

## A methodological approach to potential vegetation modeling using GIS techniques and phytosociological expert-knowledge: application to mainland Portugal

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with 3 figures and 3 tables

Dedicated to Salvador Rivas-Martínez

**Abstract.** An attempt to obtain a consistent spatial model of natural potential vegetation (NPV) for the mainland Portuguese territory is reported. Spatial modeling procedures performed in a Geographic Information System (GIS) environment, aimed to operationalize phytosociological expert-knowledge about the putative distribution of potential zonal forest communities dominant in the Portuguese continental territories. The paradigm for NPV assumed was that of RIVAS-MARTINEZ (1976) and RIVAS-MARTINEZ et al. (1999), which presupposes, for a given territory, a univocal correspondence between a uniform combination of bioclimatic stage and lithology, given a biogeographical context, and a unique successional sequence leading to a single climax community (i. e. a vegetation series (VS)). Information issued from both literature and a team of phytosociologists possessing detailed knowledge about Portuguese vegetation, namely about forests and its serial vegetation, was acknowledged as a starting point for the construction of such a habitat-vegetation correspondence model. First, a bioclimatic map concerning the “Worldwide Bioclimatic Classification System” (WBCS) of RIVAS-MARTINEZ (1981–2004), obtained by multivariate geostatistical interpolation issuing from the work of MESQUITA (2005), was set. Several partial matrices, one for each biogeographical Province, combined such habitat statements to VS. Initial incoherence due to vagueness of statements led to an important amount of both superimposition of VS and habitat gaps in the matrices. Further rearrangement of the table according to known field distribution of VS by experts allowed setting an approximate univocal correspondence VS-habitat. Finally, an intersection of bioclimatic, lithology and biogeographic maps yielded over a thousand habitat combinations to be associated each to a single VS through implementation of the matrices as a set of rules. Again, inconsistencies were solved likewise, but this time by direct observation of the map by experts. Keeping of phytosociological consistency and fidelity to information on actual vegetation field distribution was always mandatory during the process.

**Abbreviations:** NPV=Natural Potential Vegetation; VS=Vegetation Series; DEM=Digital Elevation Model; WBCS=Worldwide Bioclimatic Classification System of Salvador Rivas-Martínez; GIS=Geographic Information System.

**Keywords:** Natural Potential Vegetation, phytosociology, expert-knowledge, GIS modeling, Portugal

## Introduction

In spite of earlier, more or less explicit formulations in the conceptual framework of the Zurich-Montpellier School (e.g. BRAUN-BLANQUET & PAVILLARD 1928; TANSLEY 1929; TÜXEN 1956; BRAUN-BLANQUET 1951), the use of the NPV concept was only formalized later by TÜXEN (1973). In short, it corresponds to a hypothetical vegetation state that would occur, in the actual habitat conditions, if human influence would cease and the progressive successional process was to be instantaneous. Its connotation with primitive vegetation is therefore partially possible if climate change and change in paleo-biogeographical context are not assumed as relevant (RIVAS-MARTINEZ 1994; RIVAS-MARTINEZ et al. 1999). Simultaneously, conceptual development in the study of vegetation mosaics (c.f. sigma-associations) summed up evidence that a great part of them had its origin in successional processes, being the other main process zonation in several spatial scales (BRAUN-BLANQUET 1951; TÜXEN 1956, 1973). Moreover, it was implied that difficulties in telling apart both processes are weaker in zonal territories influenced by humans because succession tends to dominate. Nevertheless, most authors avoided formalization of a functional link between the two facts, even for forest euclimatopes (i.e. linking explicitly vegetation mosaics and succession leading to NPV; e.g. TÜXEN 1977, 1978, 1979). Even recently, THEURILLAT (1992a, 1992b) and MORAVEC (1998) account extensively for the comparison of the two alternative views of mosaics (sigma-associations). However, as both vegetation mosaics and NPV were consensually accepted, the association of the two, as an integrated single concept to stand for a general model of succession, appeared only in RIVAS-MARTINEZ (1976). Therefore, for this author, plant community mosaics are, in zonal biotopes, mainly the result of succession and therefore stages of a successional sequence (or sequences) that lead ultimately to climax or NPV (RIVAS-MARTINEZ 1976, 1987; RIVAS-MARTINEZ et al. 1999). Thus, it is implied in this concept that any set of connate biotopes that are uniform in habitat conditions (*teselae*) exhibit, in principle, a single successional sequence (VS) and also a single climax plant community, which corresponds to NPV.

The status of NPV – encompassing successional events leading to climax – as scientific concept, in any of the current formulations by phytosociologists, is debatable. Much criticism dating back from GLEASON (1926, 1939) is still frequent, issuing from mainstream vegetation ecologists (e.g. WHITTAKER 1951; NAVEH & WHITTAKER 1980; CONNELL & SLATYER 1977; GLENN-LEWIN 1980, PEET & CHRISTENSEN 1980). On the other hand, evi-

dence of a great degree of coherence in forest successional processes at the meso-scale and related to bioclimate has been demonstrated (DAVIS et al. 1986; BOX 1981). Moreover, even assuming its usefulness as a landmark for thinking about vegetation, some problems seem to remain: i) from the epistemological point of view, it could be a teleological concept: it implies inversion of temporal causality; but in fact all predictions do so (CAPELO 2003); ii) NPV statements are difficult to formulate as falsifiable hypothesis (GODRON 1981); iii) verification can be carried out only where putative climax-communities are present, which is nowadays only a small part of the territory in many developed countries.

