

- Küchler, A.W. (1964) *Potential natural vegetation of the conterminous United States*. Special Publication No. 36, American Geographical Society, New York.
- Lexer, M.J., Honninger, K., Scheifinger, H., Matulla, Ch., Groll, N., Kromp-Kolb, H., Schadauer, K., Starlinger, F. & Englisch, M. (2002) The sensitivity of Austrian forests to scenarios of climatic change: a large-scale risk assessment based on a modified gap model and forest inventory data. *Forest Ecology and Management*, **162**, 53–72.
- Liu, H., Wang, L., Yang, J., Nakagoshi, N., Liang, C., Wang, W. & Lv, Y. (2009) Predictive modeling of the potential natural vegetation pattern in northeast China. *Ecological Research*, **24**, 1313–1321.
- Miyawaki, A. (1998) Restoration of urban green environments based on the theories of vegetation ecology. *Ecological Engineering*, **11**, 157–165.
- Moravec, J. (1998) Reconstructed natural versus potential natural vegetation in vegetation mapping – a discussion of concepts. *Applied Vegetation Science*, **1**, 173–176.
- Mücher, C.A., Hennekens, S.M., Bunce, R.G.H., Schaminée, J.H.J. & Schaepman, M.E. (2009) Modelling the spatial distribution of Natura 2000 habitats across Europe. *Landscape and Urban Planning*, **92**, 148–159.
- Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and methods of vegetation ecology*. John Wiley & Sons, New York.
- Pickett, S.T.A., Cadenasso, M.L. & Meiners, S.J. (2009) Ever since Clements: from succession to vegetation dynamics and understanding to intervention. *Applied Vegetation Science*, **12**, 9–21.
- Ricotta, C., Carranza, M.L., Avena, G. & Blasi, C. (2002) Are potential vegetation maps a meaningful alternative to neutral landscape models? *Applied Vegetation Science*, **5**, 271–275.
- Rodwell, J. & Patterson, G. (1994) *Creating new native woodlands*. HMSO, London.
- Rosati, L., Marignani, M. & Blasi, C. (2008) A gap analysis comparing Natura 2000 vs National Protected Area network with potential natural vegetation. *Community Ecology*, **9**, 147–154.
- Schulze, E.D., Beck, E. & Müller-Hohenstein, K. (2005) *Plant ecology*. Springer, Berlin-Heidelberg.
- Strand, E.K., Vierling, L.A., Bunting, S.C. & Gessler, P.E. (2009) Quantifying successional rates in western aspen woodlands: current conditions, future predictions. *Forest Ecology and Management*, **257**, 1705–1715.
- Tüxen, R. (1956) Die heutige potentielle natürliche Vegetation als Gegenstand der Vegetationskartierung. *Angewandte Pflanzensoziologie*, **13**, 5–42.
- Verheyen, K., Fastenaekels, I., Vellend, M., De Keersmaecker, L. & Hermy, M. (2006) Landscape factors and regional differences in recovery rates of herb layer richness in Flanders (Belgium). *Landscape Ecology*, **21**, 1109–1118.
- Walker, D.A., Reynolds, M.K., Daniëls, F.J.A., Einarsson, E., Elvebakk, A., Gould, W.A., Katenin, A.E., Kholod, S.S., Markon, C.J., Melnikov, E.S., Moskalenko, N.G., Talbot, S.S., Yurtsev, B.A. & the other members of the CAVM Team (2005) The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, **16**, 267–282.
- Westhoff, V. & van der Maarel, E. (1973) The Braun-Blanquet approach. *Ordination and classification of communities* (ed. by R.H. Whittaker), pp. 617–726. *Handbook of Vegetation Science*, Vol. 5. Junk, The Hague.
- Willis, K.J. & Birks, H.J.B. (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science*, **314**, 1261–1265.
- Willis, K.J., Bennett, K.D., Froyd, C. & Figueroa-Rangel, B. (2007) How can a knowledge of the past help to conserve the future? Biodiversity conservation strategies and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 175–186.
- Zerbe, S. (1998) Potential natural vegetation: validity and applicability in landscape planning and nature conservation. *Applied Vegetation Science*, **1**, 165–172.
- Zou, S., Cheng, G., Xiao, H., Xu, B. & Feng, Z. (2009) Holocene natural rhythms of vegetation and present potential ecology in the Western Chinese Loess Plateau. *Quaternary International*, **194**, 55–67.

