The relevance of the concept of potential natural vegetation in the Anthropocene

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Abstract

Background: The concept of potential natural vegetation (PNV) embodies mature vegetation capable to survive under the environmental conditions of a site. Despite its widespread use, its applicability under the current level of human impacts on the environment has been criticised.

Aims: We re-examine the original publication of the PNV concept and its development over time to identify the sources of tension between theory and application and to direct the discourse onto a common ground of understanding. Our focus is the relationship between human impacts and PNV.

Arguments: Based on extended excerpts and detailed interpretation, we affirm that PNV applies to a specific point in time. Consequently, it is independent of any realised vegetation including past undisturbed (pre-human) vegetation. We track possible routes and reasons for alternative interpretations. We identify PNV as a mental concept, a neutral model, that represents baseline vegetation potential that excludes contemporary human management but includes past environment modifying impacts. We address how a concept reflecting unmanaged vegetation can be important for application in a world transformed by humans.

Conclusions: Rather than abandoning the concept, we advocate adhering to using it in the original sense of its definition. This way PNV can serve research as a neutral model and support sustainable land use planning.

Keywords: anthropogenic biomes, climate change, multiple potential natural vegetation (MPNV), natural vegetation, neutral model, reconstructed vegetation map

Introduction

Vegetation maps are always models in the broad sense, whether they are produced directly as a human interpretation of observed patterns in the field, via interpretation of remote sensing or through a computer model (e.g. Pedrotti 2004). Typically, vegetation maps are expected to provide a representation of actual vegetation. Maps of potential natural vegetation (PNV), on the other hand, are models of hypothetical vegetation that prevailing environmental conditions would allow to exist at a given time. The production of PNV maps has a long tradition (e.g., Tüxen 1956; Bohn 1981; Neuhäuslová et al. 2001; Fischer et al. 2019; Peng et al. 2019; Ochs et al. 2020) and PNV maps have been employed for a wide range of purposes such as landscape evaluation, identifying revegetation targets, defining seed transfer zones (e.g. listed in Somodi et al. 2017 and Hengl et al. 2018; demonstrated in Török et al. 2018 and Cevallos et al. 2020). However, the concept of PNV has been subject to criticism recently (e.g., Chiarucci et al. 2010; Birks 2019). While most works on PNV maps have followed the original concept defined by Tüxen (1956), some authors have been using it differently. This has resulted in attributing a meaning to the PNV term without reference to a definition (e.g. Cha 1997) or usage of the term, while referring to a similar, but not identical term, as definition (e.g. Notaro 2008; Levavasseur et al. 2012). Other authors have used PNV even more broadly, applying it to encompass the potential distribution of individual species, primary productivity and biomes (e.g., Hengl et al. 2018). However, as the concept of PNV possesses a precise definition by Tüxen (1956) any new alternative related concept would require to have its own definition and name to distinguish it from PNV. Adherence to the definition of PNV by Tüxen (1956), would make many of the concerns raised about the use of the concept irrelevant. In this paper we revisit the original German language publication by Tüxen (1956) to provide a conceptually precise English definition and explanation of PNV.

While PNV has been applied in global (e.g., Levavasseur 2012; Hengl et al. 2018) and

regional scale studies (Hickler et al. 2012; Fischer et al. 2019), others have called into question the very meaningfulness of the PNV concept (e.g., Chiarucci et al. 2010; Birks 2019). The divergence of views is particularly strong in respect to applying the concept to a world co-shaped by nature and humans in the Anthropocene (Crutzen 2002, 2006). The latest example of a critique of the PNV concept with an emphasis on the role of human impact on vegetation is that by Birks (2019, p. 280-281), which specifically motivated us to revisit the original concept and to outline a clear framework for its appropriate application.

Many aspects of the critique levelled by Birks (2019) represent common contemporary concerns related to the impacts of human activities on the biosphere. Thus, addressing the concerns raised by Birks (2019) offers a starting point for addressing the issue of PNV and its relevance in the Anthropocene. To identify the roots of divergent interpretations of PNV and the resulting ramifications in its application, as well as to create a common ground of understanding, we revisit the original definition by Tüxen (1956). We present a full interpretation of the text to clarify the original starting point for the concept, and allay concerns that we perceive have derived from a subsequent 'drift' in the way it has been used.

