FORUM
The concept of potential natural vegetation: an epitaph?

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Abstract

We discuss the usefulness of the concept of *Potential Natural Vegetation* (PNV), which describes the expected state of mature vegetation in the absence of human intervention. We argue that it is impossible to model PNV because of (i) the methodological problems associated to its definition and (ii) the issues related to the ecosystems dynamics. We conclude that the approach to characterizing PNV is unrealistic and provides scenarios with limited predictive power. In places with a long-term human history, interpretations of PNV need to be very cautious, and explicit acknowledgement made of the limitations inherent in available data.

Keywords: Mature vegetation; Succession; Vegetation dynamics; Vegetation modelling; Vegetation types.

Introduction

Reconstructions of *Potential Natural Vegetation* (PNV) have been widely used in vegetation survey and restoration, but recent exchanges in the literature have questioned the basic concept adopted to define PNV. Using palynological records, de Nascimento et al. (2009) found that before human settlement, the fo-

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rests in La Laguna, Tenerife, were dominated by *Quercus* and *Carpinus*; two genera that are not currently considered as native to this archipelago. In a provocative commentary, Carrión & Fernández (2009) stated that the findings of de Nascimento et al. (2009) falsify the phytosociological expectation (del-Arco et al. 2006) that the mature vegetation in this area should, in the absence of human interference, be dominated by the *Lauro-Perseetum indicae* or *Monteverde forest* (better known as 'Laurel *forest*'). To support their claim, de Nascimento et al. (2009) reported an increase of Laurel forest species in the last two millennia, when humans exploited the islands and both *Quercus* and *Carpinus* disappeared.

The commentary of Carrión & Fernández (2009) prompted a heated debate about the merits and demerits of the florist–phytosociological approach (see Farris et al. 2010; Loidi et al. 2010) and the validity of the PNV concept. Here, we continue the discussion of Carrión & Fernández (2009) by arguing that PNV can hardly be defined because of (i) methodological problems associated with its definition and (ii) problems related to the ecosystem's dynamics.

PNV and Related Concepts

The idea that a final stage of vegetation exists for any given site dates back to, at least, the concept of *climax* that was introduced in 1885 by Hult (Clements 1936). Controversy surrounded the concept of climax (e.g. Selleck 1960), and eventually it was substituted by the concept of PNV (Tüxen 1956). PNV was intended to express the mature vegetation that would establish given a particular set of environmental constrains, but excluding the effects of humans. Tüxen (1956) defined PNV as the "*hypothetical natural status of vegetation [...] that could be outlined for the present time or for a certain earlier period, by taking away human impact on vegetation.*" Tüxen also stated that, "*imaginable influences of climatic changes that could occur during long-term succession should be avoided.*" To characterize PNV, he suggested that an assumption that the vegetation was in equilibrium with the current

climate conditions was necessary. Later, Westhoff & van der Maarel (1973) defined the PNV as "*the vegetation that would finally develop in a given habitat if all human influences on the site and its immediate surroundings would stop at once and if the terminal stage would be reached at once*."

This concept was later refined. Kowarik (1987) noted that the PNV of a given area could be irreversibly affected by major human interventions, such as the introduction of exotic species or soil removal. In the Czech Republic, the concept of environmentally adapted natural vegetation was developed as a consequence of severe large-scale pollution impacts (Neuhäusl 1984). Following the idea that PNV cannot be identified without taking into account the human effect, Leuschner (1997) introduced the concept of *Potential Site-adapted Vegetation* (PSV), as the vegetation that would finally develop taking into account all "*succession-related changes in soil and nutrient stocks, and in this sense, differs from the PNV. By accounting for succession processes, PSV would represent an extension of the original PNV concept for those sites where soil regeneration is an important process in the context of landscape planning and forest management*" (Ricotta et al. 2002). A related alternative concept to that of PNV, the *Potential Replacement Vegetation* (PRV), was proposed by Chytrý (1998); this represents the abstract and hypothetical vegetation in equilibrium with the climatic and soil factors currently affecting an area, with the external environmental factors, such as air pollution, and with an abstract anthropogenic influence, such as management. Different PRV types are possible in each site depending on the anthropogenic influences (Chytrý 1998). A related concept is that of *Naturalness*. Peterken (1996) defined five types of naturalness, among which both *Potential Naturalness* (e.g. the vegetation that would result if human influences were removed and the resulting succession took place in a single instant) and *Future Naturalness* (i.e. the vegetation that would eventually arise from existing forests if human influence was completely and permanently removed) match the PNV concept. Peterken (1996) acknowledged that future naturalness cannot be predicted, but is likely to be different from the potential naturalness.