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The concepts of potential natural vegetation (PNV) and other abstractions (trying to pick up fish with wet hands)

ABSTRACT

This note follows from an earlier Commentary published in *Journal of Biogeography* (Carrión & Fernández, 2009, **36**, 2202–2203), which provided palaeoecological data, and two replies in the form of

Correspondence (Loidi *et al.*, 2010, **37**, 2209–2211; Farris *et al.*, 2010, **37**, 2211–2213). The latter papers attempt to invalidate the palaeoecological database as a source of comparison with the maps of potential vegetation. Here, some of the different interpretations of the term ‘potential natural vegetation’ (PNV), as used by the floristic phytosociological school, are discussed. It is suggested that there is a conceptual impasse that will not have a solution until a terminological consensus is reached. This terminology will open new methodological avenues that will facilitate the entry of new information derived from historical biogeography, palaeoecology, ecology, phylogeography, and niche and community modelling. One of the main sources of conflict arises from the link made between habitats and floristically-determined associations, a confusion that has crucial repercussions in biological conservation, including in respect of the EU Habitats Directive.

Keywords Climax concept, conservation, historical biogeography, palaeoecology, phytosociology, potential natural vegetation.

This paper is a response to two papers authored by sixteen phytosociologists from Spain and Italy. The first, Loidi *et al.* (2010), presents what could be seen as the phytosociological school’s consensus position as already published, for example, by Loidi (1998) in reaction to Blanco *et al.* (1997). The latter, among others (e.g. Spribille & Ceska, 2001), claim that potential natural vegetation (PNV) has the following weaknesses: (1) the subjective character of sampling, (2) the inefficient description of human-disturbed areas, (3) the lack of regard to the role of structure in the definition of communities, (4) the confused system of nomenclature and the instability of the classification, (5) impoverished, outdated methodology, (6) lack of experimental field studies, and (7) a strong tendency to use *ad hoc* taxonomy to name phytosociological taxa.

Loidi *et al.* (2010) argue that by seeking a comparison with pristine vegetation, Carrión & Fernández (2009) are using an inexact interpretation of the concept of potential natural vegetation (PNV), even though this comparison is common in applied forestry (Higgins *et al.*, 2004). In practice, it is difficult to determine which interpretation of PNV should be adopted given that there are

a number of available concepts, as shown by the following excerpts: (1) the PNV concept 'has been formulated more in terms of a hypothesis than a prediction; it has never been intended to be a prophecy of what vegetation would be certain to establish in the absence or removal of human impact' (Loidi *et al.*, 2010); (2) PNV represents 'the plant community that "would become established if all successional sequences were completed without interference by man under the present climatic and edaphic conditions (including those created by man)"' (Farris *et al.*, 2010); or (3) PNV is defined as 'steady plant community which should be present in an area, as a consequence of the progressive succession, if there were not human influences. In practise, potential vegetation is considered synonymous to climax and to primitive vegetation (not altered yet by humans)' (Rivas-Martínez *et al.*, 2002a). So, which interpretation should we select, if any, and on what grounds?

