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Bioindication for Ecosystem Regeneration towards Natural conditions: the BERN data base and BERN model

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Abstract

The primary task of the BERN database is to document reference data on typical site parameters for the occurrence of plant communities in which their diagnostic species are in competitive equilibrium with each other and in homeostatic equilibrium with the site factors. Common approaches for the creation of a site-plant database such as ordination or bioindication based on individual species like PROPS or MultiMOVE model are of limited use because it is not possible to determine the potential occurrence of a plant species on the basis of site factors, since the competitive influences cannot be determined in advance according to current knowledge. Therefore, the BERN database takes into account the structure of plant communities with the abundance and dominance of species in the competitive equilibrium of plant communities as a reference for determining anthropogenically induced changes. Qualitative knowledge on the relationship between site types and vegetation communities is widely available, as can be seen from the extensive phytosociological publications. For this purpose, synoptic tables and their location descriptions of around 50,000 relevés were evaluated. The BERN database includes currently 887 central European plant communities and links to their diagnostically defining species composition. The database defines the niche of 2210 central European plant species for the soil properties pH, base saturation, carbon to nitrogen ratio, and wetness index and the climatic properties continentality, length of vegetation period, solar radiation and climatic water balance. The BERN model recombines the realised species niches that mainly form the competitively homeostatic structure of a plant community in order to determine the fundamental multifactorial niche of this community. The BERN database contains mainly historical recordings of more or less undisturbed sites. The BERN model (Bioindication for Ecosystem Regeneration towards Natural conditions) as an application module of the BERN database was developed to integrate ecological cause-effect relationships into studies on environmental status assessment and forecasting. The BERN database now has been published for the first time. The methodology of creating the BERN database and the BERN model are documented and applications are demonstrated with examples. The freely available database should invite you to supplement and modify it.

Keywords BERN database, BERN model, Bioindication, Plant community, Effects of air pollutant inputs on biodiversity, Effects of climate change on biodiversity

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Introduction

Background

Global warming has probably not yet reached its peak at present. Land-use changes have never been as rapid and intense as in recent decades, and a reversal of the trend is not in sight. As a result of soil chemical processes in response to anthropogenic eutrophic and/or acidifying substance inputs in recent decades, a large part of Central European sites is currently characterised by a nutrient ratio that did not exist in Central Europe before 1960. Anthropogenic sulphur and nitrogen emissions peaked in Central Europe between 1975 and 1985 [1].

The consequences have mostly been a decline in the vitality, initially of single individuals, up to the death of populations and ultimately to the loss of the plant community, which has evolved over centuries, and its ecosystem service potential at the site [2–4]. In extreme cases, polyecious species (in fragment communities) remain and derivative communities emerge [5].

A similar development of biodiversity loss is to be expected with further increasing warming and the resulting changes in bioclimatic factors.

At the latest since the signing of the Convention on Biological Diversity and still today, models are being sought [6–8] that describe the response of ecosystems and in particular the response of biodiversity to geochemical and climatic changes.

The loss of diversity of plant species due to anthropogenic influences can only be measured and evaluated in relation to a reference diversity in largely undisturbed habitats. Historical records of vegetation and site factors are of great importance for this. Although such data are available in published form, they have not yet been compiled in a database that is suitable for model-based evaluation.

It is becoming increasingly important to plan and implement measures for vegetation complexes that are important for nature conservation, forestry and agriculture in order to adapt to anthropogenic environmental changes, in addition to measures to combat the causes.

Especially for the development of management plans for areas important for nature conservation and forestry, the question of objectives for the development of vegetation types plays an increasing role. They should have the best possibilities of existence under the site conditions and utilisation to be expected or aimed for in the future. This is associated with a highly competitive stability of the species among themselves as well as full vitality as a prerequisite for the self-regeneration potential. However, a precondition for this is knowledge about the dynamics of vegetation changes as a function of changing site factors.

There are a variety of dynamic models for simulating changes in geophysical and geochemical factors, such as global and regional climate models (e.g., STAR, WETTREG), soil chemical simulation models for changes in the carbon, nitrogen and acid balance, water balance models, etc., the results of which then serve as drivers for biotic models. Coupled soil–plant models that are able to quantify potential interactions of climate change and N deposition on biodiversity are increasingly applied.