As the main points of criticism concern the relationship between human impacts and PNV (Carrión and Fernandez 2009; Chiarucci et al. 2010; Birks 2019), we closely examine:

- how past and present human impact on the environment has been represented in PNV;

- the interpretation of PNV as a mental construct (i.e., a conceptual model); and

- what benefits the use of PNV as a model offers.

In order to establish a common understanding between those who apply the concept in their research and those who reject / criticise it, we place particular emphasis on:

- a thorough introduction of Tüxen's original article and the definition of PNV in it; and

- reconstructing the process of how the interpretation of PNV with regard to the human

  factor diverged from the original definition.

We aim to bring users and critics to a common understanding by demonstrating why and how

misinterpretations have emerged.

1. Past and present human impact on the biotic and abiotic environment and its representation in PNV

Whether PNV is equal to pre-human vegetation (a state of vegetation in the past, not affected

by agriculture and other human land use) is a contentious point that has emerged periodically

in the literature. This understanding does not originate from Tüxen (1956) but prevails (e.g.

Carrión and Fernandez 2009; Sylvester et al. 2014; Birks 2019) despite clarifications based on

Tüxen's work (e.g., Härdtle 1995; Moravec 1998). In the following, we present a careful re-

examination of Tüxen's position on the issue and identify sources of the subsequent

development of interpreting PNV.

1.1. Translations of Tüxen

Most contemporary scholars access information on the definition of PNV through English

translations of one short excerpt from the original paper by Tüxen (1956) and do not consult

subsequent foundational German language papers on PNV either (e.g., Trautmann 1966,

Neuhäusl 1975, Kowarik 1987; Leuschner 1997). German has been replaced by English in

scientific communication since PNV was defined, even German-speaking researchers have to

provide today translations in their contemporary publications. Furthermore, the style of

scientific communication in German in Tüxen's time was far less concise than today's

English language communication. Therefore, selecting a short excerpt from the German text

can lead to inconsistent and incomplete view of what PNV is according to Tüxen and the

researchers who have followed his school of thought in applying the concept. In the absence

of an authoritative, peer-reviewed translation of the original article, here we present a

collection of translated sections to provide a complete and contradiction-free picture of

Tüxen's definition, which is based on the full paper.

The following excerpt from the original manuscript is the one that typically emerges in

the literature with different translations (Tüxen 1956, p. 5):

> "ein gedachter natürlicher Zustand der Vegetation […], der sich heute oder für einen
> bestimmten früheren Zeitabschnitt entwerfen lässt, wenn die menschliche Wirkung auf
> die Vegetation unter den heute vorhandenen oder zu jenen Zeiten vorhandenen
> gewesenen übrigen Lebensbedingungen beseitigt und die natürliche Vegetation, um
> denkbare Wirkungen inzwischen sich vollziehender Klima-Änderungen und ihrer Folgen
> auszuschliessen, sozusagen schlagartig in das neue Gleichgewicht eingeschaltet gedacht
> würde."

Following as much as possible the German wording a conceptually precise translation would

read as:

> 'a hypothetical natural state of vegetation [...] which can be drawn for today or for given
> previous time periods with the human impact on vegetation under the environmental
> conditions in the target period (present or previous, respectively) removed. For this
> hypothetical state, natural vegetation is assessed as if appearing in this new equilibrium
> quasi promptly, excluding possible climate changes and their effects that could occur in
> the meantime'

The above excerpt stresses that:

(1) PNV explicitly refers to a definite point in time, i.e., today's PNV is likely to be

    different from the PNV of any point in time in the past (Figure 1, 'original Tüxenian

    PNV' column).

(2) While contemporary human management of vegetation is disregarded when estimating

    PNV, past lasting human impact on abiotic environmental factors that may constrain

    vegetation is accounted for (Figure 1, 'active human management' and 'environmental

conditions' columns respectively). In other words, abiotic environment-shaping human

impact is regarded as part of the forces that have formed the environment by the given

point in time.

In the words of Tüxen (1956, p. 6):

"Der Unterschied zwischen einer früheren und der heutigen potentiellen natürlichen

Vegetation zeigt sich am eindringlichsten an Pflanzengesellschaften, die sich heute nach

dem Aufhören des menschlichen Einflusses auf irreversibel veränderten Standorten

einstellen würden, wie sie in altbesiedelten Gebieten in großer Ausdehnung vorkommen."