Thus, a variety of concepts have been proposed to define the final stages of vegetation dynamics. The possibility of mapping these potential vegetation types has also been discussed for ecosystem management (Zerbe 1998). But are PNV and related concepts, given present knowledge of vegetation dynamics and the needs of conservation planning, really useful?

Methodological Problems Associated to the Definition of PNV

Basically, PNV is a synonym for the final successional stage of vegetation that is identified on the basis of the existing mature stages. Carrión & Fernández (2009) referred to the identification of PNV as an inferential process using the floristic–phytosociological approach. However, this cannot be defined as part of an inferential process because of (at least) three main problems.

The first problem is that most phytosociological data consist of subjective samples of vegetation and, as such, do not allow for generalization about repeatable vegetation units (Chiarucci 2007; Lájer 2007). The vegetation units resulting from this type of survey often represent what is perceived by the surveyor as being 'typical,' 'expected' or 'usual' rather than the units that would be identified using objective and repeatable approaches. Sampling techniques have been much improved in phytosociology and descriptive vegetation science, but subjective aspects (e.g. the use of physiognomic vegetation types for stratifying sampling) are still used and can hardly be avoided (Økland 2007). In other words, it is difficult to reach consensus in recognizing the existing vegetation units, so it must be harder to reach consensus for the characterization of PNV types that lack examples in the real world.

The second problem is the choice of spatial scale in which PNV should be defined. Scale is usually defined in terms of *grain* and *extent*. Vegetation units are typically defined using small grain, such as data coming from plots or relevés, whilst the PNV concept applies at much larger grains, for example in a whole geographical region, and involves extent-related properties. Almost all biodiversity properties are scale-dependent, with species richness being the most investigated (Connor & McCoy 1979; Turner & Tjørve 2005); however, species co-occurrence and species constancies are also considerably affected by spatial scale components (Otypková & Chytrý 2006; Dengler 2009) and this affects the definition of existing and potential vegetation types. In addition, the grain used in data collection for vegetation description has changed over the years: Chytrý & Otýpková (2003) found that the plot size used in phytosociological data collection decreased significantly during the period 1970-2000, but the effects of this on vegetation classification are unclear. Otypková & Chytrý (2006) observed that different vegetation units (based on species composition) are potentially observed in the same area if classification or ordination is performed using different grain sizes.

These studies gave inconsistent results for data collected at different but very close grain sizes (plot sizes were within the same order of magnitude); more significant problems could exist when defining the species composition for potential vegetation types, on larger grain size and extent, on the basis of existing vegetation types described at small grain size.

The third problem is the use of projections of the inferences across space in time. Temporal inferences regarding vegetation succession are based on few data points, since long-term data sets have only existed for the last decades and benchmarks of species composition in pristine vegetation are scarce, at least in Europe. Palaeoecological reconstructions (e.g. Mitchell 2005; Willis & Birks 2006) have revealed huge inconsistencies between the expected vegetation before and after human occupation. The competing theories of the pristine European temperate forest, namely the 'closed forest hypothesis' (e.g. Peterken 1996) and the 'savanna-like landscape hypothesis' (e.g. Vera 2000), have both received support from palaeoecological records (Mitchell 2005). One solution for avoiding the difficulties in characterizing PNV through time is to consider that it should represent the vegetation that would come to existence at once (Westhoff & van der Maarel 1973; Härdtle 1995), but this approach is hardly defensible, since vegetation succession is a process that is intrinsically related to time scale and environmental conditions, which are likely to change with time. As stated by Farris et al. (2010) and Loidi et al. (2010), the PNV is better referred to as a prediction based on the most mature vegetation stage that can currently be observed in a given site. In fact, the proposed vegetation succession is typically based on *space-for-time* substitution, whereby the final successional stages of vegetation in a particular place are identified from vegetation units occurring elsewhere. The use of space-for-time substitution to derive PNV is risky because it is unable to replicate the historical contingencies that determined the size and composition of regional and local species pools. Moreover, a true validation of the inferences is not possible due to lack of appropriate benchmarks for testing and the existence of possible alternative mature, stable states (Beisner et al. 2003; Decocq 2006).