On the other hand, an operational concept of NPV can be envisaged (CAPELO op. cit.). Actually, the determination of NPV for a given biotope – even barren or deprived of mature vegetation – can be viewed as an act of extrapolation from the nearest location where actual vegetation is taken as climax and where habitat features are analogous to the former. In fact, this is the general practice of phytosociologists and has the advantage of referring to actual vegetation (care should be taken, as in any extrapolation, regarding habitat changes not perceived by the researcher; stochastic effects, extrapolation over biogeographical sector limits and the eventual presence of relictual vegetation, etc.). In spite of doubts, NPV has proved to be, to say the least, “a useful entelechy” and of great heuristic and practical value in the scope of vegetation science (GEHÚ & RIVAS-MARTINEZ 1980). Its usefulness and adequacy for vegetation landscape analysis, as well as for nature-planning programs, was empathized by SCHWABE (1997) and PEDROTTI (2004).

In the Iberian Peninsula, the 1:400,000 maps for Spain (RIVAS-MARTINEZ 1987) are an example of such operational concept of NPV. As to Portugal, in spite of a wealth of knowledge in the conceptual framework of NPV sensu S. Rivas-Martínez, no such maps exist.

In general, mapping NPV in a GIS environment can be acknowledged either by i) incorporation or computational formalization of expert knowledge or ii) using more objective methods, by inductive statistical construction of models by means of a training set (field observations of both vegetation and habitat features). In any case, it's mandatory that predictive vegetation mapping be based on the development of a model, mathematical or descriptive, followed by the application of that model to a geographic database (FRANKLIN 1995). In literature, such models – not necessarily phytosociology oriented – range from pure inductive computational approaches to formalization of expert-knowledge in a set of rules. These rules are further implemented in GIS by map algebra operations. Some approaches are hybrid and account for the two types of models. For instance, as mixed approaches are concerned, USTIN et al. (1994), in the scope of boreal forest, derived a set of rules to obtain a predicted vegetation map using literature, topographic features (i. e. from a digital elevation model (DEM)) and remotely sensed spectral variables. Similarly, SKIDMORE (1989) used a rule-based ‘expert system’ to map forest vegetation in Australia based on satellite imagery and terrain data. A priori probabilities of a forest-type occurring on

a topographic position were chosen by expert foresters, rather than induced from sampling. On the other hand, CAIRNS (2001) prefers an approach in which the vegetation model is strictly induced from a training set: general linear models (GLM), artificial neural networks (ANN) and induced classification trees are compared as predictors of vegetation type along the alpine timberline. MOORE et al. (1991) also used machine-learning approaches (CART: classification and regression trees) to vegetation mapping in GIS. - FRANKLIN (2002) used classification-trees obtained from a training set of 906 plots, where predictive variables were drawn from a DEM and from climate information. A simpler proposal for using a non-supervised classification algorithm, in the case a TWINSPAN classification (HILL 1979) derived from a VS vs. environmental feature matrix, was made by CAPELO et al. (1994) for the Lisbon area. Fitting of bioclimatic descriptors to dominant forest species in northern Europe was proposed by SKYES et al. (1996). MARTINEZ (1991) used logistic regression over DEM variables, estimated solar radiation regime and lithology to estimate probabilities of occurrence of forest-types. GONZÁLEZ (2005) used a similar approach to predictive VS distribution in the scope of climate-change scenarios in the Castilla y León region (Spain). Other models – not reviewed here – approach NPV through implementation of ecophysiological models (e.g. carbon-balance based: KAPLAN 2001; LI & SUN 1998) or biogeochemical models (WOODWARD et al. cit. SHUGART 1998; HAXELTINE & PRENTICE 1996). A descriptive model-approach is made by PALO et al. (2005), deriving a predictive map of Saare County (Estonia) vegetation using published classifications of Estonian vegetation. As predictive variables, simplified soil classes including estimates of limestone content, DEM-derived variables, and CORINE land cover (deciduous/coniferous forests) were used.

An attempt to model NPV encompassing a rule-based prediction is presented in this work. Its objectives are to test a NPV model based on phytosociological expert-knowledge, mainly for heuristic purposes, and putting together a consistent reference map of NPV. The mapping process encompasses two distinct ideas: first, predictive cartography of VS (or NPV) is based on the assumption that, given: i) a biogeographical context (Province, in the case) expressing a peculiar species pool and paleo-biogeographical history; ii) a unique combination of bioclimatic types and lithology; a single VS can be assigned to it. I.e., one can assume that  $NPV = f(\text{bioclimate, lithology, biogeography})$ . Second, belief that incompleteness or ambiguities in the model can be solved either by introduction of relevant auxiliary variables (e.g. terrain slope) or directly by field knowledge of experts.

The same approach has been followed by some of the authors elsewhere, to map the NPV of Madeira Island (Portugal), with great adherence to actual climax vegetation-type limits (CAPELO et al. 2004).

## Materials and methods

### Study area

The study area was the whole continental territory of Portugal.

### Phytosociological data sources

The main phytosociological data sources about Portuguese and Iberian VS issued from: Costa et al. (1998); Rivas-Martínez et al. (1990, 2001, 2002), Rivas-Martínez (1987), Costa (2006), Aguiar (2001), Honrado (2003), Capelo (1996) and Pinto-Gomes & Paiva-Ferreira (2005). Many other fragmentary sources were also considered from the Portuguese phytosociological literature. The final version of the list of VS occurring in Portugal and relevant to the cartographic scale in the final layout of the map (1:1.000.000 – not presented) is summarized in Table 1.

### Source maps

A simplified geological layer was produced by aggregating classes of the 1:500.000 geological map of Portugal (SERVIÇOS GEOLÓGICOS DE PORTUGAL 1992). Geological classes were simplified as to be reduced to the following coarse lithological classes: 1) alluvium, 2) arenaceous coverings, 3) siliceous sandstone, 4) non-karst limestone, 5) karst limestone, 6) paleo-dunes (podzols), 7) active dunes, 8) diorite, 9) granite, 10) sienite, 11) schist/greywacke, 12) schist/gneiss, 13) other silicates, 14) ultramafic, 15) vertic and 16) solonchaks/saltmarsh.