'The difference between past and contemporary potential natural vegetation is most

vividly demonstrated by vegetation types that would appear today after the cessation of

human influences at irreversibly altered sites, which are common in regions that have

been populated for a long time.' (translation by the authors)

Thus, Tüxen stresses the distinction between past and current PNV. He also clearly

distinguished transient human influence, the effect of which disappears after human action

ceases and persistent anthropogenic alterations to the environment. The first type of impacts is

disregarded in modelling PNV, whereas long-term impacts on abiotic conditions are

accounted for as part of the environment to which PNV refers to (Figure 1, 'environmental

conditions' column).

Tüxen (1956, p. 9) further elaborates on the difference between past and contemporary

PNV:

"Uns scheint es wichtiger, das heutige Potential der natürlichen Wuchskräfte unter den

tatsächlich vorhandenen Standortseigenschaften […], so zuverlässig wie möglich zu

erkennen, auch wenn diese durch vergangene menschliche Wirkungen geschaffen wurden

und dadurch von den früheren vorhandenen natürlichen abweichen."

'We consider it more important to recognise the contemporary potential for natural

vegetation growth under current environmental conditions as reliably as possible even if

these [environmental conditions] have resulted from past human impacts and therefore
differ from the natural conditions formerly present.' (translation by the authors)

In between the cited sections, Tüxen (1956, p. 6–7) also gives a long list of examples where
pre-human vegetation differed from the PNV in Tüxen's time, because the abiotic
environment had been altered by humans or natural processes such as (i) aggradation of soils
by adding long-lasting manure and topsoil, (ii) degradation by the formation of podzols and
hardpans, (iii) alterations of the groundwater table. Today, we would definitely add recent
climate change to the list. These examples show that Tüxen accepted both human and natural
forces in shaping the environment for it to be represented in PNV (Figure 1) and did not
intend PNV to be constructed on the basis of conditions of time periods before human
influence. Thus, Tüxen has suggested that contemporary PNV should be assessed under
current conditions, whether or not past human alterations, anthropogenic or natural climate
change have led to it. This interpretation is at odds with the suggestion that PNV should
represent vegetation in the absence of recent climate change (Birks 2019, p. 280). The
difference is likely to be due to relying on the first excerpt of Tüxen's paper (Tüxen 1956, p.
5) and particularly on its last line.

'excluding possible climate changes and their effects that could occur in the meantime'
(translation by the authors)
or
'imaginable influences of climatic changes that could occur during long-term succession
should be avoided' (translation used by Birks 2019)

The key issue is the translation of *beseitigt* as avoided by Birks (2019), whereas reading the
original German indicates that Tüxen meant removed / disregarded. The sentence analysed
here refers to the quasi-instant (*schlagartig*, or abrupt) appearance of the vegetation that the
environment would foster. It refers to the notion that PNV embodies the requirements of
mature vegetation according to the conceptual model by Tüxen and not a succession process.

This conceptual model relates site suitability to potential vegetation (in an analogous manner to species distribution models estimate environmentally suitable areas for the distribution of a species, assuming an equilibrium state between distribution potential and environment) and explicitly excludes any consideration of vegetation succession. Thus, how climate change during the successional process could affect the suitability of a site is not considered. PNV, according to Tüxen's original definition, is the potential vegetation corresponding to the site conditions at the time PNV is estimated for, irrespective of the processes involved.

