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### **Diplomarbeit von Christof Bigler (1999)**

Die vorliegende Diplomarbeit von Bigler (1999) wurde im Jahr 1999 im Rahmen des Nachdiplomstudiums in Statistik (Université de Neuchâtel) ausgeführt. Der Text wurde in einer alten Word-Version auf einem Apple-Computer erstellt. Im Jahr 2009 wurden die Dokumente auf einem Apple-Computer unter Word 2004 neu gespeichert und anschliessend zu einem einzelnen PDF-Dokument zusammen gestellt.

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Christof Bigler

Diploma Thesis

# Evaluating time series to reveal successional patterns

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# Evaluating time series to reveal successional patterns

## Abstract

Long-term investigations of vegetation changes in the Swiss National Park since 1917 allowed composing a successional series by means of merging single time series. 49 permanent plots were established on a subalpine meadow in order to observe the recovery process from pasture to forest. The time series cover an observational time span of 50 to 80 years. The current vegetation pattern of the meadows shows a patchy structure of different vegetation types. In a space-for-time substitution these patches can be assigned to the underlying successional stages. The multivariate time series, defined by the centroid of 6 species groups, were matched by an algorithm into a successional gradient, furnishing a unique and consistent solution. However, there is no possibility to test the emerging pattern, neither experimentally, nor by comparison. Its reliability is therefore as yet unknown.

This paper presents a sensitivity analysis of the algorithm. Firstly it suggests that there is a robust internal pattern of the successional processes. Second the length of the investigation period provides sufficient data to detect the successional pattern. Third the algorithm yields similar results, even when using subsets of the data. Only after reducing the number of relevés of each time series below of 50%, misinterpretations occur due to inadequate overlap of single time series.

The results suggest that partial space-for-time substitution can be extremely efficient for investigating successional patterns. Provided the sampling design is optimized for this purpose, continuous analysis and interpretation of the monitoring process may reveal the pattern in surprisingly short time.

**Keywords:** Vegetation succession; Long-term investigation; Space-for-time substitution; Ordination; Principal coordinates analysis; Ranking algorithm; Subalpine meadows; Swiss National Park.

## **Introduction**

The investigation of successional processes aims at revealing underlying ecological mechanisms. Since any biological individual or population is bound to a spatio-temporal context, the importance of temporal processes, particularly in plant ecology, should be kept in mind. The knowledge of a vegetation succession as a whole can provide a deeper understanding of inter-species relationships. Austin (1977) mentions two purposes of research on succession: detailed understanding of particular successions in order to predict and control and the detection of general rules of changes in community patterns.

Ideal conditions to study successional processes are met in the Swiss National Park (SNP). The documentation of the vegetation development dates back to the foundation of the SNP in 1914. Thanks to the far-sighting efforts of Braun-Blanquet and Stüssi who established permanent plots in order to observe the expected long-term vegetation change from pasture to forest (Braun-Blanquet 1931; Stüssi 1970), more than 100 time series are now at our disposition. Many of these permanent plots were observed over more than 50 years, some even over nearly 80 years.

There are 49 permanent plots considered in this study, mainly concentrated on one subalpine meadow on 2000 m a.s.l. Cattle and sheep, grazing on this meadow until 1914, were excluded after the foundation of the SNP, as no domesticated animals were permitted in this area any more. Subsequently the increasing population of red deer has taken the role of grazing mega-herbivores. Until 1930, the influence of deer on vegetation can be neglected. The exponentially growing red deer population reached a maximum of about 2000 animals in the SNP in the eighties.

The spotted structure of different vegetation patches on the meadow, each being in a different successional stage, is caused by temporally and spatially changing browsing patterns (Krüsi et al. 1995) as well as by endogenous forces. This vegetation structure is transferred in a space-for-time substitution (Pickett 1989) into a successional series. Merging single time series is a way to get a unique, consistent solution (Schütz et al. 1998; Wildi et al. 1999a) and allows explaining the transition of one vegetation type into another. Depending on the method used a time span of 580 years (Schütz et al. 1998)

or 360 years (Wildi et al. 1999a) can be explained with the data from the SNP. Apart from the different time scaling, both methods yield the same pattern. If the procedure turns out to be appropriate and reliable, this would imply an enormous increase of efficiency in research on succession.

This approach, if justified, would provide a contribution to answer practical questions concerning the design and analysis of long-term investigations and monitoring projects. These are, e.g., the sampling time required and the optimal selection of permanent plots.

### **Data and methods used**

We dispose of a three-dimensional data matrix of stand x species x time, consisting of 49 permanent plots considered in this analysis. The selection of stands by Braun-Blanquet and later by Stüssi was most likely preferential, in order to observe the succession on sites with “typical“ vegetation. All initial relevés were taken between 1917 and 1944, 38 of these 49 time series were continued up to present. The plot size varies between 1 and 100 m<sup>2</sup>. On average the relevés were repeated all 5 years, resulting in a total of 582 relevés. The entire set was used as reference system for the following presentations and comparisons of results.

