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Potential replacement vegetation: an approach to vegetation mapping of cultural landscapes

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Abstract. The concept of mapping potential replacement vegetation (PRV) is proposed as a parallel to potential natural vegetation (PNV). Potential replacement vegetation (PRV) 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 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.

The PRV-concept is especially useful in large-scale mapping (scales > 1 : 25 000) of small areas where replacement vegetation is the focus of attention for managers and land-use planners, for example in nature reserves where the aim is conservation of replacement vegetation managed in a traditional way, or in restoration ecology where the concept may be used for defining restoration goals and evaluating the success of restoration efforts. At smaller scales, PRV-mapping may be useful for revealing the biogeographical patterns of larger areas which may be different from the corresponding PNV patterns, because replacement vegetation and natural vegetation may respond to environmental gradients at different scales. An example of medium-scale PRV-mapping through the coincidence of diagnostic species of vegetation types, based on species distribution grid data, is presented.

In cultural landscapes, the advantage of using the PRV-concept instead of PNV is its direct relationship to the replacement vegetation. In the habitat mapping with respect to the replacement vegetation, the PRV concept yields more valuable results than the mapping of actual vegetation, as the latter is strongly affected by spatially variable anthropogenic influences which may be largely independent from climatic and soil factors.

Keywords: Coincidence mapping; Nature conservation; Plant community; Podyjí/Thayatal National Park; Potential natural vegetation; Restoration ecology; Semi-natural vegetation.

Abbreviations: PNV = Potential natural vegetation; PRV = Potential replacement vegetation

Nomenclature: Ehrendorfer (1973) for plant species; Mucina et al. (1993) and Chytrý et al. (1997) for syntaxa.

Introduction

Potential natural vegetation (PNV), introduced by Tüxen (1956), has become an important concept in applied vegetation science. The underlying idea is that the spatial variation in habitats over landscapes may be effectively described and mapped through the variation in natural vegetation. The original definition by Tüxen – see also Westhoff & van der Maarel (1973) and particularly Zerbe (1998) – relates the PNV to a given habitat, as the vegetation that would finally develop (terminal community) if all human influences would stop, and if the terminal stage would be reached at once. Irreversible or permanently effective human-induced changes in the habitats are considered in the PNV; a parallel concept which is rather related to the original habitats is the reconstructed vegetation (Neuhäusl 1963). Tüxen's definition has been successively made more precise and it has undergone different modifications (Tüxen 1963; Trautmann 1966; Neuhäusl 1975; Stumpel & Kalkhoven 1978; Kowarik 1987; Härdtle 1995; Leuschner 1997).

To avoid the uncertainties about the changes of the environment during succession (e.g. long-term climatic change or nutrient accumulation), Tüxen excluded the factor time in his definition. Stumpel & Kalkhoven (1978) argued that it is more realistic to consider a period of 50 to 150 years of succession which is a sufficiently long time to allow the vegetation to reach a (provisional) final stage but a short time for major climatic changes to take place. Most German authors, however, did not accept this modification and rather sticked to the original concept with the successional time excluded (e.g. Kowarik 1987; Härdtle 1995). Leuschner (1997) suggested a parallel concept of potential site-adapted vegetation (PSV) which is the vegetation which would develop due to secondary succession (i.e. not at once) in present habitats if the human influence would stop. He pointed out that particularly on nutrient-depleted soils the PNV and PSV may often be very different. Another item of discussion were the environmental factors affecting the habitat from outside such as air pollution. Neuhäusl (1975, 1980, 1984) elaborated a concept of the 'environmental natural vegetation' (in

German ‘umweltgemäße natürliche Vegetation’) which is essentially the PNV developed under the influence of external factors. Kowarik (1987) incorporated Neuhäusl’s ideas into the PNV-concept.

The PNV-concept has been most widely used in vegetation mapping and landscape planning in Germany (Schröder 1984), but also in, e.g. The Netherlands (Stumpel & Kalkhoven 1978), Switzerland (Brzeziecki et al. 1993), Poland (Matuszkiewicz et al. 1995), the Czech Republic (Neuhäuslová et al. 1997) and Japan (Miyawaki & Fujiwara 1988). Large-area mapping projects based on the PNV-concept include the vegetation maps of the USA (Küchler 1964) and Europe (Bohn 1995; see also Kalkhoven & van der Werf 1988 for further references).

A usual scale for PNV-maps is 1 : 25 000 and smaller, as at larger scales the uncertainty in drawing boundary lines between the hypothetical mapping units increases (Dierschke 1994). Small-scale PNV-maps are a powerful tool for describing biogeographical patterns (Matuszkiewicz 1979). Mapping at scales 1 : 25 000 - 50 000 is motivated by applications in land-use planning, nature conservation, forestry, agriculture and related fields. The most successful applications of PNV-maps are probably in the planting of native trees in urban green zones (Miyawaki & Fujiwara 1988) and the creation of new natural woodlands (Rodwell & Patterson 1994).

The application of large-scale PNV-maps becomes more problematic when managers or planners are concerned with replacement (substitute) vegetation, such as in nature reserves designed for protection of semi-natural treeless vegetation and in range management. In these cases, replacement vegetation types cannot be easily or unequivocally derived from PNV-maps; hence maps of actual vegetation are often used instead. Maps of the actual vegetation are suitable for the assessment of vegetation change by repeated mapping, but unlike PNV-maps they hardly enable comparisons among habitats defined in terms of climatic and soil factors, as the actual vegetation is very variable in time due to frequent, mostly anthropogenic disturbances and subsequent secondary succession. An additional problem is that mapping of the actual vegetation is time-consuming and hardly applicable at scales smaller than 1 : 100 000 (Trautmann 1966).