Statistical models such as NTM [9], MOVE [10], GBMOVE [11] or a process-based model such as PROPS [12] or MultiMOVE [13] predicts changes in plant species probability of occurrence in response to the changes in water, nutrient and acidity status, using plant species specific information on habitat preferences. Empirical studies of cause-effect relationships are only applicable to a limited extent for regional or even global generalisations, because they are rarely based on long-term studies, only consider a few species and have been collected under site-specific environmental factors or even in the laboratory. On the other hand, they form an indispensable basis for the calibration or validation of deterministic models. Common approaches such as ordination [14] or bioindication based on species [15–18] or ecological species groups [19] are also of limited use. All these models do not take into account the influence of competition among species.

In order to model the actual occurrence of a species, equilibrium points of the dynamic competitive forces would have to be determined [20]. However, there is a lack of sufficient knowledge about the equilibrium points among species [17]. The degree of possibility for the occurrence of a plant community can be determined [21], as this represents the current final solution of a long-term competitive equilibrium between species [22]. Therefore, the BERN database takes into account the structure of plant communities with the abundance and cover rates of species in the competitive equilibrium of homeostatic plant communities as a reference for determining anthropogenically induced changes.

Another difference to all the other models mentioned above is the BERN database with historical recordings at more or less undisturbed sites.

The BERN database now contains so many vegetation relevés that the database can be considered representative at least for Central Europe. Publication now may therefore be helpful for a number of further applications.

Objective

The task of the BERN database is to document reference data on typical site parameters for the occurrence of plant communities. The BERN database contains mainly historical recordings of more or less undisturbed sites. The BERN database takes into account the structure of plant communities with the abundance and dominance of species in the competitive equilibrium of plant communities as a reference for determining anthropogenically induced changes. Qualitative knowledge on the relationship between site types and vegetation communities is widely given in phytosociological publications. For this purpose, synoptic tables and their location descriptions of around 50,000 relevés were evaluated and compiled in a database suitable for model-based evaluation. The BERN database includes currently 887 central European plant communities and links to their diagnostically defining species composition. The database defines the niche of 2210 central European plant species for the soil properties pH, base saturation, carbon to nitrogen ratio, and wetness index and the climatic properties continentality, length of vegetation period, solar radiation and climatic water balance.

To this end, the BERN model combines the species niches that mainly form the structure of a plant community in order to determine the multifactorial niche of a plant community.

The community niche in the sense of BERN is defined as the possibility range for the existence and function of a plant community with all its constant species with respect to one or more environmental factors. The common definition of the term to a habitat that contains all biotic and abiotic environmental factors which are necessary for a particular plant or animal to live functional is not meant here.

The aggregation of species niches into community niches regarding 8 abiotic site parameters is the difference compared to existing dynamic vegetation models (PROPS, MOVE, NTM, VSD-Veg [23]). Some more empirical studies are also focussed on the relation between co-occurring plant combinations and their site parameters [24–26] but with different methods and not comparable results.

The BERN model (Bioindication for Ecosystem Regeneration towards Natural conditions) as an application module of the BERN database was developed to integrate ecological cause-effect relationships into studies on environmental status assessment and forecasting. The application of the BERN model therefore provides recommendations for development goals of sustainably self-organising vegetation types with high resilience.

The resulting recommendations are intended to promote or initialise the development of vegetation types that have a high resilience to site changes and that can develop a high ecosystem service potential, be it for the function as habitat for animal species, for primary biomass production, for carbon storage [4], to name but a few examples.

The BERN database and model has been developed in its original form nearly 20 years ago [34], but the model code and the database have not been publicly available. Since then, the model and database have been further developed and applications have been published (see Sect. 2.2). Finally, we are now able to release the actual database and code (BERN5) to the public under a creative commons licence (https://github.com/bern-model/BERN). This study explains the current status of the theory, material, methods and applications of the BERN5 database and model.

Material and methods

Basic assumptions of the BERN-database

Plant species in a homeostatic ecosystem have adapted to site-specific nutrient supply, water supply and climatic conditions through long-term evolutionary development. Therefore, changes in vegetation composition and structure can serve as indicators of changes in these parameters. They represent the current solution of the interaction between their species and the environment in a dynamic equilibrium.

“Those species that form a stable natural community have evolved in such a way that their species-specific adaptation to ecological niches minimises direct competition with other species in the community" [27]. Plant species that are embedded in a natural plant community can use this reduction in direct competitive pressure to increase their vitality and stress resilience. This increases the ability of plant species populations within a natural vegetation stand to cope with short-term as well as long-term exogenous disturbances [27].