A geomorphologic map (FERREIRA 1980) was used as an additional source of information for defining some areas, namely: i) karst or non-karst limestone (not originally in the geological map); ii) saltmarsh areas; iii) sea-cliffs. Sea-cliffs were delimited as a 200 m strip along the coast for cliffs with less than 50 m high and as a 400 m strip for those higher than 50 m.

Auxiliary layers were found to be necessary to discriminate among relevant special habitat types. Distance from sea-shore (a 500 m buffer) was used to arbitrarily separate active littoral dunes from quaternary inland dunes, not distinguished in the geological map. Quaternary dunes in the geomorphologic map were also included and then restricted to 500 m from the sea.

All this information was put together in a simplified lithology layer, consisting of 17 classes.

A 200 m cell digital elevation model (DEM) was also used for deriving topographic variables, namely slope angle.

A phytogeographic map (COSTA et al. 1998) of mainland Portugal was used for representing phytogeographical context. The study area includes four different Provinces, which divide hierarchically in Sectors, Subsectors and Superdistricts, in a total of 31 distinct units.

A bioclimatic layer was created using the maps produced by MESQUITA (2004). The bioclimatic classification used was that of RIVAS-MARTÍNEZ

Table 1. Portuguese Vegetation Series relevant to the cartographic scale.

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**Vegetation Series**


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Arbutus unedo-Quercus pyrenaica S.
Arisarctus-Quercus broteroi S.
Asparagus aphyllus-Quercus suberis S.
Daphniphyllum gnidioides-Juniperus navicularis S.
Genista falcata-Quercus pyrenaica S.
Genista hystrix-Quercus rotundifolia S.
Holcus mollis-Quercus pyrenaica S.
Juniperus lagunae-Quercus suberis S. & Ruscus aculeatus-Juniperus lagunae S.
Lonicera implexa-Quercus rotundifolia S.
Lycopodium clavatum-Juniperus nana S.
Myrica fayae-Arbutus unedo S.
Myrtillus-Quercus roboris S.
Myrica communis-Quercus rotundifolia S.
Olea sylvestris-Quercus suberis S.
Ostrya quadripartita-Juniperus turbinata S.
Phlomis purpurea-Juniperus turbinata S.
Physospermum cornubiense-Quercus suberis S.
Pyrus bourgaeana-Q. rotundifolia S. & Pistacia terebinthus-Q. broteroi S.
Quercus coccifera-Juniperus turbinata S.
Rhamnus oleoides-Quercus rotundifolia S.
Ruscus aculeatus-Quercus roboris S.
Sanguisorbo agrimonoides-Quercus suberis S.
Saxifraga spathularis-Betula celtiberica S.
Smilax aspera-Quercus suberis S. & Pistacia-Juniperus badia S.
Teucrium baeticum-Quercus suberis S.
Vaccinium myrtillus-Juniperus nana S.
Viburnum tinus-Olea sylvestris S.
Viburnum tinus-Quercus rivasmartinezii S.
Viburnum tinus-Quercus roboris S.
Riparian geosigmeta
Saltmarsh microgeosigmeta
Sea-cliff microgeosigmeta

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(1981) known as 'Worldwide Bioclimatic Classification System' (WBCS), actualised by the online version of RIVAS-MARTÍNEZ (2004) of 23<sup>rd</sup> of April 2004. Spatial interpolation of the variables necessary for the bioclimatic classification of continental Portugal according to RIVAS-MARTÍNEZ (2004), was carried out. Compensated thermicity index (*I<sub>tc</sub>*), annual ombrothermic index (*I<sub>o</sub>*), ombrothermic indexes of the summer bimonth (*I<sub>os<sub>2</sub></sub>*) and of the summer trimester (*I<sub>os<sub>3</sub></sub>*), summer compensated ombrothermic index (*I<sub>osc<sub>4</sub></sub>*) and positive temperature (*T<sub>p</sub>*) were interpolated using several multivariate geostatistical techniques. Although spatial interpolation of bioclimatic parameters is not common in ecological literature, it is a common practice for climatic parameters in the scope of mainstream climatology (e.g. CORNFORD 1999; GOOVAERTS 2000; JARVIS & STUART 2001; KYRIAKIDIS et al. 2001; BROWN & COMRIE 2002).

The best geostatistical estimator for each variable was chosen taking into account both cross validation and visual inspection of the produced maps. Knowledge of natural vegetation was considered also a good indicator for the evaluation of these maps. The best results were achieved using multiple regression followed by ordinary kriging of the residuals for *I<sub>os<sub>2</sub></sub>* and for *I<sub>os<sub>3</sub></sub>* and kriging with external drift using multiple regression as drift for all other indexes (Table 2). The independent variables used were altitude, latitude, longitude, distance to the coast and distance to the nearest river of order higher than 1 (using the common Strahler criteria).

A raster model with a resolution of 1 km was created in a GIS; (BURROGH & McDONNELL, 1998) for all independent variables, and the best model for estimating each variable was implemented for Continental Portugal, resulting in six maps. A bioclimatic diagnosis for all the studied territory was derived from these maps, using local spatial analysis operators.

A macrobioclimate map was created using map algebra, through a set of conditional statements imposed to the four ombrothermic Indexes maps according to RIVAS-MARTÍNEZ (2004). Next, a thermotypes map was produced through a set of conditional statements imposed to the macrobioclimates, compensated thermicity index and positive temperature maps. Finally, an ombrotypes map was obtained by reclassifying the annual ombrothermic index map (MESQUITA, 2005).