Ecosystems are Dynamic but the PNV Concept is not

In addition to the methodological problems previously discussed, the major conceptual problems in applying PNV to real-world vegetation are due to the ecosystems dynamics. In fact, the PNV concept assumes that one final stage in vegetation succession is reached under stable conditions. However, ecosystems rarely experience stable conditions, and instability is magnified by human action. The biotic or abiotic conditions of apparently repetitive events are rarely the same, and this can make one species dominant in a time window but not in a later replicate. As an example, *Carpinus betulus* L. was one of the dominant species in central European forests during the last (Eemian) interglacial, but it has only a marginal role in the present interglacial (Turner 2002). Heterogeneity and neutral processes should be incorporated in models of long-term vegetation dynamics, with extreme events potentially being determinants for the species success or lack of success. Further to natural variation, ecosystems are altered by millennia of human action. The major drivers of ecosystem processes that make it difficult to use the existing mature vegetation as reference for the final stages of PNV are discussed below, under a perspective that is largely, but not exclusively, European.

Large Mammals

Fauna is one of the drivers of vegetation dynamics that has dramatically changed in the last centuries and millennia, especially because of human action. Large mammals, such as the woolly mammoth (*Mammuthus primigenius* Blumenbach) or the giant deer (*Megaloceros giganteus* Blumenbach), vanished in Europe between 8 and 3.6 ky BP, very likely because of a combination of climatic changes and human hunting pressure (Stuart et al. 2004; Nogués-Bravo et al. 2008). Other large mammals survived up to recent times: the Eurasian bison (*Bison bonasus* L.) was, at the beginning of the 20th century, almost extinct, with few exemplars remaining in the Bialowieza forest, Poland; the auroch (also known as reem or ur; *Bos primigenius* Thomas), a massive wild cow that lived in European deciduous forests vanished about 350 years ago; the tarpan (*Equus ferus* Gmelin), a wild horse, became rare because of hunting and forest destruction during the Middle Ages, with the last captive individuals surviving up to the beginning of the 20th century. Large groups of such animals are shown in Pleistocene cave paintings in southern European countries, and their potential effects on forest regeneration, disturbance dynamics and species dispersal are difficult to assess. The impact of similar animals elsewhere, such as the American bison (*Bison bison* L.), on forest composition, regeneration and structure is known to be major (e.g. Towne et al.

2005; Rosas et al. 2008). Other smaller herbivores have been reduced in population or made extinct, while some others have been introduced, such as fallow deer (*Dama dama L.*) and moufflon (*Ovis musimon L.*).

The mature vegetation that we can observe nowadays, such as ancient forests, largely developed under a different interaction with wild animals than experienced by present-day vegetation. This makes it hard to use the present mature vegetation as a reference point for PNV expectations.

Forest Management

For centuries, management has dramatically impacted the species composition and structure of most European forests: for timber production, water basin protection, hunting, recreation or other uses. It has directly or indirectly favoured the dominance of certain tree species, caused the disappearance of other species and reduced the heterogeneity of natural forests. For example, wood-pastures were a common type of land use in historical times, and are still found in some areas, containing a selection of trees used for animal feeding, such as oaks for acorns. The disturbance regime of trampling and herbivory created safe sites for the establishment of non-forest species, which may persist in the forests developed on these sites (Eriksson 1996). Moreover, some species specifically regenerate in managed forests while others are known to be highly sensitive to even sporadic disturbance and many are favoured or suppressed by coppicing. Early successional divergence has been found after the conversion of coppice-with-standard forest stands into uneven-aged high forest (Decocq et al. 2004), suggesting that the so-called 'true forest species' could rather be coppice-woodland species, developed through centuries of traditional management.

It is extremely hard to assess how centuries of forest management have affected the structure and composition of existing mature forests and if present management will resemble such conditions or not. Several records have shown disagreement between palaeoecological data and present vegetation or provided evidence that the present landscape is largely due to human action. As an example, Andric & Willis (2003) found that the early Holocene vegetation of Slovenia was rather uniformly, dominated by broadleaf woodlands containing *Corylus*, *Quercus*, *Ulmus* and *Tilia*, with most of the present regional differences becoming evident following human activity between 3000 and 600 yr BP. They concluded that the present-day landscape and the differences among phytogeographical regions were due not only to climatic variation but also to the intensity of prehistoric human activity.

Wildfires and Cultural Fires

The effects of fire on vegetation dynamics are only known for limited spatial and temporal scales. The earliest evidence of human control and use of fire known today dates back as far as $0.8\,My$ BP (Goren-Inbar et al. 2004), but the human capacity to extinguish fire is recent. Consequently, wildfires were likely to be much larger than now, even in historical times, and fire regime is likely to have shifted from natural (less frequent, larger duration and extent) to cultural (more frequent, shorter duration and extent).

The effects of past fire regimes on the present forest structure and composition are largely unknown and it is, consequently, extremely difficult to assess if the present vegetation dynamics, under different fire regimes, could lead to mature forest stages as currently observed.