Loidi *et al.* (2010) and Farris *et al.* (2010) defend their methodology by attempting to discredit the results presented by Carrión & Fernández (2009) as only reviving an obsolete debate. This is hardly a robust approach to tackling a long-standing problem. The powerful quantitative tool provided by palynology can no longer be ignored on grounds of inconvenience. Loidi *et al.* (2010) argue that insurmountable difficulties exist with the use of pollen analysis, even though there are important experimental-taphonomical models that already deal with their objections (e.g. Jackson *et al.*, 1995). For instance, by using high precision dating techniques, palynology is able to develop scenarios with a well-defined temporal component. This contrasts with the definition of a succession as 'if human pressure were to be removed now, it would take a long time for a potential natural forest to grow' (Loidi *et al.*, 2010). This clearly raises problems. How much time is a long time? How long does it take to reach one of these 'steady plant communities'? How long is a 'long period of succession' *sensu* Farris *et al.* (2010)? Are we talking years, decades, centuries, millennia or millions of years? The adoption of the term 'vegetation series or sigmetum' and the use of the expression 'ecologically homogeneous units', do not provide an answer to these questions, and they denote an insistence in detecting indicator species only. In doing so it is forgotten that phytosociological associations are simply human constructs (the realm of qualitative biogeography) and not habitats (the realm of quantitative ecology).

The question must remain, where do 'natural' and 'semi-natural' fit in the phytosociological paradigm? How are they distinguished empirically and how are anthropogenic, artificial or non-natural variables identified? Here, I propose that 'natural' means free from the effects of human interference/influence and if this is accepted, the naturalness of a vegetation type could only be assessed through a long temporal perspective.

I contend that it is groundless to maintain that '*Quercus* and *Fagus* forests have been used as PNV types, as they are among the most competitive trees of the modern native dendroflora' (Loidi *et al.*, 2010). How do they firstly define and then observe competition, and under what biotic and abiotic circumstances? The greater competitive power of other species, including pines could be argued with conviction (Blanco *et al.*, 1997). Research on succession has shown that present differences in the structure and composition of vegetation communities are often the result of past exploitation and such exploitation may be spatially irregular (Pardo *et al.*, 2004). If we do wish to generalize, then perhaps the only factor that is obvious is that *Fagus* and *Quercus* are very demanding of soil depth, but the problem arises that most deep soils in the Mediterranean region today have been degraded or are under agriculture or have been urbanized. Furthermore, it is well documented that the holm oak (*Quercus ilex/rotundifolia*) is the most widespread species in some Mediterranean ecosystems because it is best adapted to human activity such as the use of wood for firewood and charcoal, the ability to regenerate after cropping, and the provision of acorns for animal food (Valbuena-Carabaña *et al.*, 2009). In this case the question must be asked, why do Loidi *et al.* (2010) suggest that the majority of modern pine woods are 'secondary' forests? And, if this is the case, why do they not present any background information to support their contention? In contrast, the palaeobotanical data from the Iberian Peninsula indicates that pines were widespread during the Late Pleistocene and Holocene and can be resilient within a succession (Carrión *et al.*, 2010).

Differing perspectives exist within the phytosociological school but have been ignored. For example, Pérez Latorre *et al.* (2004) proposed that PNV ought to be assigned to the biotope, not the vegetation (species) and that PNV ought to incorporate palaeobiogeographical data. They used such data to explain the present-day occurrence

of formations dominated by *Buxus balearica* and *Maytenus senegalensis* in a region where the PNV had been allocated to *Quercus ilex/rotundifolia*. This suggestion of conceptual adaptation has not even been mentioned in any of the subsequent revisions of the classification system of Iberian vegetation and it is absent in the glossary provided by Rivas-Martínez (2005).

The PNV concept can only become a tenable hypothesis if a general consensus is reached with respect to its meaning and a protocol is agreed in order that it can be tested. My contention is that PNV cannot provide information about changes or trends in vegetation, whether in the past or the future, simply because it is not in its nature. Decorating the PNV concept and its application with methodological novelties in mapping, stressing eventual coincidences with predictive distribution models based on current climate (Loidi *et al.*, 2010), or speculatively searching for parallelisms with the chaotic behaviour of 'strange attractors' (Farris *et al.*, 2010) will not validate the concept.