1.2. Reinterpretation of reconstructive mapping campaigns

As shown in the previous section, a careful reading of Tüxen (1956) clearly shows that PNV does not have to represent any realised vegetation (Figure 1, 'actual vegetation' column), past or present, but should reflect the potential vegetation for the given set of environmental conditions corresponding to a specific period. Why then the PNV concept has become related to past vegetation reconstructions in the literature (e.g., Carrión and Fernández 2009; Chiarucci et al. 2010; Sylvester et al. 2014)? A prominent reason for this is the divergent interpretations that have arisen shortly after the publication of Tüxen's concept. Maps that aimed at reconstructing pre-human or potential natural vegetation were produced in many countries or regions (e.g., Küchler 1964; Scamoni and Grosser 1964; Zólyomi 1967; Mikyška et al. 1968–1972; Faliński 1977; Michalko et al. 1986). However, reconstructed vegetation and PNV maps were not clearly distinguished. For several of the countries, reconstruction of past vegetation without human disturbance, i.e., pre-human vegetation, were carried out (e.g., Zólyomi 1967; Mikyška et al. 1968–1972; Michalko et al. 1986). Some of them were correctly named reconstructed vegetation maps, while others were labelled geobotanic maps or maps of the natural vegetation. Furthermore, some were merely relabelled from 'reconstruction' to 'natural vegetation' as time progressed with only minor modifications in the maps themselves (Hueck 1935–1937 vs. 1943; Zólyomi 1967 vs. 1989). In fact, Tüxen

himself has criticised the use of unspecific terminology of vegetation mapping and particularly the renaming of maps initially prepared as a reconstruction of pre-human vegetation to 'natural vegetation maps' when confronted by critiques. Tüxen (1956) himself was critical about Hueck for using the expression 'natural vegetation map' in at least four different meanings, without further specifying his understanding.

A further confusing aspect was that, even though reconstruction of past vegetation was identified as the main aim, reconstructive mappers of the 1950s and 1960s used a hybrid method. Some conspicuous human impacts (e.g., dyking of rivers) were disregarded (undisturbed floodplains were taken as a basis), however some changes to the abiotic environment (e.g., climate; Moravec 1998) were included in the models. The baseline for reconstruction was the observed distribution of the 'most' natural or 'seemingly' natural vegetation (under the abiotic conditions of their time, i.e., 1960s) rather than information on the vegetation of the past (Moravec 1998). Although many authors have clearly indicated that their objective was a map of reconstructed vegetation and the difference from mapping PNV (Neuhäusl 1975; Chytrý 2012), reconstructed vegetation maps were often viewed and referenced as potential natural vegetation maps (Bauer 2009; Abraham et al. 2016; Fekete et al. 2016). The similarities in the approaches in both cases, i.e., expert estimation of natural vegetation across areas of natural and anthropogenic land cover equally could have led to this understanding. The influence of the work by Moravec (1998) might also have been considerable by providing an important and detailed overview of central European PNV mappings in English. In his overview, he interpreted reconstructive vegetation mapping as effectively yielding PNV maps. This was reinforced by Bohn and Neuhäusl (2000/2003), who, for the lack of complete coverage of one or the other type, merged PNV and reconstructed vegetation maps to create the Natural Vegetation Map of Europe.

Clearly, the reconstructed maps of the 1950s and 1960s were not potential vegetation maps in the Tüxenian sense (Kalkhoven and Van der Werf 1988; Härdtle 1995; Chytrý 2012) as parts of changes to the abiotic environment since any possible time period hosting pre-human vegetation were disregarded. It is also true that because they were estimated from actual vegetation and not from historical/paleoecological sources, they were likely to be imprecise as reconstructions too (Moravec 1998). They could perhaps be best interpreted as maps of potentially restorable vegetation, assuming that major human alterations to the physical environment could, and would, also be reverted. The interpretation of early hybrid vegetation reconstruction maps as PNV maps (often against their authors' intention, e.g., Abraham et al. 2016; Fekete et al. 2016; Moravec 1998) probably has led to the notion that PNV equalled reconstruction of natural vegetation and thus referred to a past epoch with negligible or no human influence (Carrión and Fernández 2009; Chiarucci et al. 2010; Sylvester et al. 2014). It appears that, as a consequence, some authors expect PNV and true reconstructions based on paleoecology to be interchangeable (Carrión and Fernández 2009; Birks 2019). For example, Birks (2019, p. 281) cites Abraham et al. (2016), who have compared their quantitative vegetation reconstruction based on pollen sequences from the Czech Republic with PNV composition from Neuhäuslová et al. (1998). Neuhäuslová et al. (1998, see also Neuhäuslová et al. 2001) have prepared a PNV map as defined by Tüxen (1956) and made clear its distinctiveness from any reconstruction maps of former vegetation (Chytrý 2012). Abraham et al. (2016), on the other hand, reconstructed past vegetation. Thus, in this case two different models are compared and an agreement between the two is not necessary for either of them to be considered valid. Nonetheless, the idea of a comparison between reconstructions and PNV maps is of potential interest for the analysis of differences between current potential vegetation and past vegetation. However, conclusions regarding the

usefulness of PNV (such as "impossible to apply usefully" in Birks 2019, p. 280) cannot be drawn from such comparisons.