The methodological approach for compiling the databases is based on the following fundamental considerations: According to Tüxen [28]", a plant community is a working society selected in its species association by the site, which as a self-regulating and regenerating structure of action in competition for space, nutrients, water and energy is in a sociological-dynamic equilibrium, in which each acts on all, and which is characterised by the harmony between site and production and all life phenomena and their temporal sequence". This higher level of organisation of a plant community in the interaction with the site factors results in structural and functional properties that cannot be derived from the parts of the ecosystem. Complicated balancing processes within the community lead to a relatively stable equilibrium (“homeostasis”) [22, 29] The plant community “possesses a characteristic core of common plant species, the characteristic combination of species” [29]. Plant communities “indicate certain environmental conditions of the respective site of growth" [29]. The law of relative site constancy results from this realisation [29].

Even if the hypothesis of the plant community in "balanced equilibrium with the abiotic site factors" no longer corresponds without restrictions to the state of the art in vegetation research, since anthropogenic site changes must now be considered manifest, the above-mentioned definitions by Tüxen [28] and Dierschke [29] apply as a basis for some modelling tasks with the BERN model.

The semi-natural and non-natural forest and grassland communities defined in the phytosociological literature cannot be considered to be in equilibrium in Tüxen's sense, but they can at least be considered to be in pseudo-equilibrium. This consideration is based on the theory of the "stepped continuum" in the sense of Dierschke [29], which we follow.

Data basis

The self-organisation potential and thus the adaptive capacity of the vegetation to changing site factors, data is needed in a reference condition. For this purpose, we evaluated the spontaneously occurring plant communities from vegetation relevés that had been recorded at largely unaffected or slightly changed site factors. Very early recordings are of particular interest, preferably those dated before large scale eutrophication and acidification of ecosystems in central Europe. Only a few relevés from the time before the industrialisation wave in the second half of the twentieth century exist with measurement data of abiotic site parameters. And the available measured values from this period originate from non-standardised measurement procedures.

Many natural forests were converted to coniferous plantations as early as 1900. Large scale effects of nutrient and acid deposition starts around 1970 [1], regional effects in the industrial centres start even earlier.

However, all historic literature with old synoptic tables also contain additional verbal data on soil, water and climatic factors at the sites of the relevés. According to their (then) definition, this information could be compared with the databases of reference site types now available and thus, by analogy, site parameters could be assigned to the sites of the communities.

The BERN database serves as the basis for modelling vegetation changes. The BERN database includes plant communities with clearly definable site constancy, which made it necessary to subdivide associations into regional sub-associations. While the ecological niches of communities can overlap widely in the marginal areas (ecotones), the optimum areas should overlap only a little. Generally accessible publications of vegetation surveys in the relevant scientific literature were included. Only aggregated synoptic tables were used, and only if they were accompanied by sufficient information on the site characteristics of the relevé plots. Only those communities of forests, grasslands (including dry and wet heaths, and extensive used meadows), water bodies, bogs and swamps were included in the database that can be preserved in the long term (if necessary, taking into account conservation management, cf. Briemle et al. [31]).

The BERN database has been continuously developed (Table 1). The respective state of development was described (BERN1: Schlutow in Achermann and Bobbink [32]; [33]; BERN2: Schlutow in deVries et al. [34, 35]; BERN3: Schlutow et al. in BMVBS [36], Schlutow et al. in deVries et al. [37], BERN4: Schlutow et al. [38]). The database is now available in version BERN5 and publicly available for non-commercial purposes at https://github.com/bern-model/BERN.

For Germany, the documented synoptic tables and site factors from 45 standard works on plant sociology were evaluated. [17, 19, 39–82]

Outside Germany, further synoptic plant tables were evaluated and the corresponding data from the surveys were transferred to the BERN database. Special attention was paid to vegetation surveys from Europe east and southeast of Germany such as Poland [83, 84], the Czech Republic [85–87], Slovakia [88–91], Hungary [92, 93], Austria [94–97] Switzerland [98]and the Balkans [99, 100].

