from randomly selected individuals vs expected number of individuals within that distance (Ripley's count-distance analysis): Kenkel 1988 (Ecology 69:1017), Leemans 1990 (in Krahulec et al. : 111), 1991 (V. 93:157), Prentice & Werger 1985 (V. 63:133), Rebertus et al. 1989 (J. Ecol. 77:638), Stamp & Lucas 1990 (J. Ecol. 78:589), Skarpe 1991 (JVS. 2:565), Sterner et al. 1986 (J. Ecol. 74:621), Stewart & Rose 1990 (V. 87:101), Szwagrzyk 1990 (V. 89:11). Distance between pairs of plots (spacing) vs correlation or other statistic (e. g. , spatial autocorrelation, semivariance; incl. spectral analysis): Carpenter & Chaney 1983 (V. 53:153), Carpenter & Titus 1984 (V. 57:153), Ford & Renshaw 1984 (V. 56:113), Fortin et al. 1989 (V. 83:209), Franklin et al. 1985 (V. 64:29), Gibson 1988 (J. Ecol. 76:233), Kenkel 1988 (V. 78:45), Kenkel et al. 1989 (Can. J. Bot. 67:263), Legendre & Fortin 1989 (V. 8):107), Newbery et al. 1986 (V. 65:77), Palmer 1988 (V. 75:91), 1990 (C. 2:79), Rijnberk & During 1990 (in Krahulec et al.: 161), Robertson 1987 (Ecology 68:744), Sakai & Oden 1983 (Am. Nat. 122:489), Van der Hoeven et al. 1990 (V. 86:151), West & Goodall 1986 (Abstracta Botanica 10:187), Wildi 1990 (C. 5:51). Distance of quadrats vs fractal dimensionality: Palmer 1988 (V. 75:91). Distance between pairs of plots (spacing) vs variance based on ordination scores: Carpenter & Titus 1984 (V. 57:153). Distance of sampling units vs diversity: Oksanen 1984 (Ann. Bot. Fenn. 21:189).

Sample size vs diversity measures: Chaneton & Facelli 1991 (V. 93:143), Scheiner 1990 (V. 86:175), Stampfli 1991 (V. 96:185). Sample size vs precision of estimates: Everson et al. 1990 (V. 88:135), Floyd & Anderson 1987 (J. Ecol. 75:221). Sample size vs stability of structural measures: Orłóci & Patta Pillar 1989 (Biom. Praxim. 29:173). Sample size vs pattern detection: Cox 1987 (J. Ecol. 75:193).

P: real; D: resemblance

Plot (block) size vs species correlation (association): Bartha & Horváth 1987 (Abstracta Botanica 11:9), Hahn 1984 (Abstracta Botanica 8:35), Usher 1983 (J. Ecol. 71:945), Weir & Wilson 1987 (V. 73:81), Whittaker 1991 (V. 94:81). Plot size vs competition coefficients: Gurevitch et al. 1990 (J. Ecol. 78:727). Plot

size vs frequency distribution of quadrat resemblance: Kwiatkowska & Symonides 1985 (Acta Soc. Bot. Polon. 54:511).

Distance from plants vs species association: van Tilborgh et al. 1989 (JVS. 2:189).

Sample size vs mean distance between quadrats: Belsky 1988 (V. 74:3). Sample size vs community similarity: Lim & Khoo 1985 (Ecology 66:1682).

P: real, D: classification and ordination

Plot size vs ordination: Boerner & Cho 1987 (Bull. Torrey Bot. Club 114:173), Camiz & Gergely 1990 (Abstracta Botanica 14:83), Castro et al. 1986 (V. 68:37). Plot size vs temporal changes in ordinations: Smith & Urban 1988 (V. 74:143), Plot size vs classification: Podani 1989 (V. 83:111).

Sample size vs species clustering: Podani 1987 (C. 2:9).

Sample size vs community classification: Podani 1986 (Abstracta Botanica 10:235), Wildi 1989 (V. 83:179).

Sample size vs ordination stability: Knox & Peet 1989 (V. 80:153). Sample size vs ordination: Bridgewater 1989 (V. 81:1159), Wildi 1989 (V. 83:179).

P: data; D: resemblance

Number of species vs distance matrices: Shaukat 1989 (C. 4:163). Number of species vs distributional properties of similarity: Lim & Khoo 1985 (Ecology 66:1682).

P: data; D: ordination and classification

Number of species vs estimated gradient length: Eilertsen et al. 1990 (JVS. 1:261). Number of species vs clustering: Podani 1989 (V. 83:111), Shaukat 1989 (C. 4:163).