2. Consequences of PNV being a conceptual model

Whether modelled using data and algorithms or based on expert opinion, a PNV map does not equate to real-world vegetation cover of any time period, as seen above, thus it is clearly artificial inasmuch it is a model representation of vegetation potential. Not reflecting, and not necessarily coinciding with any realised vegetation has been seen as a drawback by some authors (Chiarucci et al. 2010, Birks 2019). In the following, we explore some advantages of PNV.

2.1. PNV does not depend on the capacity of vegetation development via succession

A prominent false expectation of PNV is that it has to be able to develop by natural succession (Grossmann et al. 1998; Chiarrucci et al. 2010; Birks 2019), despite the fact that Tüxen has repeatedly stressed that PNV is a potential state that is meant to be fitted abruptly (*schlagartig*) to the environment and PNV being a mental construct ('gedacht', 'denkbar', i.e. thinkable, imaginable). Associating PNV with succession may have stemmed from the first English-language interpretation of PNV by Kalkhoven and van der Werf (1988). Although, Kalkhoven and van der Werf (1988, p. 376) have indicated that Tüxen meant that PNV was to mean an immediate equilibrium between potential vegetation and environment, they have also indicated that PNV represented the climax state, which clearly can be interpreted as the end-product of succession.

> "The present-day terminal stage of vegetation succession which would develop under the actual environmental conditions is called, after Tuxen (1956), the potential natural vegetation of today." (Kalkhoven and van der Werf 1988, p. 376)

This is in a stark contrast with what Tüxen (1956) actually wrote about the environment –

vegetation relationship. Tüxen (1956) did not consider vegetation dynamics and the processes

involved. Tüxen's work (1956) focused on site potential and its application to forestry in the

sense it still prevails (e.g., Humphrey et al. 2003) and other land uses – in a way, presenting a

conceptual predictive vegetation map. It is unfortunate that Kalkhoven and van der Werf

(1988), who appear to have understood the concept correctly, provided a definition that

apparently has mislead many.

2.2. Interpretation of natural in the PNV term

Both Birks (2019) and Tüxen (1956) have complained about the inconsistent use of 'natural'

in vegetation science. Although Tüxen (1956) has not defined the term, his article allows to

deduce that he considered natural, within the PNV framework, the vegetation that would be in

equilibrium with the local environment at a given time (Tüxen 1956, p. 5):

> "In manchen Gebieten der Erde, wie im Hochgebirge, in der Arktis, in gewissen
> Tropenländern, in Seen, in Meeren oder an Küsten, ist die heutige reale natürliche
> Vegetation noch natürlich, d. h. im Gleichgewicht mit den abiotischen und biotischen
> Kräften des Standortes"

> 'In a few regions of the Earth, such as in high mountains, in the Arctic, in certain parts of
> the tropics, in lakes, in the seas or at the shores, the contemporary actual vegetation is
> natural, i.e., in equilibrium with the abiotic and biotic forces of the location' (translation
> by the authors)

As ecological theory has progressed since the original publication by Tüxen (1956), thanks to

palynology among other disciplines, it has been recognised that actual vegetation may not

represent an equilibrium with the environment (Svenning and Sandel 2013; Birks 2019), and

therefore may not be a reliable baseline for modelling equilibrium. However, the motivation

underlying PNV estimation for Tüxen and to its modelling today remain the same: to assess

the potential of the environment to sustain a type of vegetation. For the concept, potentiality

and self-sustaining vegetation survival are central, a theoretical equilibrium was considered

because it was believed to represent potentiality at Tüxen's time. Starting from this point,

'natural' in the context of PNV can be understood as vegetation types that can occur

spontaneously and are self-sustainable under the given environmental conditions without

active human management. Therefore, current vegetation that is present without human

management provides a reasonable baseline for PNV. Correctly identifying self-sustaining

vegetation is fundamental to PNV mapping. Knowledge form historical ecology (e.g., Molnár

et al. 2012) and paleoecology (Coffey et al. 2011) can support the identification through the

recognition of long-term vegetation patterns.