This paper focuses on the gap between the PNV-concept and the map units of the actual vegetation in areas where the interests are in replacement vegetation. The aim is to propose a concept of potential replacement vegetation (PRV) which is suitable for mapping in these areas and at the same time contains the advantages of the PNV-concept.

Relationships between PNV and replacement vegetation

As already emphasized by Tüxen (1956), particular replacement communities are confined to habitats of corresponding PNV-communities, and provided the correlations between the PNV and replacement communities are known, PNV-maps of cultural landscapes may be derived from the actual pattern of the replacement communities. Conversely, the approximate distribution of the replacement communities may be deduced from the PNV-map (see also Stumpel & Kalkhoven 1978 for a reference to the vegetation series concept).

However, only exceptionally a PNV-community has just one counterpart in the replacement vegetation and vice versa. In mapping projects where the relationships between PNV and replacement communities were clearly defined, the number of replacement communities for the study area usually exceeds the number of PNV-communities (Dierschke 1979; Janssen & Seibert 1991; Härdtle 1995). This pattern is indeed partly affected by differences among the authors in the delimitation of mapping units, but various studies repeatedly recognized a higher rate of differentiation in replacement vegetation than in PNV, at least in Central Europe where most PNV is forest. Dominant tree species in PNV-types usually have broader ecological ranges than the dominants of replacement communities – herbs, low shrubs or shrubs (Whittaker 1960). Trees level out environmental heterogeneity on the forest floor by shading, litter accumulation, and moderating temperature extremes; water is more evenly distributed over time in the forest. In the replacement communities, these overriding effects imposed by the tree canopy are removed and vegetation often tends to be more diverse in response to small-scale variation in light, temperature, nutrients and water availability. An example of this phenomenon from the floodplains in eastern Bohemia was described by Neuhäusl (1975: pp. 121-122). For ruderal vegetation, Mucina (1981) suggested that only communities rich in native species reproduce PNV patterns well, whereas relationships between the PNV and ruderal communities dominated by aliens are rather weak.

The possibility of interpreting a PNV-mapping unit in terms of two or more replacement communities precludes the applicability of PNV-maps in applied fields such as land-use planning, nature conservation and range management. Often, the relationships between PNV and replacement vegetation are rather complex and varying among areas, so the planner or manager concerned with the replacement vegetation cannot directly interpret the PNV-map without consulting a specialist in local vegetation or the author of the map.

An additional problem with the PNV-mapping arises in man-made habitats such as abandoned opencast mines or reclaimed areas in coastal land which have never supported terminal communities of natural vegetation. In these areas, corresponding PNV types are often unknown, but replacement communities adapted to these habitats may be well-known and can be used for mapping instead of hypothetical PNV-communities.

Potential replacement vegetation

Rationale and definition

The management of replacement vegetation would obviously be more effective if managers could directly use maps of replacement vegetation. Maps of actual vegetation are not always suitable for this purpose as they show vegetation patterns that are mainly controlled by the immediately effective management. These patterns may rapidly change over time as the anthropogenic influence (management) alters, and then the maps may rapidly become out-of-date. For planning purposes, however, long-term effective environmental factors associated with a given site, such as climate (including, e.g. available radiation, temperature, precipitation, wind) and soil (e.g. water relations, nutrients, pH, depth, erosion processes), are often more important than the actual vegetation state which is subject to frequent fluctuations. These environmental factors will be referred to as the site factors in the following text.

Mapping of the site factors responsible for the differentiation of replacement vegetation may be achieved by an abstract standardization of the management practice for the mapped area. For example, the whole area may be imagined as a moderately fertilized meadow mown twice a year, and different meadow communities are mapped which would be in balance with soil moisture, nutrient status or pH in each part of the area. Similarly the area may be imagined as a sheep pasture, arable field, regularly burned heathland or trampled ground, and different communities of grazed grasslands, weeds, low shrubs or trampling-resistant plants, respectively, may be mapped according to different habitat parameters that affect vegetation in addition to the management. The abstract vegetation mapped in this way should be called potential replacement vegetation (PRV).

The idea of PRV is similar to that of PNV. The principal difference between these two is the way of standardizing the present direct human impact on vegetation. In PRV, it is standardized by the uniform management, whereas in PNV, any present human impact is excluded. In this respect, PRV is related to the concepts of potential semi-natural and potential segetal vegetation as outlined by Küchler (1988). Like PNV, PRV may be constructed for present site factors or site factors of any moment in the past or future. The most typical case is the PRV corresponding to the present site factors which is the PRV of today. PRV may be defined as follows:

Potential replacement vegetation (PRV) is the 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.

Effect of time

The reference to the present site factors implies that the time necessary for the vegetation to reach the balance with its site factors and management is not considered, and the PRV is imagined as arising at once – compare the original PNV-definition in Tüxen 1956 (Zerbe 1998). This means that in some cases the replacement vegetation which actually develops at a site after a certain management is applied, may be different from the PRV constructed for this management.

A possible mechanism responsible for such deviations may be the inhibition of succession (Connell & Slatyer 1977). For example, if grazing is taken as the abstract management in an area which is an arable field at present, the PRV is a pasture community, e.g. the *Lolio-Cynosuretum*. In actual vegetation, however, the grazed grassland in a recently abandoned field, may either develop towards the *Lolio-Cynosuretum*, or be invaded by a strong competitor such as *Calamagrostis epigejos*. This species rapidly spreads and forms monodominant stands which cannot be removed by grazing. The result of the secondary succession is a *Calamagrostis epigejos* community and not the *Lolio-Cynosuretum* which is constructed as the PRV.