Soil

Another important and scarcely known factor is soil development and carbon accumulation. The role of soil in controlling pre-human vegetation is hard to assess, especially in the Mediterranean where the millennial history of clear-cutting, burning and grazing have heavily impacted the soils. Examples of ancient forest soils still exist, but it is hard to assess how, in the absence of human disturbance, the process of accumulation of organic matter would affect the geochemical properties of the forest soil, the small-scale heterogeneity of the understorey and the regeneration of several forest species. Dead wood and litter have been collected for centuries in most temperate and Mediterranean areas and, even if the accumulation process is now re-established in some managed or protected areas, the long-term effects on vegetation structure and composition are scarcely known. Atmospheric deposits such as nitrogen and biocides are also likely to impact chemical and biotic properties of soils (e.g. mycorrhizae).

Changes in the soil properties during the last centuries are directly related to the presence of mature vegetation stages, but it is uncertain whether the same processes are involved in the present ecosystems dynamics. For example, in Central Europe, where the concept of PNV was developed, the naturalness of soil conditions that were influencing

vegetation dynamics during the previous centuries has to be questioned. In medieval times only about 10% of the original forest cover remained and most of the landscape was used for agricultural or grazing purposes. Thus, large parts of forests that have been considered natural have developed on former agricultural soils. This type of problem provides a clear idea of how the future mature stages of vegetation could differ significantly from existing ones.

Biological Invasions

Biological invasions cause substantial changes to ecosystems and a growing literature addresses their impacts on succession. Using long-term permanent plot data, Yurkonis et al. (2005) suggested that exotic species reduced the rate of establishment of natives, by saturating germination sites. When an invasive plant species becomes part of a community, long-term changes are expected on both species composition and ecosystem functioning (Strayer et al. 2006). The invaders can cause resources to be no longer available to native species, and can alter abiotic characteristics of the ecosystem, as is common with *Robinia pseudoacacia* L. in Europe or various legume trees in tropical savannahs. Biogeochemical cycles, water availability and soil properties may change, which in turn modify the species composition of the plant communities. By imposing new environmental filters, such an invader may become an ecosystem engineer, and dramatically alter the course of the potential mature stage of succession.

Pests and diseases are also able to durably alter the species composition of plant communities. Even if biological invasions are often recognized as a side effect of globalization, they might have played a significant role in controlling successional pathways far into the past. Palynological records show that an extension of *Fagus grandifolia* Ehrh., *Acer saccharum* Marshall, *Quercus* and *Ulmus* in NE America followed the mid-Holocene decline of the canopy-dominant *Tsuga canadensis* (L.) Carriére (ca. 4700 yr BP) due to a pathogenic outbreak. *T. canadensis* took about 2000 yr to recover and, in this time-window, the species-poor conifer forest was replaced, as mature stage, by a species-rich deciduous forest (Fuller 1998). The recent Dutch elm disease has annihilated a large proportion of the dominant *Ulmus* species of late-successional alluvial forests in Europe (*Querco-Ulmetum* forests) and in North America (*Ulmus americana* L. forests), causing a shift in the canopy species.

The above examples provide evidence of how biological invasions can alter the expected vegetation dynamics in an unpredictable way, making it almost impossible to include them in a PNV expectation.

Concluding Remarks

The PNV concept is plagued with problems. The idea that PNV can be characterized by reference to existing mature vegetation ignores that vegetation is dynamic and may continuously change into non-analogue assemblages of species. The PNV is a static concept and thus it completely overlooks biological uncertainties and natural temporal variability. Models for long-term vegetation dynamics cannot be fully deterministic because of the existence of environmental heterogeneity and random neutral processes (e.g. Keith et al. 2008). Modelling long-term vegetation dynamics requires complex simulations where demographic, ecophysiological and ecological factors are combined (e.g. Thuiller et al. 2008; Brook et al. 2009). In places with long-term human history, models assuming equilibrium of plant species with current climate conditions are more difficult and prone to errors (Baselga & Araújo 2010); in such cases, the PNV expectations need to be very cautious and acknowledge explicitly the limitations inherent in the data.

A change of paradigm is required to move from a static and unrealistic concept of PNV to a dynamic and more useful concept of vegetation. A starting point is to model individual species distributions and investigate potential associations that might emerge when environmental conditions change. The dominance, or distribution of single species, or the forest structure can be modelled with some accuracy using existing tools (e.g. Nonaka & Spies 2005), but modelling the composition of vegetation has been shown to be a difficult endeavour (Baselga & Araújo 2010). Unless new research demonstrates the potential uses of the PNV and the circumstances in which its predictions are accurate, we propose that the concept should be abandoned.

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