Vegetation under ongoing management (Figure 1, 'active human management' and 'actual

vegetation' columns) is clearly not considered natural in the PNV framework. On the other

hand, indirect human impacts such as pollution that affect the environment are widely present

today. They form part of the environmental background conditions (Figure 1, 'environmental

conditions' column) and as such they modify the environment, which, in turn, affects the

potential for a site to support a specific type of vegetation. Therefore, for PNV mapping, the

assessment of contemporary environmental conditions (see Tüxen's definition of PNV at a

given time point) needs to include the overall not management-related human impact that is

present. We believe that the understanding of PNV as self-sustaining vegetation is congruent

with the theory by Tüxen, and it is also compatible with current ecological understanding by

dropping the condition of an equilibrium between environment and vegetation.

2.3. The relevance of PNV in the Anthropocene

One reason, why PNV is pronouncedly distinct from actual vegetation and thus its

conceptual nature stands out is that the Earth's surface has been greatly transformed by

humans. This notion is reflected in the remarks by Birks (2019, p. 281) whereby "the PNV concept should be discontinued and replaced by what Ellis and Ramankutty (2008) describe as »[p]utting people in the map: anthropogenic biomes of the world«". However, this statement misses that actual and potential vegetation are clearly different. Anthropogenic biomes by Ellis and Ramankutty (2008) reflect the actual vegetation and other land cover together. These authors have classified current global land cover into self-sustaining or natural vegetation, transformed vegetation and built environment. Their approach could serve as an analogue to PNV, interpreted as landscape potential for human use, i.e., whether a place is more likely to be used for settlement, agriculture or left for nature and in what proportion. Appropriate models could be built to answer such questions, however, the results would be different from those arrived at by mapping PNV. Tüxen (1956) himself has stressed that PNV is a potential, whether it is estimated for the present, or for an earlier time period, it may well be different from the realised vegetation. Certainly, arriving at projecting the PNV at a point in time can make use of palynological knowledge. If environmental requirements of a vegetation type are identified based on the environmental conditions of an earlier period, when the vegetation type occurred there, this knowledge can be utilised in the estimation of present-day or future PNV as well. Naturally, this is more of a theoretical possibility as information on values of environmental variables in the past are typically not as detailed as that for the present.

Furthermore, it makes PNV even more of an operational concept if we adapt it to the current ecological understanding of stochasticity in vegetation development and thus of the probabilistic element in the identity of vegetation type growing given a specific combination of environmental factors. We agree with critiques (Jackson 2013; also endorsed in Birks 2019, p. 281) that:

"actual vegetation that develops at a site may not resemble a particular PNV ideal, but

could instead represent one of any number of potential outcomes".

The concept of multiple potential natural vegetation (MPNV) proposed by Somodi et al.

(2012, 2017) is an extension of the PNV concept in that direction. It is based on Tüxen's

principles but interprets PNV as the probability distribution of several possible self-sustaining

vegetation types at a location (Figure 1, 'multiple potential natural vegetation (MPNV)'

column). The MPNV of pre-human times with no human disturbance would naturally be

different from the realised vegetation in that only one vegetation type can be realised in a

location. To the contrary, MPNV represents both uncertainty of prediction (i.e., uncertainty in

which vegetation type is potential, such as reflected in the Multiple Scenario Approach to

vegetation reconstruction; Bunting and Middleton 2009), and the stochasticity in the identity

of self-sustaining vegetation in the same environment (c.f. multiple stable states; e.g. Baker

and Walford 1995; Petraitis 2013).

3. Benefits of PNV as a model

The most widespread use of PNV today is modelling potential vegetation distribution both at

the global and regional scales (Reger et al. 2014; Fore and Hill 2017; Hengl et al. 2018;

Fischer et al. 2019; Peng et al. 2019). The applications of PNV principles to generate global

and regional maps rely on modelling the environment - vegetation relationships (Somodi et al.

2012). Thus, PNV maps actually characterise the abiotic environment through the 'eyes' of

the vegetation. PNV assigns the characteristic vegetation type, or distribution of vegetation

types (if MPNV is used) to a location which is/are most likely to persist under those

conditions. This set of formalised relationships allows to model expected vegetation and thus

growing potential and revegetation/remediation possibilities for specific sites (Somodi et al.