Another problem may appear where the actual seed bank does not contain diaspores of the species typical of the predicted PRV and the former dispersal routes are no longer effective due to increased habitat fragmentation or shifts in land-use (Bakker et al. 1996; Poschlod et al. 1998). The mere application of the management typical of the target PRV community would possibly lead to the development of a strongly impoverished vegetation type in this case.

Exclusion of the factor time in the PRV-concept is especially important in restoration ecology where the PRV provides a reference to define restoration goals and evaluate success of restoration efforts (White & Walker 1997). For actually directing ecological succession towards the PRV, often other measures must be taken than the management linked to the target PRV types (Luken 1990).

If the restoration includes manipulation of site factors, the PRV of the future – which considers the altered habitat – should be constructed rather than the PRV of today, if we wish to define the restoration goals.

Environmental factors considered for the construction of potential replacement vegetation

The environmental factors considered for the construction of PRV include (1) natural site factors; (2) irreversible and permanently effective anthropogenic changes of the site factors; (3) external environmental factors under long-term anthropogenic control; (4) management of given type and intensity.

The factors under (1) and (2) are the same as in the original PNV-concept of Tüxen (1956). The former include in particular climatic factors, physical and chemical properties of the soils and moisture regime. The latter include anthropogenic changes such as lowering of the groundwater, creation of artificial lakes, podsolization under secondary heathlands, soil erosion, accumulation of sediments in floodplains, peat extraction and building asphalt roads.

External environmental factors under long-term anthropogenic control specifically include the effects of air pollution. For example, under increasing atmospheric nitrogen deposition, Dutch heathlands, originally dominated by low shrubs, mainly *Calluna vulgaris* and *Erica tetralix*, change into *Deschampsia flexuosa*- and *Molinia caerulea* grasslands, respectively (Aerts & Heil 1993). If management by grazing is considered in the areas of original heathlands, the resulting PRV-type will be a grassland which is adapted to the present level of nitrogen deposition.

Anthropogenic site changes that would be compensated by the existence of PRV, or by the management involved, are not to be considered in the PRV-mapping. For example, if PRV – corresponding to management that does not include fertilization – is constructed at a site which is heavily fertilized at present, current high soil nutrient concentration due to fertilization is not considered. Similarly, compacted soil in trampled habitats is not considered as a factor influencing the PRV if the imaginary management consists of ploughing.

Management

One site may support a variety of different PRV communities, depending on the type, intensity and frequency of underlying management. For example, a gentle slope with a brown soil at middle altitudes of Central Europe may support a *Pastinaco-Arrhenatheretum* meadow if mown twice a year and moderately fertilized, the *Rumex obtusifolius-Dactylis glomerata* meadow if mown three (or four) times a year and heavily fertilized, the *Lolio-Cynosuretum* pasture if regularly grazed, the *Lolio-Plantaginetum* dominated by rosette plants and short grasses if heavily trampled, or the weed community *Spergulo-Scleranthetum annui*, if used for corn production. The choice of management used for the PRV-construction depends on the purpose of the study. If necessary, two or more areas with different management may be delimited in a map (see Case study 1).

If the management involved supports a temporarily variable vegetation, a season or successional age must be also considered in the construction of a PNV. For example, segetal weeds exhibit a considerable seasonal variation and some researchers distinguish series of different communities at one site in the course of a year (Kropáč et al. 1971; Holzner 1973). In this case it is necessary to define whether spring, summer or autumn community types are to be constructed as the PRV. Another example includes the communities with directional temporal changes such as forest clearings, in which the successional age must be defined in PRV-construction.

Effects of changes in the local flora

Species that once belonged to the species assemblage of replacement communities under traditional management should be considered in the PRV-construction even though their diaspores are absent from the contemporary landscape or their dispersability is limited (Poschlod et al. 1998).

On the other hand, invasive species should be taken into account provided they are adapted to the underlying management of given PRV-types. For example, *Amaranthus powellii* which is alien to Central Europe should be considered as a stable component of some potential weed communities in Central European arable fields because it is well adapted to the standard types of management. On the contrary, *Heracleum mantegazzianum* or *Reynoutria japonica* which often invade Central European mesic meadows after their abandonment, cannot be considered in the case of PRV constructed as a meadow mown twice a year, because their invasion would be prevented by regular mowing.

Case study 1: Large-scale PRV-mapping

Study site

The study site is located at the eastern edge of the Podyjí National Park near the village of Popice (S. Czech Republic) at ca. 48° 49' 20" N,16° 00' 50" E (Fig. 1). It includes a broad valley with a small creek and adjacent gentle slopes over granitic bedrock at an altitude of 270 - 360 m.

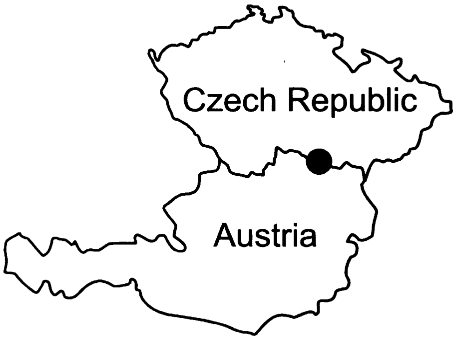

Fig. 1. Location of the study site in Case studies 1 and 2.

It is a cultural landscape with fragmented stands of both native and exotic trees, meadows (intensively managed, traditionally managed and abandoned), formerly grazed dry grasslands and heathlands, arable fields, vineyards and a built-up area of the village. The potential natural vegetation of the area includes deciduous broad-leaved forests of the *Melampyro nemorosi-Carpinetum, Primulo veris-Carpinetum, Pruno-Fraxinetum,* and *Sorbo torminalis-Quercetum* (Chytrý & Vicherek 1995).