The estimation of cover-abundances accords with the system of Braun-Blanquet (1964), a scale in 8 steps. Subsequently, the values were back-transformed to percentage cover (van der Maarel 1979; Wildi & Orłóci 1996). As described in detail in Schütz et al. (1998) the species were summarized in 6 species groups (“Aconitum“, “Carex“, “Deschampsia“, “Festuca“, “Pinus“ and “Trisetum“). The names of the groups stem from dominant species.

The algorithm proposed by Wildi et al. (1999a) provides a deterministic approach as to merge several time series into a single successional series. Plausible results can only be expected if the data quantity and quality are sufficient, i.e. single time series have to show a minimum temporal overlap and low random variation. The first requirement can only be fulfilled if each successional section is documented by an adequate number of time series.

The Euclidean distance serves as resemblance measure (Orlóci 1978; van der Maarel 1980):

$$d(r_s, r_t) = \sqrt{\sum_{i=1}^n r_{si}^2 - 2 \sum_{i=1}^n r_{si} r_{ti} + \sum_{i=1}^n r_{ti}^2}$$

where  $n$  is the number of species groups,  $r_{si}$  the percentage cover of the  $i$ th species group in relevé  $r_s$  and  $r_{ti}$  the percentage cover of the  $i$ th species group in relevé  $r_t$ . Computing the distances of all possible pairs of relevés provides a symmetrical resemblance matrix. For the time-series-merging procedure this matrix has to be calculated just once. All computations were performed with an extended version of Mulva5 (Wildi & Orlóci 1996).

The two most similar relevés of a first selected plot and a second plot were brought in correspondence, i.e. we used them as fix points in time for both time series on a successional scale. We proceeded with all other time series in the same fashion. The smallest Euclidean distance, considering all relevés of a time series, was extracted and every plot was attached to the successional scale, corresponding to the fix points. The resulting structure can be understood as minimum spanning tree (Gower & Ross 1969), which represents a unique and consistent solution with mean values, furnished by the algorithm (Wildi et al. 1999a).

The next step included taking the average of the percentage cover values of all corresponding relevés of each time step (Schütz et al. 1998) yielding finally a successional series. Postulating regular time intervals and a high temporal dependence of consecutive relevés (Legendre & Fortin 1989) it can be assumed that the axis is composed of discrete time steps each corresponding to roughly 5 years. The term successional series is used for the result of the time-series-merging procedure, exhibiting the pattern of the succession.

From this successional series a new resemblance matrix is calculated, again the Euclidean distance is used and provides the input for principal coordinates analysis (PCOA) (Orlóci 1978; Gauch 1982). The graphical presentation in reduced space allows a reasonable interpretation of the successional sequence (Nichols 1977; Allen & Shugart

1983). Since non-linear vegetation data appear in general as “horse-shoe“ (Austin 1976; Orłóci 1978; Wildi 1999b), more than just one component of the ordination should be considered (Johnson & Goodall 1979). The points, representing the states in time, are then linked chronologically (Swaine & Greig-Smith 1980). In this study the primary interest is not put on the ecological interpretation of the ordination scores, but on the comparison of two or more jointly analyzed data sets (Austin 1977). Combining a priori the original data set and one or several subsets of these data makes sense (Fewster 1987) since similar data points pertain to the same axes and are represented spatially close to each other (Nichols 1977). Sound conclusions concerning relationships of ordinated data points in vegetation studies are still subject to some limitations (Orłóci 1978; Wilson 1981).

Searching for a subset of time series explaining as much as possible was finally done using a ranking algorithm (Orłóci 1978; Wildi & Orłóci 1996) with the van der Maarel coefficient (van der Maarel 1979). This method should reveal the potential concerning optimal selection of permanent plots. The van der Maarel coefficient

$$d(r_s, r_t) = \frac{\sum_{i=1}^n r_{si} r_{ti}}{\sum_{i=1}^n r_{si}^2 - \sum_{i=1}^n r_{si} r_{ti} + \sum_{i=1}^n r_{ti}^2}$$

is a resemblance measure, where  $n$  is the number of species groups,  $r_{si}$  the percentage cover of the  $i$ th species group in relevé  $r_s$  and  $r_{ti}$  the percentage cover of the  $i$ th species group in relevé  $r_t$ .

## **Results**

### *Sensitivity analysis of the algorithm*

Since quality of data is very often dependent on the sampling design we would like to know how results would change with respect to the reference system if we had sampled in a different way. In order to test the reliability and robustness of the time-series-generating algorithm different subsets were used, derived from the original data. Time series were truncated at the beginning and/or at the end, entire time series or all relevés before or after a specific date were omitted.

The resulting successional series of the original data yielding 73 time steps, labelled with “series 00”, was used as reference system to be compared with results from the reduced data sets. Results were compared in form of direct gradient analysis (fig. 1) with successional time as single, unidirectional gradient or as joint ordination diagrams of a PCOA, representing a low-dimensional subspace with a maximum of variability explained (fig. 2). The comparison of two plots in direct gradient analysis, each with six curves according to the number of species groups, is much more complex than the comparison of two curves in the same PCOA.