Niche and community modelling are more promising methods by which to address issues of future vegetation explicitly. Niche modelling for individual species has developed over the last ten years, and can provide a basis for successful correlation with palaeodistribution data (Rodríguez-Sánchez *et al.*, 2010). Modelling large multispecies datasets at community level can also be used as an alternative to the phytosociological 'series' in detecting shared patterns of plant species' responses to environmental change (Ferrier & Guisan, 2006). In order to successfully manage the selection of conservation areas we require that both niche and community modelling should recognize that models for long-term vegetation dynamics cannot be fully deterministic, but should take into account environmental stochasticity, including biotic interactions (Gilman *et al.*, 2010), and that we might need to improve and generalize empirical testing. So the need for temporal series of data is again inescapable.

At this point, it is worth stressing that the static habitat types of the EU Habitats Directive, whilst being a laudable initiative, do not adequately take into account the degree of alteration suffered by our ecosystems or the historical causes of such modifications. They give rise to bizarre situations in which: some shrublands are protected to the detriment of original forests; cultural formations of Fagaceae are protected instead of original pine woods; dehesas (anthropogenic) are taken as remnants of original

forest; and where the interspecific is taken uncritically in preference to the intraspecific diversity of broadly distributed taxa (Valbuena-Carabaña *et al.*, 2009).

Phylogeographical data cannot be neglected. In the Iberian Peninsula, such data coincide with palaeoecological information to show that tree range dynamics are constrained by both deterministic and stochastic processes (e.g. historical contingencies and metacommunity assembly dynamics) acting on different spatial and temporal scales (Rodríguez-Sánchez *et al.*, 2009, 2010), and producing histories that conflict with the phytosociological interpretation for a number of species, such as *Pinus pinaster*, *Pinus pinea*, *Castanea sativa*, *Laurus nobilis* and *Olea europaea*. An outstanding case is provided by Gil *et al.* (2004), who have shown that the English elm (*Ulmus procera*), a variety of the field elm (*Ulmus minor*), is derived from a single clone that the Romans transported from Italy to the Iberian Peninsula, and from there to Britain, for the purpose of supporting and training vines. The English elm was introduced in the calcareous enclaves of the Iberian Peninsula, which are natural areas of its congeners, and in other areas of the siliceous Iberia where it would not constitute a natural element of the riparian vegetation. It must be noted, however, that the phytosociological schemes developed for the siliceous areas consider *Ulmus minor* to be an essential species of the riparian potential forest, and three syntaxonomical associations have been established for the species (Rivas-Martínez *et al.*, 2002b).

It is true that Carrión & Fernández (2009) may have been at fault in linking the phytosociological school to the PNV concept. Nevertheless, it is also important to highlight the fact that the overuse of jargon and complicated terminology is a major problem that confronts the phytosociological approach to vegetation science, and which has confounded non-phytosociologists. Seemingly technical words and terms (e.g. sigmetum, geosigmetum, microgeosigmetum, expleogeosigmetum, fractogeosigmetum, climaci-fractogeosigmetum) have created a smokescreen behind which there lies an impenetrable tangled world.

Paraphrasing Sir Arthur Conan Doyle, 'it is a capital mistake to theorize before one has data. Insensibly one begins to twist facts to suit theories, instead of theories to suit facts'. Faced with the avalanche of new information, perhaps the phytosociologists, like the ecologists before them, will have to learn to live without a general theory.