2012, Han et al. 2021). Several publications have pointed out the possible uses of PNV (Zerbe

1998; Hengl et al. 2018; Ochs et al. 2020), such as identifying the naturalness of vegetation

stands, setting revegetation targets and assessing the level of land degradation. There are also several examples of using PNV for setting a target of ecological restoration, in the sense of creating an ecosystem on degraded land (Miyawaki et al. 1987; Török et al. 2018).

PNV has important potential for science, because it provides a benchmark (neutral or even null model; Ricotta et al. 2002; Bryn et al. 2013), against which the ecological consequences of land-use can be estimated. A prominent concern by Birks (2019) was that the PNV concept would not be applicable under changing abiotic conditions. Model-based PNV estimation can actually foster the assessment of potential impact of climate change as long as vegetation - environment relationships can be expected to remain constant and vegetation types to remain coherent. Such expectations are more realistic when the comparison is made to assess short-term changes. Particularly, the existence of no-analogue communities from the past warn us that modern vegetation types will not necessarily hold through time (Williams and Jackson 2007, Birks 2019). Non-analogue climates in the twenty-first century are expected to arise primarily in the tropics and subtropics (Williams and Jackson 2007), therefore the application of PNV for climate change impact assessment needs particular attention in those regions. Clearly, emerging knowledge of the extent and timing of the emergence of non-analogue climates triggering non-analogue communities (Veloz et al. 2012) provides valuable guidance on the extent PNV, or predictive vegetation models in general, can be considered reliable in estimating future distribution patterns of today's vegetation types.

Using the assumptions (i.e., future climates will be similar to those of today's, but distributed geographically differently and with vegetation types remaining coherent), it is straightforward to extrapolate the PNV for climate change scenarios. Values of climate and other environmental background variables can be updated to reflect the climate change scenarios and thus model future PNV (Fischer et al. 2019; Peng et al. 2019). It is acknowledged that vegetation response to environmental change is not instantaneous and thus

may lag behind the change in site potential. However, we emphasise again that PNV does not target modelling of the actual vegetation of a given time period (cf. Figure 1, 'actual vegetation' and 'original Tüxenian PNV' columns). If actual vegetation and PNV differ, it may indicate important tensions between suitability and realisation (as in Peng et al. 2019).

Thus, PNV, particularly MPNV, is a potential tool to assess the possible impact of climate change on vegetation at variable spatial scales. Tüxen (1956) has clearly expressed that PNV can refer to any time point in the past. Although, he himself did not mention a possibility of PNV in the future, the same logic that applies to past can be applied to scenarios describing a likely future state of the environment. Thus, PNV allows the assessment of climate change impacts on the vegetation potential at diverse spatial scales. Projected future (M)PNV can help us to identify what kind of possible natural environment to expect around us, and thus formulate plans regarding the conservation and wise use of ecosystem services. Importantly, in addition to climate change, the impacts of any scenarios of environmental change or human modification can be explored projecting PNV, e.g., dam removal as in Ochs et al. (2020).

Conclusions

Examination of the original German text and of subsequent literature confirm that the potential natural vegetation (PNV) concept by Tüxen (1956) is an approach well developed to handle human modifications to the environment and their effects on potential vegetation. Specifically, PNV embodies the vegetation that could survive (but not necessarily develop by succession) under the environmental conditions present at a particular point in space and time without active human management. This way PNV provides a baseline, a neutral model to assess the divergence of the observed vegetation from the theoretically site-adapted. Furthermore, PNV modelled for hypothetical environmental conditions (formulated as scenarios) can also be used for comparing the impacts of environmental changes. Thus, rather

than abandoning the PNV concept we advocate its informed use in the sense described in the

original article.

Disclosure statement

No potential conflict of interest was reported by the authors.