The effect of removing 2, 4, 6 or 8 relevés at the beginning of each single time series is shown in fig. 2, displaying the resulting successional series in ordinated form. According to the increasing number of omitted relevés per time series the trajectories are termed as “series 20”, “series 40”, “series 60” and “series 80”. Apart from a delayed beginning of the succession in the top left corner, the first three reduced series feature a good correspondence to the reference curve. The result of shortening the time series by 1, 2, 3 or 4 relevés at the beginning and at the end can be seen in fig. 3. All chronologically linked series, except “series 44”, reasonably reflect the structure of the original data “series 00”. The transitions between “series 33” and “series 44” and between “series 60” and “series 80” indicate the critical point where the data quantity is not sufficient to reconstruct the successional series properly.

Excluding 11 of the total of 49 time series, with each of the 11 permanent plots representing a part of the succession with *Carex* as dominant species group, the ordinated successional curve is practically identical to the reference curve. Some deviations can



be established around the knee in the middle of the curve, which in all ordinations represents the transition from *Carex* species to *Pinus* species, suggesting the influence of *Carex* as important species group in this successional stage.

### *Sampling time*

The dependence of the number of time steps generated and the number of relevés is shown in fig. 4. There are two categories of points that can be distinguished. Dots signify successional series where time series were shortened or completely omitted. Asterisks as symbols include successional series where underlying time series were selected according to ranking algorithms with respect to cover a maximum amount of variability. Different lengths of investigation periods can give us indications about the time required to get a realistic and plausible model. The question of sampling time can be answered by means of fig. 5 illustrating again trajectories projected into a two-dimensional space. Four successional series were created, where all relevés from the single time series after a certain date were removed. E.g. "series 1953" designates the successional series, where the relevés taken after 1953 were omitted. It can be seen that the first three trajectories "series 1953", "series 1962" and "series 1972" contain too less data to depict the pattern achieved by "series 00". The series are misinterpreted due to a lack of relevant information. As an example time series with *Aconitum* as dominant species group were placed in a late instead of an early stage of the succession. Apparently only after 1982 the trajectory approaches the reference curve. This can be seen in "series 1982" fitting quite well the reference curve.

Instead of sampling intensively during a short time (see fig. 5) we can reduce the data quantity by extending time interval of sampling while extending overall observation time. This allows retaining the data quality, if the different vegetation types are documented by several time series. If so, artificial successional gaps in the successional series may not occur. Taking every second relevé of each time series, i.e. sampling in 10-yr intervals, resulted in diminishing the number of total relevés to 301 and halving the number of time steps down to 37. Maybe due to an insufficient number of time series covering the first successional phase, there occurred some deviations from the reference curve. Both the *Aconitum* and *Deschampsia* peaks moved to a later stage, but still appeared before the

Festuca dominating phase. The corresponding ordination diagram suggests similar conclusions. In terms of resemblances there is a lack of fit particularly at the beginning and at the end of the trajectory. But in general the curve is quite well described. Shortening time series even further can lead to additional problems in the analysis. The shorter the time series, the more probable is the last relevé of one time series connected to the first relevé of any other time series. Consequently, real overlaps get scarce. Fusing the two most similar relevés, in spite of the presence of a successional gap, is considered by the algorithm as best solution. In fig. 6 we can recognize an increase of the portion of the number of single overlaps with decreasing number of relevés. The portion of single overlaps is indicative for the portion of successional gaps. The number of 270 relevés seems to be a breaking point. Below this, the proportion of single overlaps increases drastically. In other words reducing the data under a threshold of 50% can lead to a strongly increasing proportion of potential successional gaps in the present case.

#### *Optimal selection of permanent plots*

As we already pointed out, both data quantity and data quality have an impact on the results. In this paragraph the study is focused on optimal selection of permanent plots in order to explain the succession. Different ranking strategies were compared so as to enhance the quality of results with respect to the best possible fit of the ordinated successional series. Fig. 4 suggests in general a better performance of the ranking method, i.e. we need 2 – 6 times less relevés to achieve the same number of time steps than without ranking algorithm.

In the sequel one case of such a ranking procedure is discussed. The question arises how to select permanent plots after having taken one relevé of each plot at the same point in time. For this purpose all 44 time series starting before 1943 were chosen. The first relevé taken after 1938 and before 1943 was extracted for each time series. We used the van der Maarel coefficient to avoid over-representation of time spans where variability is high (fig. 1). The ranking algorithm yielded 16 relevés, explaining more than 99% of the variability of the 44 initial relevés. In a next step the corresponding time series were subjected to the time-series-merging procedure. Even though only 199 relevés were used, we received 51 time steps (fig. 7), yielding a remarkably similar representa-

tion of the reference curve (fig. 1). In fig. 8 not only the ordinated successional series of the 16 selected time series is shown ("series rank"), but also the resulting trajectory of the 44 time series considered in this approach ("series all"). The starting and end phases are almost the same in both curves, "series rank" as well as "series all". Only the transition between Carex- and Pinus-dominance, i.e. the knee in the top right corner, shows minor deviations.