Table 2. Mean square error (MSE) and determination coefficient ( $R^2$ ) for the best methods used to interpolate the bioclimatic indexes (adapted from MESQUITA 2005).

Index	Best interpolation method	MSE	$R^2$
<i>T<sub>p</sub></i>	Kriging with external drift using mult. regression as drift	5532.1	0.928
<i>I<sub>tc</sub></i>	Kriging with external drift using mult. regression as drift	243.4	0.958
<i>I<sub>o</sub></i>	Kriging with external drift using mult. regression as drift	3.0656	0.801
<i>I<sub>os<sub>2</sub></sub></i>	Multiple regression & ordinary kriging of the residuals	0.0257	0.882
<i>I<sub>os<sub>3</sub></sub></i>	Multiple regression & ordinary kriging of the residuals	0.0648	0.882
<i>I<sub>osc<sub>4</sub></sub></i>	Kriging with external drift using mult. regression as drift	0.1978	0.861

In order to produce a unique bioclimatic layer, the thermotypes and ombrotypes maps were converted from raster to polygon layers, to allow vector-based operations. The maps were then intersected, and a global Bioclimatic map of Continental Portugal was produced. The final map consists of forty-six distinct thermotype horizon vs. ombrotype horizon combinations ranging from thermo to oro-mediterranean or temperate and from semi-arid to ultra-hyperhumid.

### Expert knowledge incorporation and GIS modelling

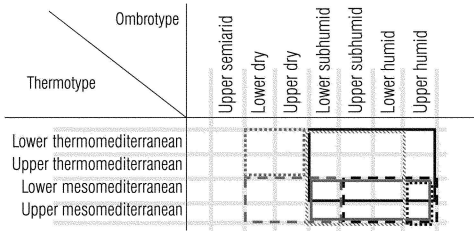
The methodological procedures occurred in several stages. The first one consisted of consulting experts and literature to delineate a set of rules to associate univocally habitat to VS.

The first phase of the rule-creation process was to compile statements about the habitat range concerning these variables alone – bioclimate (i.e., thermotype and ombrotype), lithology, biogeography – and the correspondent VS in a set of two-way graph contingency tables, in order to cross-check the possibility of obtaining univocal correspondence. One table was put together for each of the four phytogeographical Provinces, according to the phytogeographical typology of COSTA et al. (1998), and group of analogous lithology types (see Fig. 1 as an example). The set of habitat statements, being typically empirical vague ones, led, as expected, to a high degree of habitat superimposition, therefore two or more VS corresponded to a given habitat combination. Since fragmentary or superimposed habitat concepts about VS issuing from experts could contribute to inconsistency, the tables were carefully analyzed and tentatively arranged by experts to achieve univocal correspondence, while keeping consistency with a priori phytosociological knowledge of community distributions.

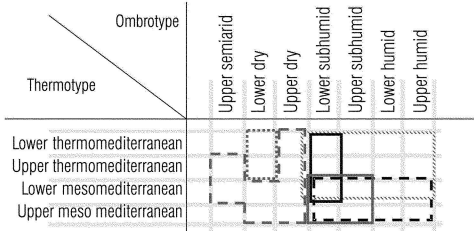
The next stage consisted of intersecting the three layers containing the information necessary for the spatialization of the model previously created. The map thus obtained summed up to 1163 different habitat combinations. The rules issued from the matrices were applied to this map, as a first attempt to spatialize them, therefore implementing the model in a map. It was then possible, by visual inspection of this map, to evaluate the habitat-VS model produced and to identify its main problems, namely gaps and VS superimposition areas.

Thus, as the last step of the process, for each polygon in the map expressing a doubtful habitat-VS combination, the known field distribution of dominant forest communities (personal knowledge and literature) was used by a group of experts to solve ties, gaps and inconsistencies and assign them to a single VS. Sometimes mosaics of two or more VS had to be accepted in polygons. The first type of constraint forcing the use of mosaics relates to lack of discrimination among lithology types relevant to vegetation response, but absent in the geological map (e.g. sandstone vs. limestone of the same geological age; depth of basalt-derived soils assumed as discriminant between oleaster (*Olea europaea* subsp. *sylvestris*) and cork-oak (*Quercus suber*) series). The second type attempts to express an actual mixture in a

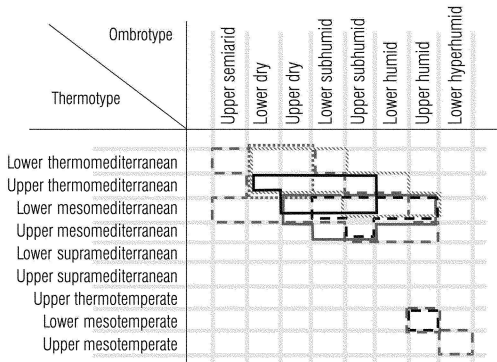




1. Habitat ranges directly issued from experts



2. Habitat ranges re-arranged by experts



3. Habitat ranges in the final map.

VS of Luso-Estremadurensian Province:

- *Arbutus unedo*-*Quercus pyrenaica* S.
- *Asparagus aphyllus*-*Quercus suber* S.
- ..... *Euphorbia*-*Quercus canariensis* S.
- - - *Myrica*-*Quercus rotundifolia* S.
- - - *Pyro bourgaeana*-*Quercus rotundifolia* S. + *Pistacia terebinthi*-*Q. broteroi* S.
- *Sanguisorbo agrimonoides*-*Q. suber* S.
- ..... *Teucrium baeticum*-*Quercus suber* S.

Figure 1. Habitat range changes for the set of siliceous luso-estremadurensian province VS during the expert-knowledge acquisition process, as an example.

small-scale level of several VS. The later can be due to small-scale topographic or edaphic variation not expressed in any of the habitat information layers (due to its scale) or to the actual interpenetration of forest-types during quaternary or contemporary times. One last reason relates to the impossibility of experts to tell apart habitat features of the VS.