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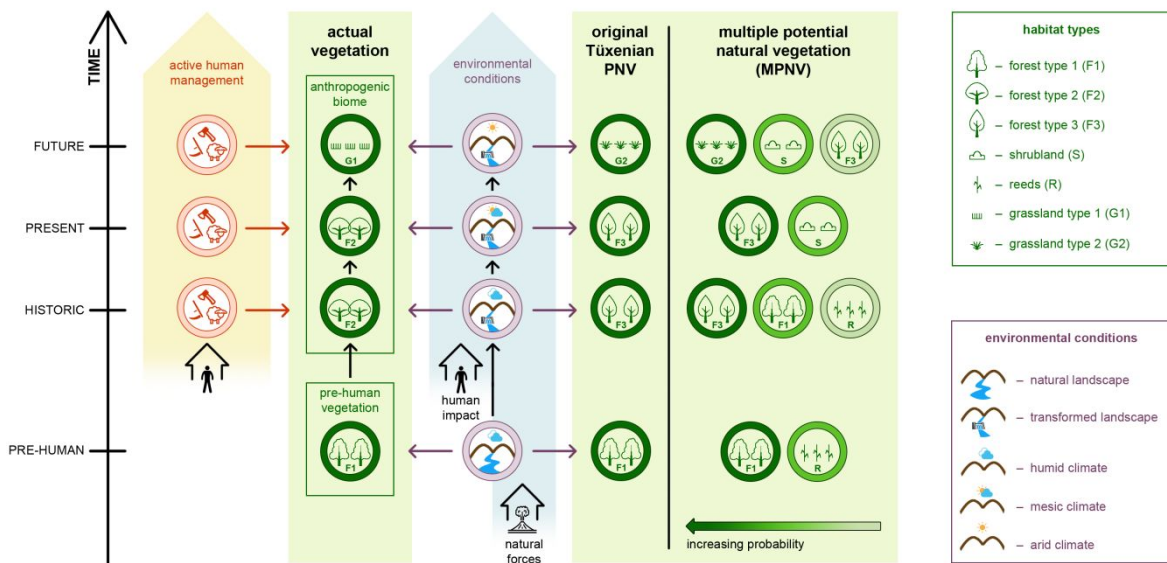
Figures

Figure captions

Figure 1. Conceptual figure demonstrating the relationship between actual and potential vegetation in different time horizons. Two potential vegetation approaches are shown: potential natural vegetation (PNV) corresponding to the original Tüxenian definition (Tüxen, 1956) and multiple potential natural vegetation (MPNV; Somodi et al. 2012, 2017). The contrast of the deterministic nature of the Tüxenian PNV concept and the probability distribution of vegetation in case of the MPNV concept is displayed by the single, 'certain' vegetation (i.e. green circles) vs. multiple vegetation types of different probability levels (i.e. different shades of green). PNV and MPNV are contrasted by actual observable vegetation for characteristic points in time. Actual vegetation is shaped by environmental conditions (wide light blue arrow) and human management (wide yellow arrow; since humans started to affect environment). Environmental conditions themselves are also influenced by humans since historic times.

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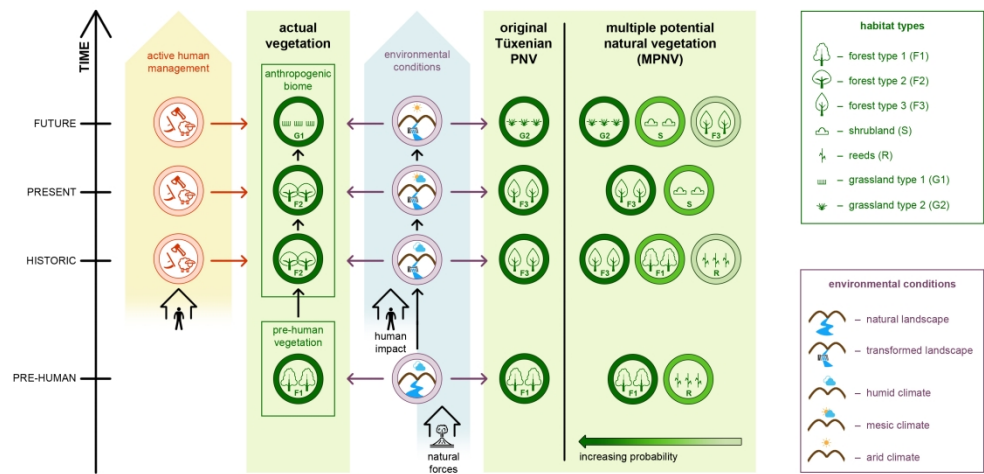51
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