Methods

After a preliminary survey of vegetation types in a wider area, the vegetation was mapped in early October 1997 in a rectangular plot of 1.80 km × 0.65 km. Two kinds of maps, i.e. actual vegetation and PRV, were prepared simultaneously. The maps were sketched in the field at a scale of 1 : 10 000, using a 1 : 5 000 aerial photograph as a guide for the location of boundaries. As the area is situated in the buffer zone and the so-called second protection zone of the national park and the main aim of land-use planning is conservation of traditionally managed species-rich grasslands and heathlands, the traditional management of these vegetation types was considered in the PRV-construction. Two types of traditional management used to be practised in the area: (1) grazing, mainly by sheep on slopes with shallow and rather dry, low-productive soils, and (2) mowing twice a year, combined with moderate fertilization, at productive sites in the mesic to moderately wet floodplain. Consequently, the deforested area (including isolated woodland patches smaller than 2 ha) was divided into two zones with different management, i.e. grazing and mowing. In each of these zones the PRV was mapped independently, considering the respective management. The currently forested area constituted another zone, where the PNV was constructed instead of the PRV. It would indeed have been possible to construct the PRV also for the forested area; however, there was no practical reason for doing that because the land-use plans for the study area did not suppose the enlargement of the treeless area. Therefore, a combined PRV/PNV-map was prepared which is optimal for management planning of both treeless and forest vegetation. The built-up area in the village was not mapped. Knowledge of the relationships between particular types of replacement vegetation, site factors and management was crucial in the field mapping. Mapping units defined in the actual vegetation map largely included floristic types based on local species combinations, whereas the PRV-map was mainly based on associations defined by the Braun-Blanquet approach, which are valid over larger areas.

Results and Discussion

The following points can be made as a result of the comparison of the maps of actual and potential replacement vegetation (Fig. 2):

1. The actual vegetation map includes more mapping units than the PRV map.
2. The actual vegetation map shows a complex land-use pattern influenced by manifold types of the past, recent and present human activities in the study area. To some extent, this anthropogenic pattern masks the natural site factors such as moisture, soil fertility etc. The PRV-map, on the other hand, reveals this natural pattern very well with apparent differences between the floodplain and the adjacent slopes.
3. Some mapping units of actual vegetation fit perfectly to the PRV-mapping units; some others tend to produce groups embedded in one mapping unit of the PRV. On the other hand, some mapping units of actual vegetation extend over two or more units of PRV. This is particularly the case with actual vegetation units that are subject to strong human impact such as weed communities of arable fields. Also, actual communities with strong dominants that modify their environment such as *Calamagrostis epigejos* or *Robinia pseudacacia* may extend over several PRV-mapping units.

Case study 2: Medium-scale PRV-mapping through coincidences of indicator species

Study site

The medium-scale study was performed in the Podyjí/Thayatal National Park with some adjacent areas on the border between the Czech Republic and Austria. The study area includes the wider surroundings of the site from Case Study 1, being roughly bound by the towns of Vranov n.D., Znojmo and Retz.