## Results

Table 3 summarizes the evaluation of the first map produced (Fig. 2), by comparison to the final map (Fig. 3). Analysing this table, it stands out that less than half the habitats are considered correctly assigned to a single VS (44.3 %); more than one third are not assigned to any VS (36.7 %); also some relevant amount of incorrect (11.5 %) or overlapping VS also occurs (7.5 %). The main factor apparently justifying the great deal of occurring habitat combinations without a VS assigned to are: i) experts weren't a priori aware of some unexpected bioclimate-lithology combinations in their study areas; ii) expert unawareness of some lithology types in their areas; iii) bioclimatic parameters interpolation errors; iv) errors in the geologic and geomorphologic maps; v) small differences among the maps used arising from the use of different data and from errors in the georeferencing of printed maps; vi) and, finally, inconsistency in some VS limits, apparently suggesting a frontier among contiguous biogeographical units slightly different from that of the biogeographical map. It should be noted that, at the time (COSTA et al. 1989) the bioclimatic model assumed in the making of the biogeographical map was more informal than the one used here. Further discrepancy could arise from differences between informal perception of bioclimatic limits by experts and those issued by the bioclimatic model.

The map resulting of the implementation of the habitat-VS model is presented in Fig. 2. The final map produced, prepared for printing at the scale 1 : 1.000.000, is presented in Fig. 3.

In literature, evaluation of predicted maps is usually made through visual inspection (e.g. NICOLAU 2000) and extensive verification by a statistically

Table 3. Summary of first VS spatialization attempt by direct rule implementation. VS are considered "correctly assigned" according to the final map. VS "not assigned" stands for undefined habitat-VS combinations in the rules.

	Habitat combinations		Percentage of study area
	number	percentage	
Habitat-VS correctly assigned	515	44.3	43.8
Habitat-VS incorrectly assigned	134	11.5	17.2
Several VS overlapping in one habitat	87	7.5	14.6
Habitat not assigned to any VS	427	36.7	24.4

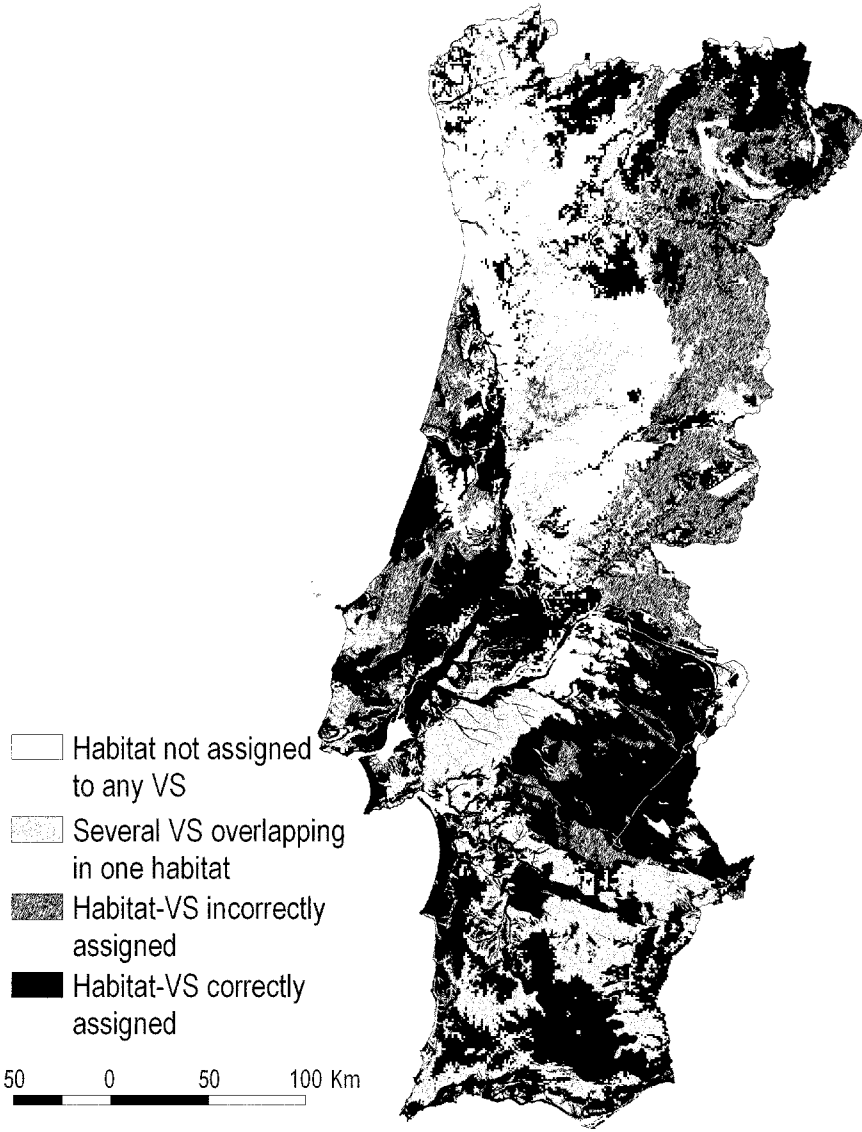


Figure 2. Territorial distribution of predicted VS status by applying directly the set of habitat-VS correspondence rules as issued from re-arranging the matrix by experts (see also Tab. 3).

significant set of field observations, so that error estimates can be derived (e.g. GOODALE et al. 1998; BROWN & COMRIE 2002). However, none of these methods can be formally applied to the produced map, due to the