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REFERENCES

- Blanco, E., Casado, M.A., Costa, M., Escribano, R., García Antón, M., Génova, M., Gómez, A., Gómez, F., Moreno, J.C., Morla, C., Regato, P. & Sainz, H. (1997) *Los bosques ibéricos. Una interpretación geobotánica*. Planeta, Barcelona.
- Carrión, J.S. & Fernández, S. (2009) The survival of the 'natural potential vegetation' concept (or the power of tradition). *Journal of Biogeography*, **36**, 2202–2203.
- Carrión, J.S., Fernández, S., González-Sampérez, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., López-Merino, L., López-Sáez, J.A., Fierro, E. & Burjachs, F. (2010) Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. *Review of Palaeobotany and Palynology*, doi:10.1016/j.revpalbo.2009.12.007.
- Farris, E., Filibeck, G., Marignani, M. & Rosati, L. (2010) The power of potential natural vegetation (and of spatial-temporal scale): a response to Carrión & Fernández (2009). *Journal of Biogeography*, **37**, 2211–2213.
- Ferrier, S. & Guisan, A. (2006) Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, **43**, 393–404.
- Gil, L., Fuentes-Utrilla, P., Soto, A., Cervera, M.T. & Collada, C. (2004) English elm is a 2,000-year-old Roman clone. *Nature*, **431**, 1053.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology and Evolution*, **25**, 325–331.
- Higgins, G.T., Martin, J.R. & Perrin, P.M. (2004) *National survey of native woodland in Ireland*. A report submitted to National Parks & Wildlife Service, Department of the Environment, Heritage & Local Government, Dublin.
- Jackson, S.T., Webb, T., III, Prentice, I.C. & Hansen, J.E. (1995) Exploration and calibration of pollen/vegetation relationships: a PC program for the extended R-value models. *Review of Palaeobotany and Palynology*, **84**, 365–374.
- Loidi, J. (1998) Sobre "Los bosques ibéricos". *Lazaroa*, **19**, 183–188.
- Loidi, J., del Arco, M., Pérez de Paz, P.L., Asensí, A., Díez Garretas, B., Costa, M., Díaz González, T., Fernández-González, F., Izco, J., Penas, A., Rivas-Martínez, S. & Sánchez-Mata, D. (2010) Understanding properly the 'potential natural vegetation' concept. *Journal of Biogeography*, **37**, 2209–2211.
- Pardo, F., Gil, L. & Pardos, A. (2004) Structure and composition of pole-stage stands developed in an ancient wood pasture in central Spain. *Forestry*, **77**, 67–74.
- Pérez Latorre, A., Navas, D., Gavira, O., Caballero, G. & Cabezudo, B. (2004) Vegetación del Parque Natural de las Sierras Tejeda, Almijara y Alhama (Málaga-Granada, España). *Acta Botanica Malacitana*, **29**, 117–190.
- Rivas-Martínez, S. (2005) *Avances en geobotánica. Discurso de Apertura del Curso Académico de la Real Academia Nacional de Farmacia del año 2005*. Available at: <http://www.ucm.es/info/cif/book/ranf2005.pdf>.
- Rivas-Martínez, S., Penas, A., Luengo, M.A. & Rivas-Sáenz, S. (2002a) *Worldwide bioclimatic classification system. Review of definitions*. Available at: <http://www.globallbioclimatics.org/book/review.htm>.
- Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousã, M. & Penas, A. (2002b) Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklist of 2001. *Itinera Geobotánica*, **15**, 5–922.
- Rodríguez-Sánchez, F., Guzmán, B., Valido, A., Vargas, P. & Arroyo, J. (2009) Late Neogene history of the laurel tree (*Laurus L.*, Lauraceae) based on phylogeographical analyses of Mediterranean and Macaronesian populations. *Journal of Biogeography*, **36**, 1270–1281.
- Rodríguez-Sánchez, F., Hampe, A., Jordano, P. & Arroyo, J. (2010) Past tree range dynamics in the Iberian Peninsula inferred through phylogeography and palaeodistribution modelling: a review. *Review of Palaeobotany and Palynology*, doi:10.1016/j.revpalbo.2010.03.008.
- Spribile, T. & Ceska, A. (2001) Book review: Spanish botanists treat North American vegetation. *Botanical Electronic News*, **276**. Available at: <http://www.ou.edu/cas/botany-micro/ben/ben276.html>.
- Valbuena-Carabaña, M., López de Heredia, U., Fuentes-Utrilla, P., González-Doncel, I. & Gil, L. (2009) Historical and recent changes in the Spanish forests: a socio-economic process. *Review of Palaeobotany and Palynology*, doi:10.1016/j.revpalbo.2009.11.003.

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