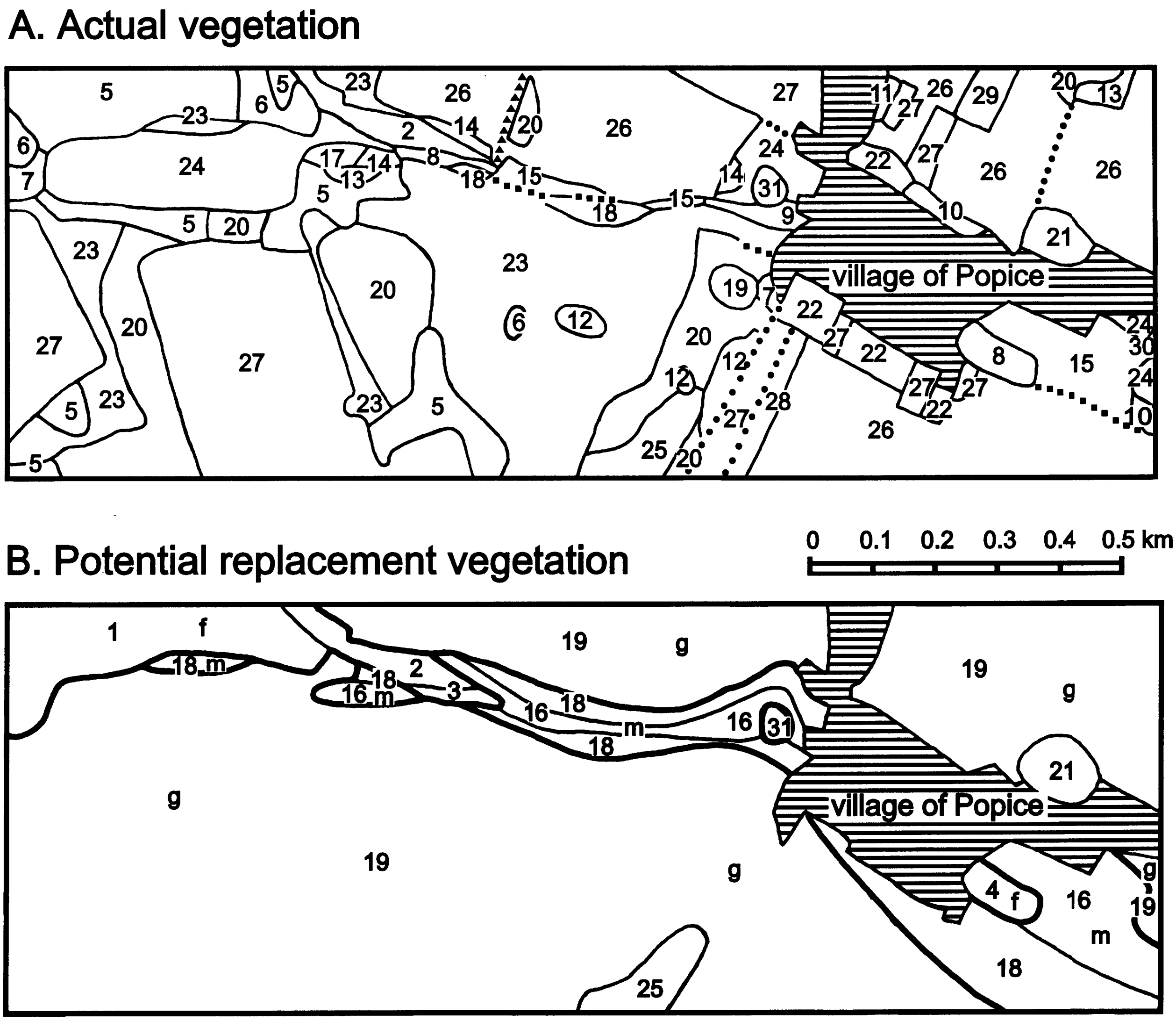

Fig. 2. Comparison of the maps of actual vegetation (**A**) and potential replacement vegetation (**B**). For practical purposes, the area was divided into three portions in the PRV-mapping, including the area potentially suitable for mowing, the area potentially suitable for grazing, and the area with forest. In the former two areas, mowing and grazing were respectively considered as an abstract management, and the forest was mapped as the PNV. Thick lines in B are boundaries of the areas with different management: m = mowing, g = grazing, f = forest. **Woody vegetation:** 1. *Sorbo torminalis-Quercetum*; 2. *Melampyro nemorosi-Carpinetum*; 3. *Stellario-Alnetum glutinosae*; 4. *Pruno-Fraxinetum*; 5. *Quercus petraea* forests with an anthropogenic admixture of *Pinus sylvestris*, *Betula pendula* and *Robinia pseudacacia*; 6. *Pinus sylvestris* plantations; 7. *Robinia pseudacacia* groves; 8. *Alnus glutinosa* groves with nitrophilous species; 9. *Acer campestre* groves with nitrophilous species; **Shrub vegetation:** 10. *Sambucetum nigrae*; 11. *Lycietum halimifolii*; 12. *Sarothamnus scoparius* community; 13. *Rosa canina* successional community; **Grasslands:** 14. *Phragmitetum communis*; 15. *Urtica dioica-Phragmites australis-Calamagrostis epigejos* community; 16. *Scirpo-Cirsietum cani*; 17. *Galium boreale-Carex curvata* community; 18. *Pastinaco-Arrhenatheretum*; 19. *Potentillo arenariae-Agrostietum vinealis*; 20. *Potentillo arenariae-Agrostietum vinealis, Arrhenatherum elatius* variant; 21. *Avenulo pratensis-Festucetum valesiacae*; 22. *Arrhenatherum elatius* dominated dry grassland with ruderal species; 23. *Arrhenatherum elatius-Calamagrostis epigejos* species-poor grassland; 24. *Dactylis glomerata-Plantago lanceolata* intensively managed dry meadow; **Heathlands**: 25. *Carici humilis-Callunetum*; **Weed communities**: 26. *Euphorbio exiguae-Melandrietum noctiflori*; 27. *Echinochloo-Setarietum pumilae*; **Ruderal communities:** 28. *Dauco-Picridetum*; 29. *Agropyron repens* community; 30. *Sisymbrio-Atriplicetum nitentis*; **Aquatic vegetation:** 31. Aquatic vegetation of a small fishpond; **Linear vegetation structures**: triangles = Fruit trees; squares - *Populus canadensis*; circles = *Ligustro-Prunetum* and *Rosa canina* community.

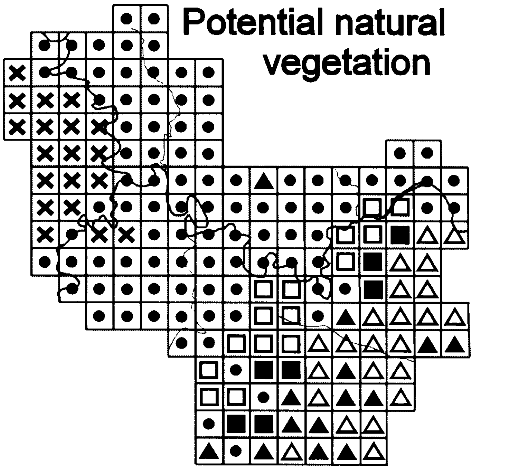

Fig. 3. Dominant PNV-types in individual grid squares derived from the 1 : 25 000 PNV-map of the area (Chytrý & Vicherek 1995). Each cell measures 0.6' of latitude and 1' of longitude, i.e. ca. 1.1 km × 1.2 km. Cross = *Melico-Fagetum*; full circle = *Melampyro-Carpinetum*; empty square = *Festuca ovina-Quercus petraea* comm.; full square = *Sorbo torminalis-Quercetum*; empty triangle = *Primulo veris-Carpinetum*; full triangle = *Potentillo albae-Quercetum.*

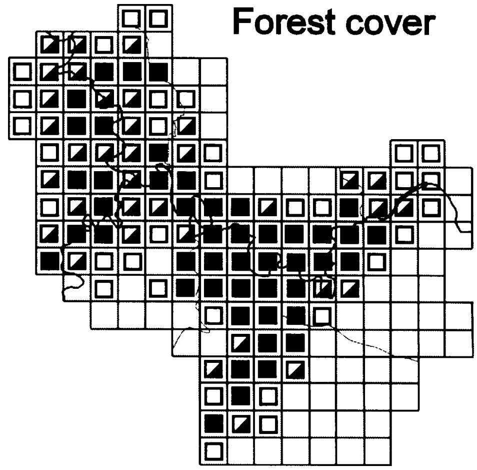

Fig. 4. Actual forest cover in the area derived from a topographic map. Full square = 90 - 100 % of the cell covered with forest; semi-open square = 50 - 90 %; open square = 10 - 50 %; empty cell = 0 - 10 %.