## **Discussion**

For the study in question the focus is upon investigation of successional processes, but not on explication of causality. We want to discuss the results in the light of consistency and plausibility, always with respect to the reference system. Pickett (1989) mentions that the successful application of space-for-time substitution relies on the availability of data of long-term phenomena. Furthermore, the pattern can only be detected, if considerable successional change can be observed. In the present data set, both conditions are satisfied.

### *Advantages of real data*

Very often methods are tested using artificial or well-known data sets (Wildi 1988). Real data have the property of showing a certain complexity compared to artificial data (Wilson 1981; Allen & Shugart 1983). The data set used is provided with the necessary density regarding repetitions of relevés and extends over a sufficient long time span. But there is no possibility to test the emerging pattern of the successional series.

Fusing species to species groups (Schütz et al. 1998) diminishes the overall variability, since single, in abundance strongly varying species lose weight. Therefore, dramatically fluctuating abundances of single species do not occur, but instead clear trends due to smooth curves of species groups can be recognized.

### *Interpretation of ordinated time series*

Comparing successional series by reducing dimensionality with eigenanalysis has been done by several authors. Principal components or coordinates analysis has the advan-

tage over direct gradient analysis to allow a simple comparison of two curves with time intervals individually stretched or shortened. Austin (1977) described an Australian rain-forest succession and analyzed a lawn succession under different conditions by ordinating time series in form of trajectories. Wildi (1988) used ordination methods to unfold trends in permanent plots. He applied correspondence analysis as well as a variant of principal components analysis on untransformed data and data smoothed by linear regression. Simulations of long-term, complex forest succession were performed by Allen & Shugart (1983). They used ordination of PCA on species-level as a powerful tool to explain successional processes controlled by competition or climatic factors.

In the study presented the first two components explained between 86.1% and 92.6% of the variability. Therefore the two-dimensional joint ordinations were considered as covering enough potential regarding the explanation of the forces driving the succession (Nichols 1977). Further knowledge of the species or species groups is a necessary prerequisite for the interpretation of ordinations (Austin 1977).

The *Aconitum*, *Carex* and *Pinus* species groups can be regarded as being stable communities dominating without any external support. At the other side the *Trisetum* community for instance is dependent on being grazed by ungulates. *Aconitum* only occurs at very nutrition-rich sites. *Carex*, either dominated by *Carex sempervirens* or *Nardus stricta*, can cover large areas (Stüssi 1970) and *Pinus* leads to forest stage and finally to climax (see fig. 1).

### *Robustness of the algorithm*

The dependence of the number of time steps on the number of relevés (fig. 4) corroborates the validity of the algorithm proposed by Wildi et al. (1999a). The algorithm is not very sensitive towards omitting time series if these time series are associated with a well-covered successional section. Of particular interest is here the beginning of the original successional series (fig. 1), covered just by three time series or the very last part, covered by only one time series. Such delicate sections can lead to misinterpretation from the side of the algorithm, if corresponding time series are omitted.

The effect of data reduction is only recognizable after having removed an essential part, i.e. more than 50%, of each time series (fig. 2 and 3). These results give insight into the

effects of fundamental data structure and the mechanism of the algorithm and indicate firstly a robust internal pattern of the successional process. Secondly the length of the investigation period provides sufficient data to detect the successional pattern. And thirdly the algorithm yields similar results, even when using subsets of the data. The category with dots as symbols in fig. 4 follows a slightly sigmoidal curve with tendency to linearity, the other category suggests being distributed logarithmically. Both thought trend lines show an asymptotic behaviour converging towards an upper limit. These findings and the well-known succession in direction of a climax typical for this area lead to the conclusion that we have not considered the last successional stage in our data. This would be the so called *Rhododendro-Pinetum cembrae* forest with *Pinus cembra* as dominating species. Until to the predominance of this slow-growing tree there may pass some hundred years (Ellenberg 1996). Observations made in the understory of the adjacent forest suggest that this last successional step has already started there.

#### *Artificial successional gaps*

A failure of the algorithm, i.e. merging time series over artificial successional gaps or misinterpretation of data due to a lack of important time series can be prevented. All regional existing vegetation types should be documented by several time series. Furthermore vegetation changes should be observed during a sufficient long time span in order to avoid too many single overlaps. As an additional requirement the relevés have to be taken at regular time intervals, but not necessarily in the same years with respect to different time series.

This demand on regularity in physical time does not imperatively coincide with ecological time (Wildi et al. 1999a). The time which is needed to pass a successional section can vary from site to site, affected by differently paced vegetation changes. Such a distortion of time axis leads to an irregular shift of individual relevés of different time series. Plots can persist in a kind of waiting position, until endogenous or exogenous forces reinitiate the succession. This phenomenon can be observed e.g. at some intensively browsed *Trisetum* areas, existing already for decades.