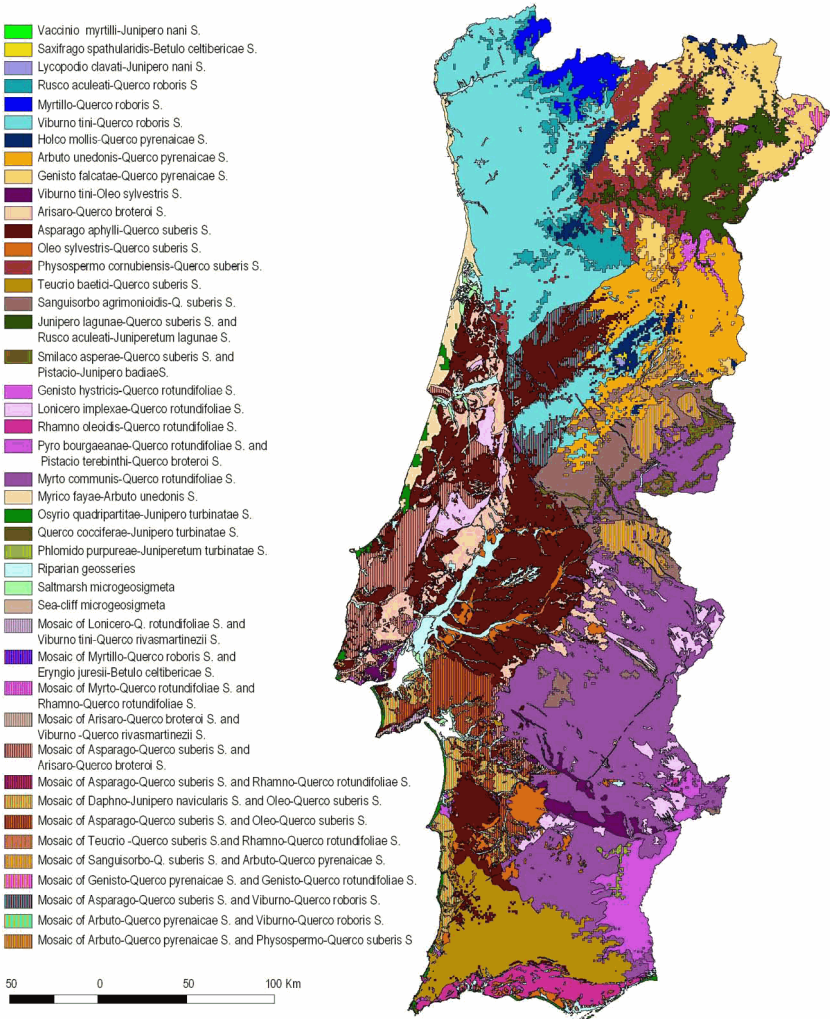


Figure 3. Map of Natural Potential Vegetation (Vegetation Series) of mainland Portugal. Reduced depiction from the original 1:1.000.000 map.

nature of inferences leading to NPV and the method of expert knowledge incorporation. It should be noted that putative successional relationships of actual vegetation to NPV could be used as verification criteria. Nevertheless, it was such knowledge that was in fact used by experts to establish the VS range in territories with no mature forests. Therefore, circular reasoning would be involved. An alternative procedure would be evaluation by an

independent group of experts or extensive field verification. The only possible evaluation of the produced map, at this stage of work, is a comparison made a posteriori with the VS map of Spain (RIVAS-MARTÍNEZ 1987) along the Portuguese-Spanish border, which yields a great deal of coherence.

## Conclusion

While being, by large, a subjective exercise, it is acknowledged that the attempt now presented to map NPV in mainland Portugal has both heuristic and practical value, as it stands as a possible first consistent reference framework for Portuguese NPV. Nevertheless, it is clear that the current status of knowledge about VS-habitat relationships, as formalized by phytosociologists in the form of simple diagnostic statements, is insufficient for NPV modeling without introducing a great degree of subjective judgment in the process. However, it is likely that, in the current NPV modeling approach, better results can be achieved by introducing other habitat variables, namely those assumed to be related to VS mosaics. Accordingly, FRANKLIN (1995) suggests a set of DEM-derived variables, such as slope-angle, slope curvature or specific catchment area. Others include remotely sensed variables, in concrete soil-moisture indexes. Moreover, further validation of the model and map could be approached by extensive confrontation with a large data set of geo-referenced field observations of ecologically mature natural forest remnants or correspondent diagnostic serial stages.

In the scope of further research in Portuguese NPV, such an effort towards greater verification and performance of NPV models will be of great importance. Furthermore, an effort to produce objective quantification of habitat features of syntaxa and sigma-syntaxa involved in VS, namely a more complete characterization of ecological amplitudes, would surely contribute to better success in modeling.

## References

- Aguiar, C. (2001): *Flora e Vegetação da Serras da Nogueira e do Parque Natural da Monteseinho*. PhD thesis (unpublished). – Instituto Superior de Agronomia, Lisboa
- Box, E. O. (1981): *Macroclimate and plant forms: an introduction to predictive modeling in phytogeography*. – *Tasks for Vegetation Science*, vol. I – Dr. Junk. The Hague. 258 pp.
- Braun-Blanquet, J. (1951): *Pflanzensoziologie*. Ed. 2. – Springer, Wien. 631 pp.
- Braun-Blanquet, J. & Pavillard, J. (1928): *Vocabulaire de sociologie végétale*. Ed. 3. – Roumégous & Déhan, Montpellier. 23 pp.
- Brown, D. P. & Comrie, A. C. (2002): *Spatial modeling of winter temperature and precipitation in Arizona and New Mexico, USA*. – *Climate Research* 22(2): 115–128.
- Burrough, P. A. & McDonnell, R. A. (1998). – *Principles of geographical information systems*. Oxford University Press, Oxford. 333 pp.
- Cairns, D. M. (2001): *A comparison of methods for predicting vegetation type*. – *Plant Ecology* 156: 3–18.
- Capelo, J. (1996): *Esboço da paisagem vegetal da bacia portuguesa do rio Guadiana*. – *Silva Lusitana* 4 (special number): 13–64.