Taxonomic level vs community classification: Elsol & Clifford 1988 (V. 78:103), Podani 1986 (Abstracta Botanica 10:235), 1989 (V. 83:111).

P: resemblance; D: ordination

Shortest path adjustment vs ordinations: Bradfield & Kenkel 1987 (Ecology 68:750).

P: classification or ordination; D: derived variables

Number of clusters vs a goodness criterion: Castillo et al. 1991 (JVS. 2:73), Dale 1988 (C. 3:11), Dale et al. 1986 (C. 1:35), 1988 (V. 76:113), Gao 1991 (C. 6:15), Marsili-Libelli 1989 (C. 4:95), Noest & Maarel 1989 (V. 83:157), Popma et al. 1983 (V. 52:65). Number of clusters vs similarity of classifications: Wilson 1989 (J. Ecol. 77:223).

Number of dimensions vs stress: Tong 1988 (V. 79:65).

P: classification; D: classification

Fuzziness vs fuzzy clustering: Podani 1990 (C. 5:17).
Parameter lambda vs flexible SAHN clustering: Podani 1989 (V. 81:61).

P: ordination; D: ordination

Degree of correlation of oblique ordination axes (delta) vs unipolarity: Oksanen 1985 (Ann. Bot. Fennici 22:263).

Weighting factor vs ordination: Oksanen 1987 (V. 72:51).

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Bibliography

This list includes references made in the main text of the paper and other sources of information on the present subject, not cited but considered very important for further orientation.

- Cain, S. A. & G. M. de O. Castro. 1959. Manual of vegetation analysis. Harper, New York.
- Cliff, A. D. & J. K. Ord. 1981. Spatial processes. Models and applications. Pion, London.
- Cormack, R. M. & J. K. Ord (eds). 1979. Spatial and temporal analysis in ecology. Internat. Co-operative Publ. House, Burtonsville, MD, USA.
- Dévai, I., K. Horváth & P. Juhász-Nagy. 1971. Some problems of model building in synbiology. Part I. Spatial diversity process of the binary type in a simple situation. Annal. Univ. Sci. Budapest, sect. biol. 13:19-32.
- Diggle, P. J. 1979. Statistical methods for spatial point patterns in ecology. In: Cormack & Ord, pp. 95-150.
- Goodall, D. W. 1974. A new method for the analysis of spatial pattern by random pairing of quadrats. Vegetatio 29:135-146.
- Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of structure in plant communities. Ann. Bot. (London) N. S. 16:293-316.
- Greig-Smith, P. 1983. Quantitative plant ecology. 3rd ed. Blackwell, Oxford.
- Juhász-Nagy, P. 1967. On some 'characteristic areas' of plant community stands. Proc. Colloq. Inf. Theory, Bolyai Math. Soc., Debrecen, Hungary, pp. 269-282.
- Juhász-Nagy, P. 1976. Spatial dependence of plant populations. Part 1. Equivalence analysis (an outline of a new model). Acta Bot. Acad. Sci. Hung. 22:61-78.
- Juhász-Nagy, P. & J. Podani. 1983. Information theory methods for the study of spatial processes and succession. Vegetatio 51:129-140.
- Kershaw, K. A. 1957. The use of cover and frequency in the detection of pattern in plant communities. Ecology 38:291-299.
- Kershaw, K. A. 1961. Association and co-variance analysis of plant communities. J. Ecol. 49:643-654.
- Krahulec, F., A. D. Q. Agnew, S. Agnew & H. J. Willems (eds). 1990. Spatial processes in plant communities. Academia, Prague.
- Ludwig, J. A. 1979. A test of different quadrat variance methods for the analysis of spatial pattern. In: Cormack, R. M. & J. K. Ord (eds), pp. 289-303.
- Orlóci, L. & M. M. Mukkattu. 1973. The effect of species number and type of data on the resemblance structure of a phytosociological collection. J. Ecol. 61:37-46.
- Palmer, M. W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. Vegetatio 75:91-102.
- Podani, J. 1984. Spatial processes in the analysis of vegetation: theory and review. Acta Bot. Acad. Sci. Hung. 30:75-118.
- Ripley, B. D. 1978. Spectral analysis and the analysis of pattern in plant communities. J. Ecol. 66:965-981.
- Ripley, B. D. 1981. Spatial statistics. Wiley, New York.
- Watt, A. S. 1947. Pattern and process in the plant community. J. Ecol. 35:1-22.
- Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.
- Willems, J. H. & R. Bobbink. 1990. Spatial processes in the succession of chalk grassland on old fields in the Netherlands. pp. 237-249 in Krahulec et al. (1990).

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