### *Consequences for the practice*

Sampling time and optimal selection of permanent plots have practical importance in monitoring projects. Increasing converging curves in ordinations suggest vegetation patterns moving towards a stabilizing state and are an indication for the sampling time necessary to reliably compose a successional series. Allen & Shugart (1977) confirm that a general trend is evident if trajectories show a parallel or similar structure.

The ranking method presented as an example in this paper shows at least in the slow-developing successional phases a distortion problem, i.e. in the *Carex* and *Pinus* dominated parts, due to overweighting of the fast-changing phase at the beginning with higher variability. This transformation effect of time scale has to be considered while interpreting the ordination diagram.

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## **Figures**

- Fig. 1: Successional series of the original data. The 73 time steps are the result of 582 relevés, distributed on 49 single time series. Given are the cover abundances in percentage of six species groups.
- Fig. 2: Joint ordination of the resulting original succession “series 00” and four versions of reduced data sets after having cutted away 2 (“series 20”), 4 (“series 40”), 6 (“series 60”) and 8 (“series 80”) relevés at the beginning of each single time series. Shown are the first and second components. The arrow indicates the direction of the succession.
- Fig. 3: Joint ordination of the resulting original succession “series 00” and four versions of reduced data sets after having cutted away 1 (“series 11”), 2 (“series 22”), 3 (“series 33”) and 4 (“series 44”) relevés at the beginning and at the end of each single time series. Shown are the first and second components. The arrow indicates the direction of the succession.
- Fig. 4: Dependence of the number of time steps and the number of relevés. Dots signifie successional series where single time series were shortened or completely omitted, asterisks as symbols include successional series where time series were selected according to ranking algorithms.
- Fig. 5: Joint ordination comparing four successional series where the relevés after 1953 were omitted (“series 1953”) etc. and the original successional series (“series 00”). Shown are the first and second components. The arrow indicates the direction of the succession.
- Fig. 6: Dependence of the percentage of number of single overlaps per number of time series on the number of relevés.
- Fig. 7: Successional series with 51 time steps. The underlying 16 time series, including 199 relevés, were selected by a ranking algorithm.
- Fig. 8: Joint ordination of the resulting successional series of 44 time series (“series all”) and the 16 time series (“series rank”) selected according to the ranking algorithm. For further explanations see text. Shown are the first and second components. The arrow indicates the direction of the succession.