- (2003): Conceitos e métodos da fitossociologia. Formulação contemporânea e métodos numéricos de análise da vegetação. – Estação Florestal Nacional, Oeiras. 107 pp.
- Capelo, J., Costa, J. C. & Lousã, M. (1994): Distribuição das series de vegetação climatófilas da região de Lisboa segundo padrões edáficos e mesoclimáticos. – Anais do Instituto Superior de Agronomia 44(1): 281–301.
- Capelo, J., Sequeira, M., Jardim, R., Costa, J. C. & Mesquita, S. (2004): Guia da excursão geobotânica dos V Encontros ALFA 2004 à Ilha da Madeira. – Quercetea 6: 5–45.
- Connell, J. H. & Slatyer, R. O. (1977): Mechanisms of succession in natural communities and their role in community stability and organization. – Amer. Nat. 111: 1119–1144.
- Cornford, D. (1999): Using Variograms to Evaluate a Model for the Spatial Prediction of Minimum Air Temperature. – in Atkinson, P. M. & Tate, N. J. (Eds.): Advances in Remote Sensing and GIS Analysis, pp. 97–117. John Wiley and Sons, West Sussex.
- Costa, J. C. (2006): Checklist dos sintaxa de Portugal. Continente e Ilhas. – Associação Lusitana de Fitossociologia 33 pp. (unpublished).
- Costa, J. C., Aguiar, C., Capelo, J. H., Lousã, M. & Neto, C. (1998): Biogeografia de Portugal Continental. – Quercetea 0: 5–56.
- Davis M. B., Woods, K. D., Webb, S. L. & Futyma, R. P. (1986): Dispersal versus climate: expansion of *Fagus* and *Tsuga* into the Upper Great Lakes region. – Vegetatio 43(1/2): 93–104.
- Ferreira, D. B. (1980): Mapa Geomorfológico de Portugal. – Instituto Geográfico e Cadastral, Lisboa.
- Franklin, J. (1995): Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. – Progress in Physical Geography 19(4): 474–499.
- (2002): Enhancing a regional vegetation map with predictive models of dominant plant species in chaparral. – Applied Vegetation Science 5: 135–146.
- Géhu, J.-M. & Rivas-Martínez, S. (1980): Notions fondamentales de phytosociologie. – Ber. Int. Sympos. Vereinigung Vegetationsk. [1980]: 5–33.
- Gleason, H. A. (1926): The individualistic concept of the plant association. – Bulletin of the Torrey Botanical Club 53: 7–26.
- (1939): The individualistic concept of the plant association. – American Midland Naturalist 21: 92–110.
- Glenn-Lewin (1980): The individualistic nature of plant community development. – Vegetatio 43(1/2): 141–146.
- Godron, M. (1981): Symposium on vegetation dynamics in grasslands, heathlands and mediterranean ligneous formations. Preface. – Vegetatio 11(46/47): VII–VIII.
- González, S. D.R. (2005): El cambio climático y su influencia en la vegetación de Castilla y León (España). – Itinera Geobotanica 16: 1–534.
- Goodale, C. L., Aber, J. D. & Ollinger, S. V. (1998): Mapping monthly precipitation, temperature, and solar radiation for Ireland with polynomial regression and a digital elevation model. – Climate Research 10 (1): 35–49.
- Goovaerts, P. (2000): Geostatistical approaches for incorporating elevation into the spatial interpolation of rainfall. – Journal of Hydrology 228: 113–129.
- Haxeltine, A. & Prentice, I. C. (1996): An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. – Global Biogeochemical Cycles 10(4): 693–709.
- Hill, M. O. (1979): TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and the attributes. – Cornell University, Department of Ecology and Systematics, Ithaca, N. Y.