The dominant bedrock types are granitoids and ancient metamorphic rocks (gneiss, mica schist), with local intrusions of marbles and patchy sediments of the Quarternary. Upper Tertiary sediments and loess occur in the southeastern part. The altitude ranges from 536 m in the northwest to 208 m in the east. Accordingly, the climate gradually changes from cooler and wetter in the northwest to warmer and drier in the southeast (see Chytrý& Tichý 1998 for climatic details). The larger part of the area is forested, with *Quercus-Carpinus*, *Fagus*, thermophilous *Quercus* and acidophilous *Quercus* forests being the most widespread PNV types (Chytrý & Vicherek 1995). Simplified maps of PNV and actual forest cover are shown in Figs. 3 and 4.

Methods

The idea of coincidence mapping of species indicative of particular syntaxa (Rodwell & Winstanley 1994; Rodwell et al. 1995) was applied to the computerized flora database of the Distribution Atlas of Vascular Plants in the Podyjí/Thayatal National Park (Grulich 1997). Coincidence maps are obtained from grid data on species occurrence by mapping joint occurrences within a group of species. Dot sizes in grid cells are proportional to the number of species of the group present. If a group of species indicative of a particular vegetation type is mapped, the resultant coincidence map may be taken as a reasonable prediction of the presence of that vegetation type. The flora database used in the current study included presence data for vascular plants on a 0.6 × 1' grid, which corresponds approximately to 1.1 × 1.2 km recording units. Two PRV-maps were prepared, based on different management types: a map of grasslands/heathlands and a map of summer weed communities of cereal fields. After a preliminary survey of the replacement vegetation in the area, the five most widespread phytosociological alliances of grassland/heathland and three associations of weeds were respectively selected as PRV-mapping units. Indicator species of these mapping units were chosen according to Mucina et al. (1993) and personal field experience of the study area. The number of indicator species per mapping unit varied from 6 to 23; this list may be obtained from the author upon request. By coincidence mapping of the indicator species for each mapping unit, predictive distribution maps were prepared in which the probability of occurrence of the particular mapping unit is expressed as a proportion of its indicator species recorded in each grid square. Maps for individual mapping units were combined by plotting, in each grid square, the mapping unit with the highest proportional representation of indicator species.

Results

The coincidence maps for individual plant communities (Figs. 5 and 6) revealed clear patterns which were mainly determined by abiotic site factors, while the actual forest cover affected the result to a small extent only.