Fig. 1

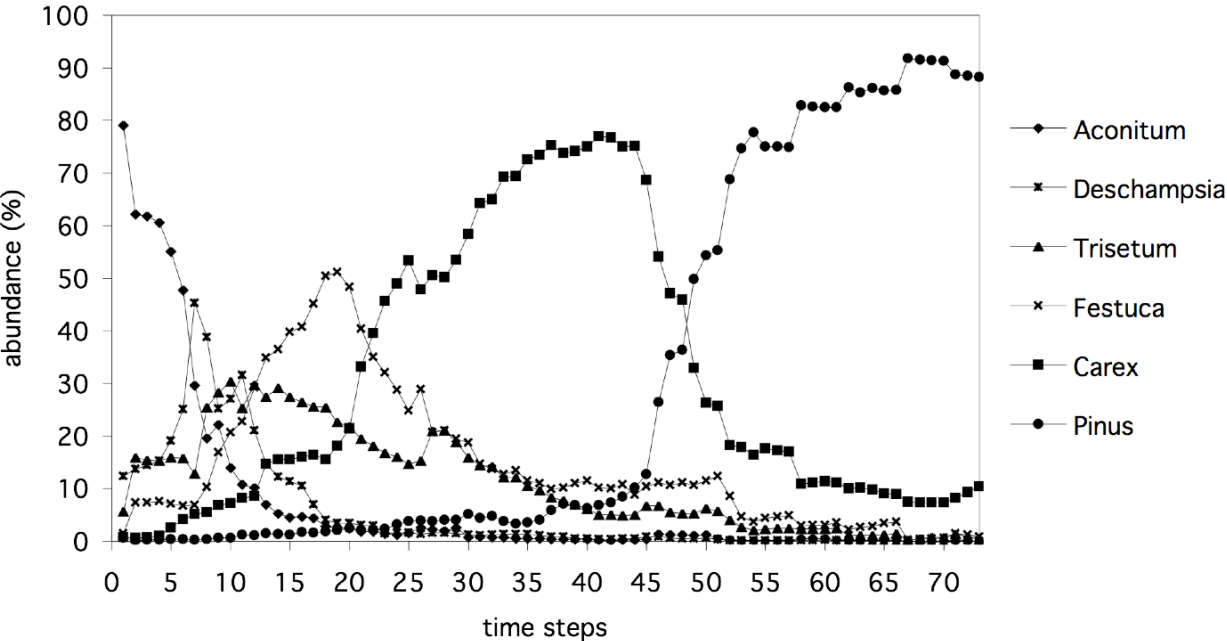


Fig. 2

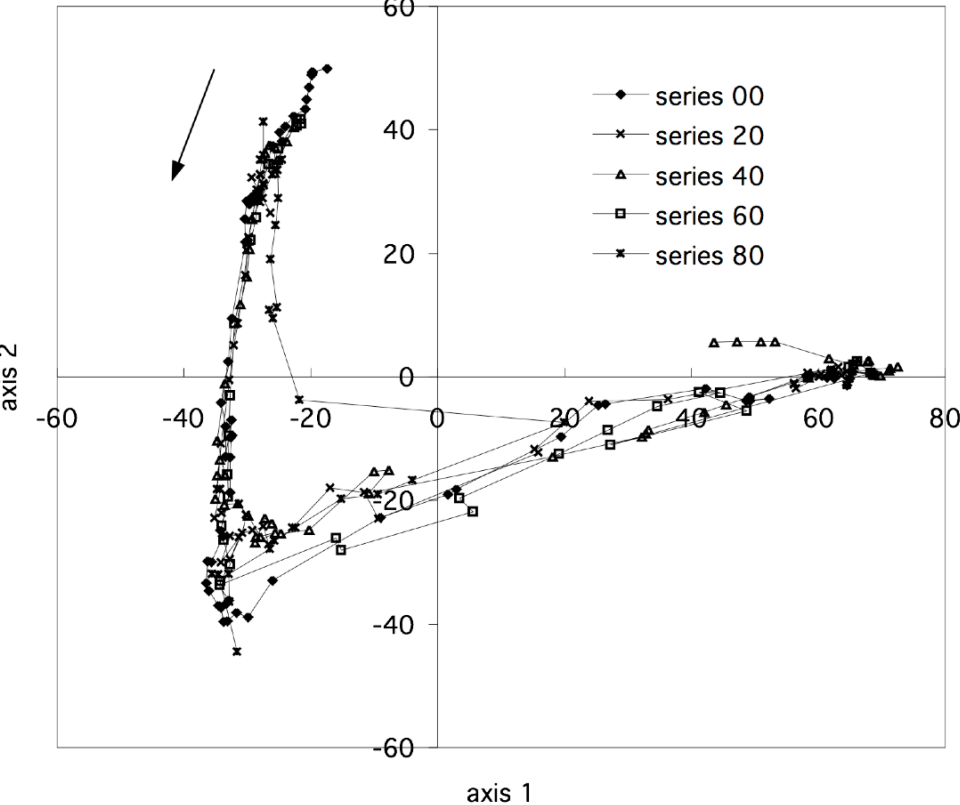


Fig. 3