- Honrado, J. (2003): Flora Vascular e Vegetação Natural do Parque Nacional da Peneda-Gerês. PhD Thesis. – Universidade do Porto.
- Jarvis C. H. & Stuart N. (2001): A comparison among strategies for interpolating maximum and minimum daily air temperatures. – *Journal of Applied Meteorology* 40(6): 1075–1084.
- Kaplan, J. (2001): Geophysical applications of vegetation modeling. – Lund University. Sweden. 114 pp.
- Kyriakidis, P. C., Kim, J. & Miller, N. L. (2001): Geostatistical mapping of precipitation from rain gauge data using atmospheric and terrain characteristics. – *Journal of Applied Meteorology* 40 (11): 1855–1877.
- Li, D. Q., Sun, C. Y. & Zang, X. S. (1998): Modelling the net primary productivity of the natural potential vegetation in China – *Acta Botanica Sinica* 40(6): 560–566.
- Martinez, J. M. (1991): Modelización de la vegetación potencial en la cuenca alta del río Narcea (Astúrias-España). – <http://www6.uniovi.es/usr/juantxo/Seminario/frames/Portada.html>
- Mesquita, S. (2005): Modelação Bioclimática de Portugal Continental. – Masters Degree Thesis (unpubl.). 129 pp.
- Moore, D. M., Lees, B. G. & Davey, S. M. (1991): A new method for predicting vegetation distributions using decision-tree analysis in a geographic information system. – *Environmental Management* 15(1): 59–71.
- Moravec, J. (1998): Reconstructed natural versus potential natural vegetation in vegetation mapping – A discussion of concepts. – *Applied Vegetation Science* 1(2): 173–176.
- Naveh, Z & Whittaker, R. H. (1980): Structural and floristic diversity of shrublands and woodlands in Northern Israel and other Mediterranean areas. – *Plant Ecology* 41(3): 171–190.
- Nicolau, R. (2002): Modelação e Mapeamento da Distribuição Espacial da Precipitação – Uma Aplicação a Portugal Continental. Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa. PhD Thesis, (unpubl.). 356 pp.
- Palo, A., Aunap, R. & Mander, U. (2005): Predictive vegetation mapping based on soil and topographical data: A case study from Saare County, Estonia. – *Journal for Nature Conservation* 13: 197–211.
- Pedrotti, F. (2004): Cartografia Geobotanica. – Pitagora Editrice Bologna. 236 pp.
- Peet, R. K. & Christensen, N. L. (1980): Succession: a population process. – *Vegetatio* 43(1/2): 131–140.
- Pinto-Gomes, C. & Paiva-Ferreira, R. (2005): Flora e Vegetação. Barrocal algarvio. Tavira-Portimão. – Comissão coordenação e desenvolvimento regional do Algarve. 354 pp.
- Rivas-Martínez, S (1976): Sinfitosociología, una nueva metodología para el estudio del paisaje vegetal. – *Anales Inst. Bot. Cavanilles* 33: 179–188.
- (1981): Les étages bioclimatiques de la végétation de la Péninsule Ibérique. – *Anales Jard. Bot. Madrid* 37(2): 251–268.
- (1987): Memória del Mapa de Séries de Vegetación de España 1: 400.000. MAPA. – ICONA Madrid. 268 pp.
- (1994): Dynamic-zonal phytosociology as landscape science. – *Phytocoenologia* 24: 23–25.
- (2004): Global Bioclimatics (versión 23-04-04) – Phytosociological Research Center. <http://www.globalbioclimatics.org>.
- Rivas-Martínez, S., Díaz, T. E., Fernández-González, F., Izco, J., Loușă, M. & Penas (2002): Vascular Plant Communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. – *Itinera Geobotanica* 15(1): 5–432.

- Rivas-Martínez, S., Fernández-González, F., Loidi, J., Lousã, M. & Penas, A. (2001): Syntaxonomical check-list of vascular plant communities of Spain and Portugal to association level. – *Itinera Geobotanica* **14**: 5–341.
- Rivas-Martínez, S., Lousã, M., Diaz, T. E., Fernandez-Gonzalez, F., & Costa, J. C. (1990): La vegetación del sur de Portugal (Sado, Alentejo y Algarve). – *Itinera Geobotanica* **3**: 5–126.
- Rivas-Martínez, S., Sanchez-Mata, D. & Costa, M. (1999): North American boreal and western temperate forest vegetation (syntaxonomical synopsis of the potential natural plant communities of North America, II). – *Itinera Geobotanica* **12**: 5–316.
- Schwabe, A. (1997): Sigmachorology as a subject of phytosociological research: a review. – *Phytocoenologia* **27**(4): 463–507.
- Serviços Geológicos de Portugal (1992): Carta Geológica de Portugal na escala 1:500.000. – SGP, Lisboa.
- Shugart, H. H. (1998): Terrestrial ecosystems in changing environments. – Cambridge University Press. UK. 537 pp.
- Skidmore, A. (1989): An expert system classifies eucalypt forest types using Thematic Mapper data and a digital terrain model. – *Photogrammetric Engineering and Remote Sensing* **52**: 779–786.
- Skyles, M. T., Prentice, I. C., Cramer, W. (1996): A bioclimatic model for the potential distributions of north European tree species under present and future climates. – *Journal of Biogeography* **23**: 203–233.
- Tansley, A. G. (1929): Succession, the concept and its values. – *Proc. Int. Congr. Plant Sci. Ithaca* **1926**: 677–686.
- Theurillat, J. P. (1992a): L'analyse du paysage végétale en symphytocoenologie: ses niveaux et leurs domaines spatiaux. – *Bull. Ecol.* **23**: 83–92.
- (1992b): Étude et cartographie du paysage végétal (symphytocoenologie) dans la région d' Aletsch (Valais, Suisse). Développement historique et conceptuel de la symphytosociologie, niveaux de perception, méthodologie, applications I. – Texte. – *Beiträge zur geobotanischen Landesaufnahme der Schweiz* **68**. Commission géobotanique de l'Académie Suisse des Sciences Naturelles. Krypto F. Flück-Wirth. Lausanne et Genève. 384 pp.
- Tüxen, R. (1956): Die heutige potentielle natürliche Vegetation als Gegenstand der Vegetationskartierung. – *Angew. Pflanzensoziologie, Stolzenau* **13**: 5–42.
- (1973): Vorschlag zur Aufnahme von Gesellschaftskomplexen in potentiell natürlichen Vegetationsgebieten. – *Acta Bot. Acad. Sci. Hung.* **19**: 379–384.
- (1977): Zur Homogenität von Sigmassoziationen ihrer syntaxonomischen Ordnung und ihrer Verwendung in der Vegetationskartierung. – *Doc. Phytosociol. N. S.* **1**: 321–327.
- (1978): Assoziationskomplexe (Sigmeten) und ihre praktische Anwendung. – *Ber. Int. Symp. Int. Vereinigung Vegetationsk.* 1977, 535 pp.
- (1979): Sigmeten und Geosigmeten, ihre Ordnung und ihre Bedeutung für Wissenschaft, Naturschutz und Planung. – *Biogeographie* **16**: 79–92.
- Ustin, S. L., Szeto, L.-H., Xiao, Q.-F., Hart, Q. J. & Kasischke, E. S. (1994): Vegetation mapping of forested ecosystems in interior central Alaska. – *Proceedings IGARSS '94*. Piscataway, NJ: IEEE Inc: 229–31.
- Whittaker, R. H. (1951): A criticism of the plant association and climatic climax concepts. – *Northwest Science* **25**: 17–31.

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