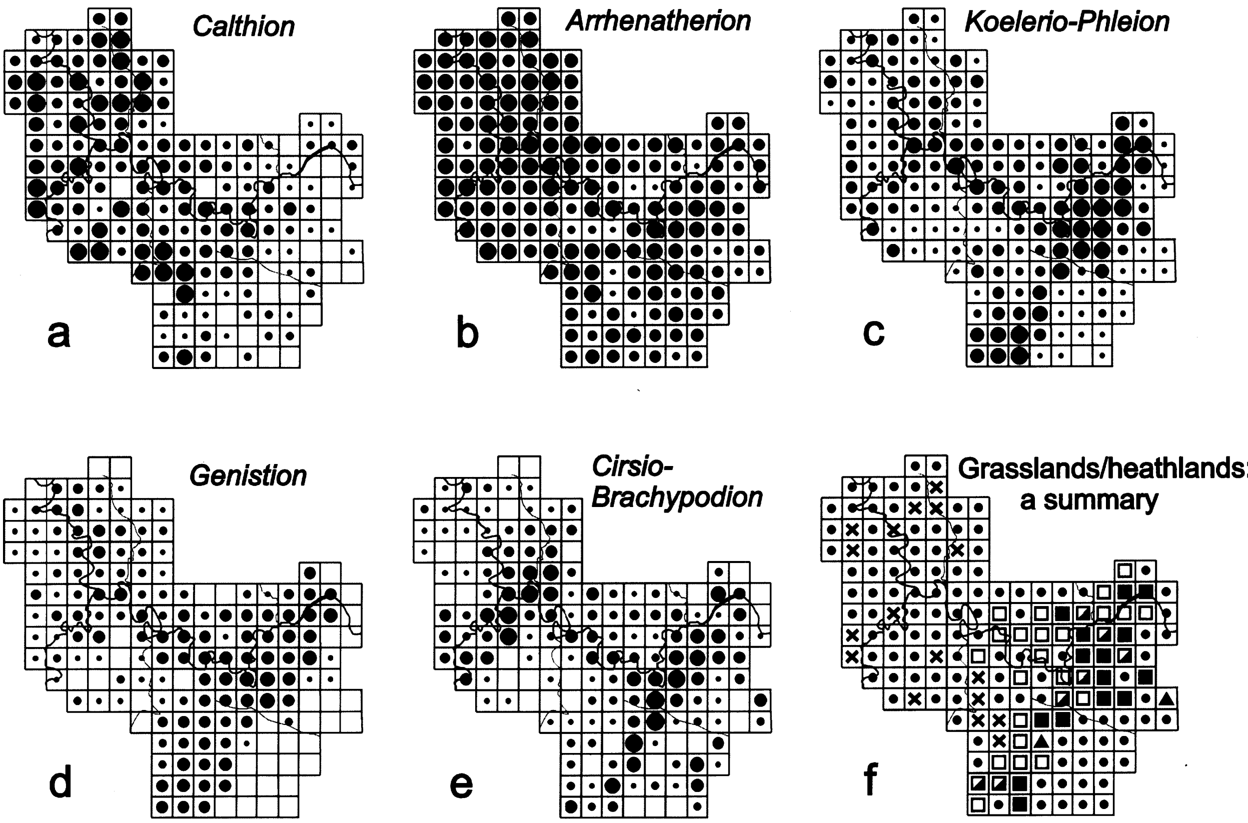

Fig. 5. Coincidence mapping of grasslands and heathlands. Proportional representation in each grid square of the diagnostic species for different syntaxa (**a - e**) is indicated by the size of circles. In **f**, the syntaxon with the highest proportional representation of its diagnostic species is mapped in each grid square: cross = *Calthion*; full circle = *Arrhenatherion*; empty square = *Genistion*; full square = *Koelerio-Phleion*; semi-open square = equal proportion of the *Genistion* and *Koelerio-Phleion* species; full triangle = *Cirsio-Brachypodion.*

On the grassland/heathland map (Fig. 5), the wet meadows of the *Calthion* were mainly predicted in the western part of the area (higher altitudes, cooler and wetter) and the mesic meadows of the *Arrhenatherion* were shown to be widespread over the whole area. The acidophilous dry grasslands of the *Koelerio-Phleion* and the *Genistion* heathlands had approximately the same pattern with high probabilities of occurrence in the river valley and in a SW-NE belt in the eastern part of the area where siliceous bedrock is combined with a warm and dry climate. The basiphilous dry grasslands of the *Cirsio-Brachypodion* possessed a similar pattern, but there was an additional distribution centre on marble in the western part of the area. The occurrence probabilities for each of the above-mentioned vegetation types were low at the southeastern edge of the area, i.e. in the landscape with Tertiary sediments and a warm/dry climate which is largely dominated by arable fields.

The combined map predicted the *Arrhenatherion* as a dominant PRV-type in the western and central part of the area and at its southeastern edge. The *Calthion* was mapped in isolated grid squares in the western and central part of the area. The *Koelerio-Phleion* and *Genistion* were predicted in the above-mentioned belt in the eastern part, and the *Cirsio-Brachypodion* was shown as a rare type predicted in two squares of the eastern part only. Except for the *Genistion*, there was significant resemblance between the distributions predicted by the combined PRV-map and the actual distributions of the vegetation types recorded in the field (χ^2, $P < 0.01$). The lack of correspondence for the *Genistion* has two possible causes. First, the actual *Genistion* heathlands mainly occur in a mosaic with the more widespread *Koelerio-Phleion* dry grasslands, and for many grid squares where both the vegetation types actually occur, the *Koelerio-Phleion* was predicted in the map. Second, several squares with predicted *Genistion* are situated in areas covered by acidophilous forests where no open heathlands occur at present, but heathland species are common in those forests.

The map of weed communities (Fig. 6) showed a different pattern from the grassland/heathland map. In

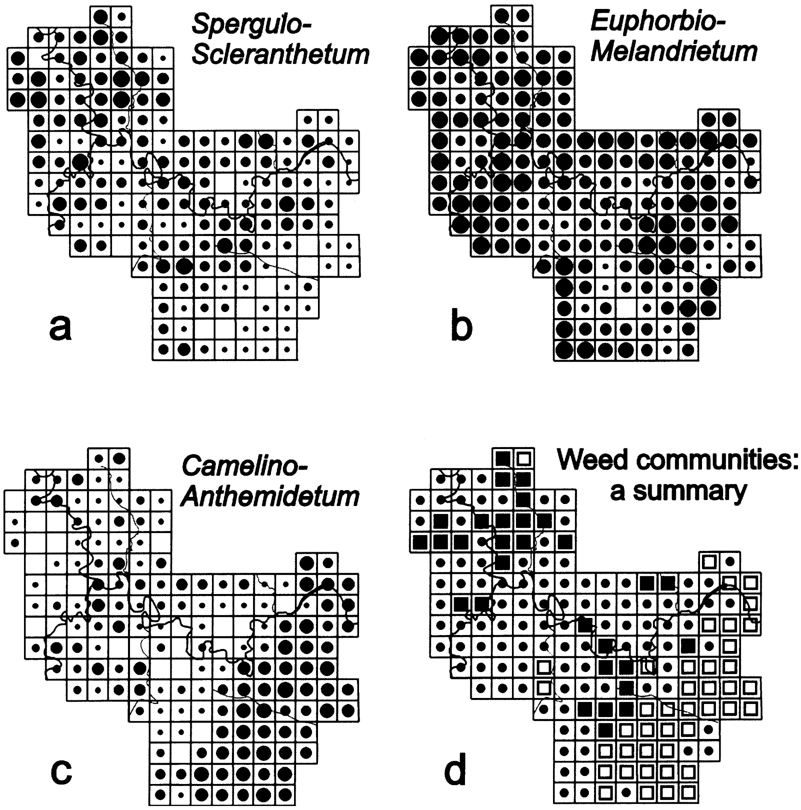

Fig. 6. Coincidence mapping of weed communities. Proportional representation in each grid square of the diagnostic species for different syntaxa (**a - c**) is indicated by the size of circles. In **d**, the syntaxon with the highest proportional representation of its diagnostic species is mapped in each grid square: full square = *Spergulo-Scleranthetum*; full circle = *Euphorbio-Melandrietum*; open square = *Camelino-Anthemidetum.*

the coincidence maps the *Spergulo-Scleranthetum* was predicted mainly in the western and central part of the area, the *Camelino-Anthemidetum* in the eastern, and the *Euphorbio-Melandrietum* over the whole area. The combined map did not reveal the SW-NE belt of the landscape in the eastern part of the area which is evident in the grassland/heathland map. A clear boundary was revealed only along the eastern edge of this belt between the *Euphorbio-Melandrietum* and *Spergulo-Scleranthetum* in the area of granite and gneiss on the one hand, and the *Camelino-Anthemidetum* on Tertiary sediments on the other hand.