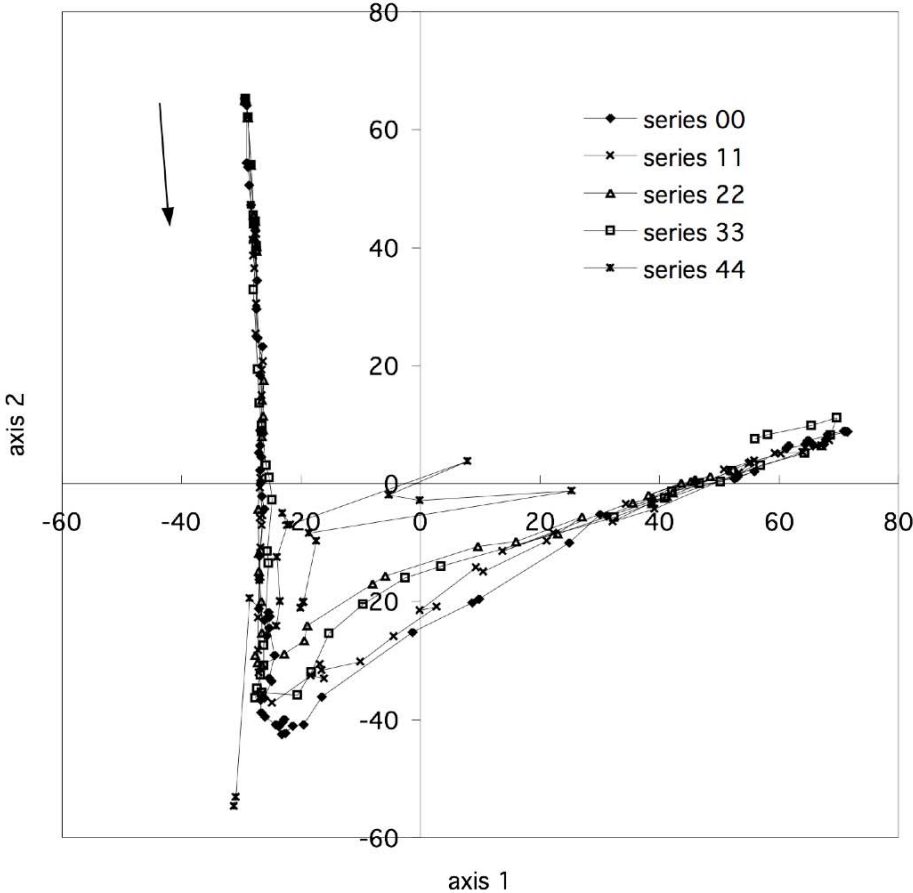


Fig. 4

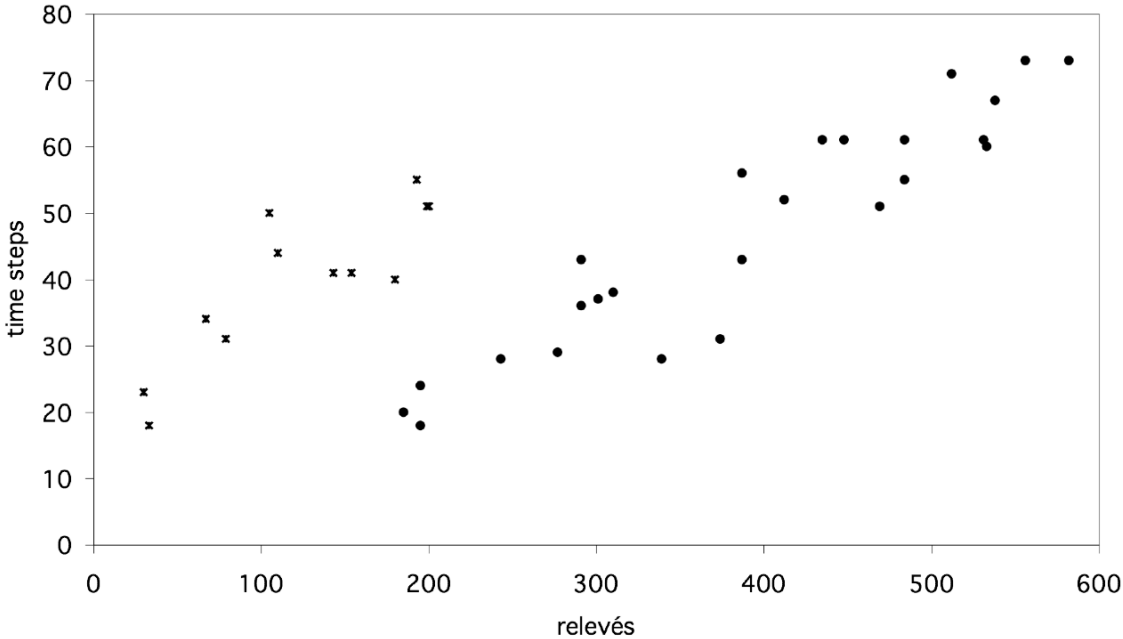


Fig. 5

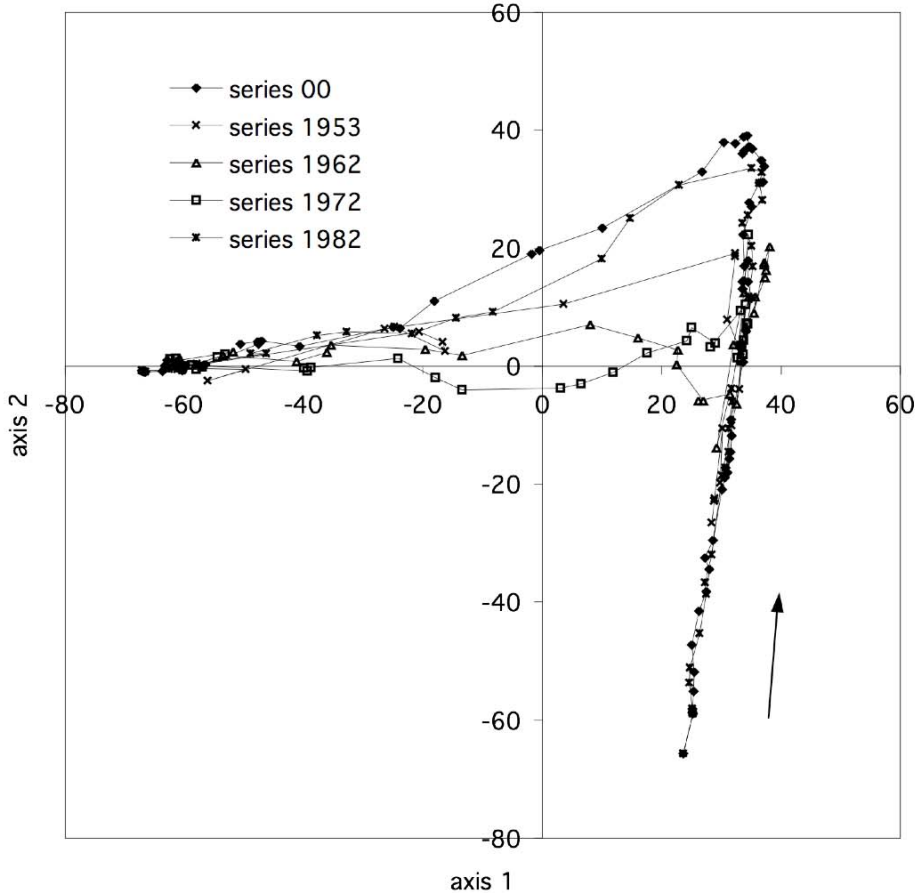


Fig. 6

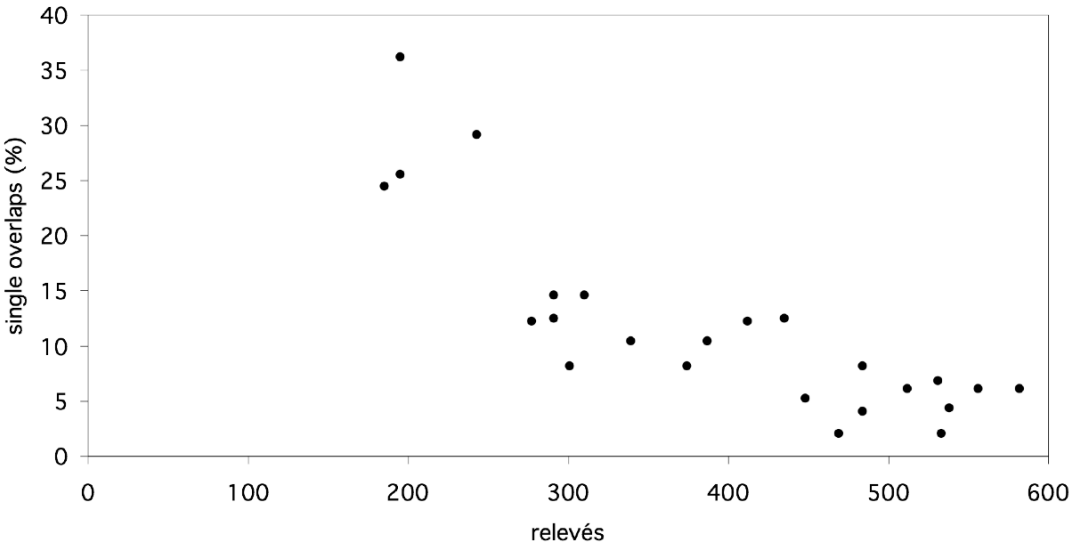


Fig. 7

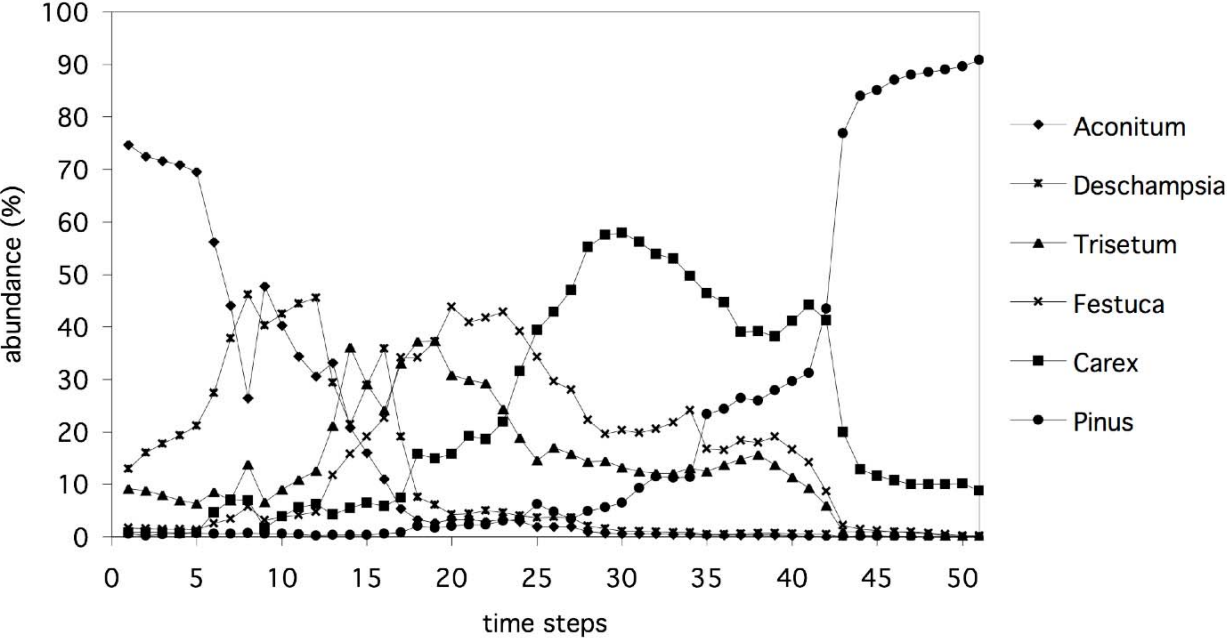


Fig. 8