The relationships between the PNV and predicted distribution of potential replacement communities were

Table 1. Contingency table analysis between the PNV (rows) and predicted occurrence of PRV-communities (columns). Yates correction was used if the number of observations in one cell of the contingency table was < 5. Only positive relationships are shown. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$.

	Calthion	*Arrhena-therion*	*Koelerio-Phleion*	*Genistion*	*Cirsio-Brachy-podion*	*Spergulo-Scleran-thetum*	*Euphorbio-Melan-drietum*	*Camelino-Anthemi-detum*
Melico-Fagetum	–	–	–	–	–	–	–	–
Melampyro-Carpinetum	–	–	–	–	–	–	***	–
Festuca-Quercus comm.	–	–	–	**	–	*	–	–
Sorbo-Quercetum	–	–	***	–	–	–	–	–
Potentillo-Quercetum	–	–	–	–	–	–	–	***
Primulo-Carpinetum	–	–	–	–	–	–	–	***

generally weak, particularly in the grassland/heathland mapping (Table 1). In the mapping of weed communities, highly significant positive relationships were detected between the *Euphorbio-Melandrietum* and *Melampyro-Carpinetum* and between the *Camelino-Anthemidetum* and *Potentillo-Quercetum/Primulo-Carpinetum*. The *Melico-Fagetum* showed no relationship with any of the replacement communities.

Discussion

The weak relationship between the PNV- and PRV-maps, as well as the differences between the two PRV-maps, may result from the failure of the coincidence mapping method due to (1) unsuitable choice of mapping units; (2) unsuitable choice of species for the definition of mapping units; (3) poor quality of the floristic data. However, objective causes may be involved as well, notably the different kinds of response of each vegetation type (PNV, grasslands/heathlands, weeds) to abiotic site factors in the landscape.

The choice of mapping units was based on several years of fieldwork in the area, and the quality of floristic data was reasonably good, with 109 - 572 species records per quadrat. The choice of species was based on the standard literature and expert knowledge, so the chosen species should sufficiently characterize particular mapping units. The bottleneck of the method's proper functioning may be the uneven occurrence frequency of the chosen species in the study area. If a certain mapping unit is based on more common species than the others, its occurrence probability will be overestimated. Therefore the knowledge of the selected species is important for the interpretation of the results (Rodwell & Winstanley 1994). However, significant relationships between the PRV and actual vegetation in the grassland/heathland mapping, limited effect of the present land use (forested vs. agricultural areas) on predicted pattern and the fieldwork-based expert knowledge suggest that the coincidence mapping method produces reasonable results.

It is therefore likely that different patterns in the PNV and PRV are, at least to some extent, attributable to the different responses of the individual vegetation types to environmental factors. The most striking differences may possibly be interpreted as follows:

1. None of the PRV-maps detected a pattern corresponding to the potential beech forests in the western part of the area. Actually there is no sharp environmental boundary between the *Melico-Fagetum* and *Melampyro-Carpinetum* forests and accordingly the vegetation boundary is fuzzy (Chytrý & Vicherek 1995). Possibly the change in replacement vegetation in response to the relatively homogeneous environment of the transitional area is less pronounced than the change in the natural forest vegetation.

2. The *Arrhenatherion* grassland was predicted both in the area of potential *Melampyro-Carpinetum* on siliceous bedrock in the cooler/wetter part of the area and in the area of potential *Primulo-Carpinetum* on Tertiary sediments of the warmer/drier southeast. Probably both areas have a similar degree of water availability because the lower rainfall in the southeast is compensated by better water-storage capacity of the deeper soils.

3. Weed communities did not reflect the SW-NE belt of siliceous bedrock in warmer/drier areas which was clearly revealed by the PNV and grassland/heathland maps. Probably the weed communities have broader ranges compared to forest or semi-natural grasslands because the uniform agricultural management is a superior factor affecting the floristic differentiation (Trautmann 1966; Janssen & Seibert 1991; Seibert & Conrad-Brauner 1995).

Conclusions

Mapping the PRV is a useful alternative to mapping the PNV or actual vegetation, provided the purpose of the mapping is the management of replacement vegetation or defining restoration goals, and the main interest is in site factors independent of the actual state of vegetation. The method may be successfully applied at large (> 1 : 25 000) and perhaps also medium (1 : 25 000 to 1 : 200 000) scales. The large-scale maps are especially useful tools for nature conservation and land-use planning; a comparison between the PRV-map and the actual vegetation map may be used to define the degree of departure of the actual vegetation from its target state. The medium-scale maps are more valuable for revealing the biogeographical patterns in the landscape; these maps may be based on the grid data on species distribution. As each type of the replacement vegetation and the natural vegetation may respond to different environmental factors, potential maps of the different types of replacement vegetation may produce different patterns which need not necessarily fit the PNV-pattern. A joint analysis of a series of such maps may contribute to a more precise biogeographical analysis of a landscape.

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