The standard works cited above of the scientific literature on plant sociology that were evaluated for the creation of the BERN databases always contain, in addition to the synoptic table for a plant community, descriptions of the reference places with regard to the abiotic site factors and lists of the reference places names that were attached to the synoptic table. As of 4/2023, the BERN5 database contains the data sets given in Table 2.

The available synoptic tables which were published under the same community's name, including the same authorship, have been summarized on the basis of the recognized syn-ecological differential species in such a way that it has been possible to differentiate site varieties and micro-climatically conditioned sub-associations or vicariant communities. This approach has

Table 1 Development of the BERN database since 2002

Status	Relevés	Communities	Plant species	Site parameter	Sources
BERN1	5.218	186	720	4	2
BERN2	28.907	285	1.040	5	24
BERN3	40.000	688	1.940	6	30
BERN4	45.157	692	1.970	8	42
BERN5	50.224	886	2.210	8	63

Table 2 Number of records in the BERN5 database as of 4/2023

Stand	BERN5 (2023)
Number of vegetation relevés summarised in synoptic tables (Europe), with description of typical site factors	50224
Of which vegetation relevés of communities occurring in Germany	25602
Number of synoptic tables analysed	1248
Vegetation relevés with site-specific measured values of soil chemistry (Europe-wide)	965
Of which Level II sites in Germany	85
Of which Level II sites in other European countries	600
Of which other vegetation surveys with soil chemistry data in Germany	229
Number of reference soil profiles of the soil overview map 1:1 million of Germany with site-typical measured values of soil chemistry, which were assigned to the plant communities as typical in the BERN database by expert opinion	674
Plant species with species-specific ecological niches for 8 site parameters	2210
Plant communities with derived non-linear ecological niches for 8 site parameters	887

proven to be successful, especially under the aspect that the 8-dimensional community niches from the BERN model should overlap as little as possible in their optimum ranges in order to be able to serve as indicators for site factors.

Due to the fact that most of the synoptic tables dates from before 1960, some of the names of the communities used are unusual today. There are two reasons why the BERN database deviates from the latest internationally agreed nomenclatures. Since old synoptic tables were adapted as far as possible for the natural communities, the reference to the source should also be preserved in the name of the community. Another reason was that in more recent nomenclatures, communities are grouped together but differ in terms of geographic distribution or site preferences. In the BERN database, emphasis was placed on ensuring that the multi-factorial ecological niches of the communities overlapped as little or not at all in their optimum ranges. Therefore, it was necessary to include communities individually in the database with their early published synoptic table, which are now included in another community under a different name. This disadvantage of the BERN database was tried to overcome by adding the EUNIS code. But for the purpose of modelling vegetation development series and species structure in response to changing site factors, this disadvantage could be accepted. The official community´s names according to the Federal Agency for Nature Conservation [101] were added in the Synonyms column, preceded by the statement "included in": where appropriate.

In the BERN database, plant communities with a clearly definable site constancy are included, which made it necessary to subdivide associations into regional subassociations. While the ecological niches of communities can overlap widely in the marginal areas (ecotones), the optimum areas should overlap as little as possible.

The location information on the vegetation relevés taken from the scientific literature was transferred to the geographic information system ArcGIS (Fig. 1) and thus the climate values of the raster data sets of the German Weather Service [102] or the European climate map [103] for the long-term mean 1961–1990 were determined. For the forest communities for which historical relevés were evaluated, the 1951–1980 climate statistics [103] has been used.

Non-local-specific site data, e.g., those that only name a region, were georeferenced only if the named region is smaller than the area of the corresponding climate region type in which the region is located. For each community, there is both local-specific information on the site and information on the region. The site-specific information allows the determination of ranges of climate values. Site regions were located with one coordinate (centroid) in such a way that the point lies within the ranges from the site-specific site data. Some site information was too vague to be located.

In contrast to the climate data, the soil data were not extracted from a soil map on the basis of the locations. The soil type, moisture, substrate and nutrient conditions at the community-typical reference sites were at least specified in the description for each synoptic table. Based on this information, comparable reference soil profiles from the database for the soil overview map 1:1 million of Germany [104], the Eurosoil database [105, 106] and Europe-wide Level II soil profiles [107] could be analogously assigned.

„From the reference profiles of the BÜK1000N and Level II databases, the soil parameter values that are most likely to be encountered at the typical sites of a plant community by analogy can be taken.

A soil chemical parameter value for a reference profile is calculated from the horizontal measured value data by averaging, weighting the respective horizon

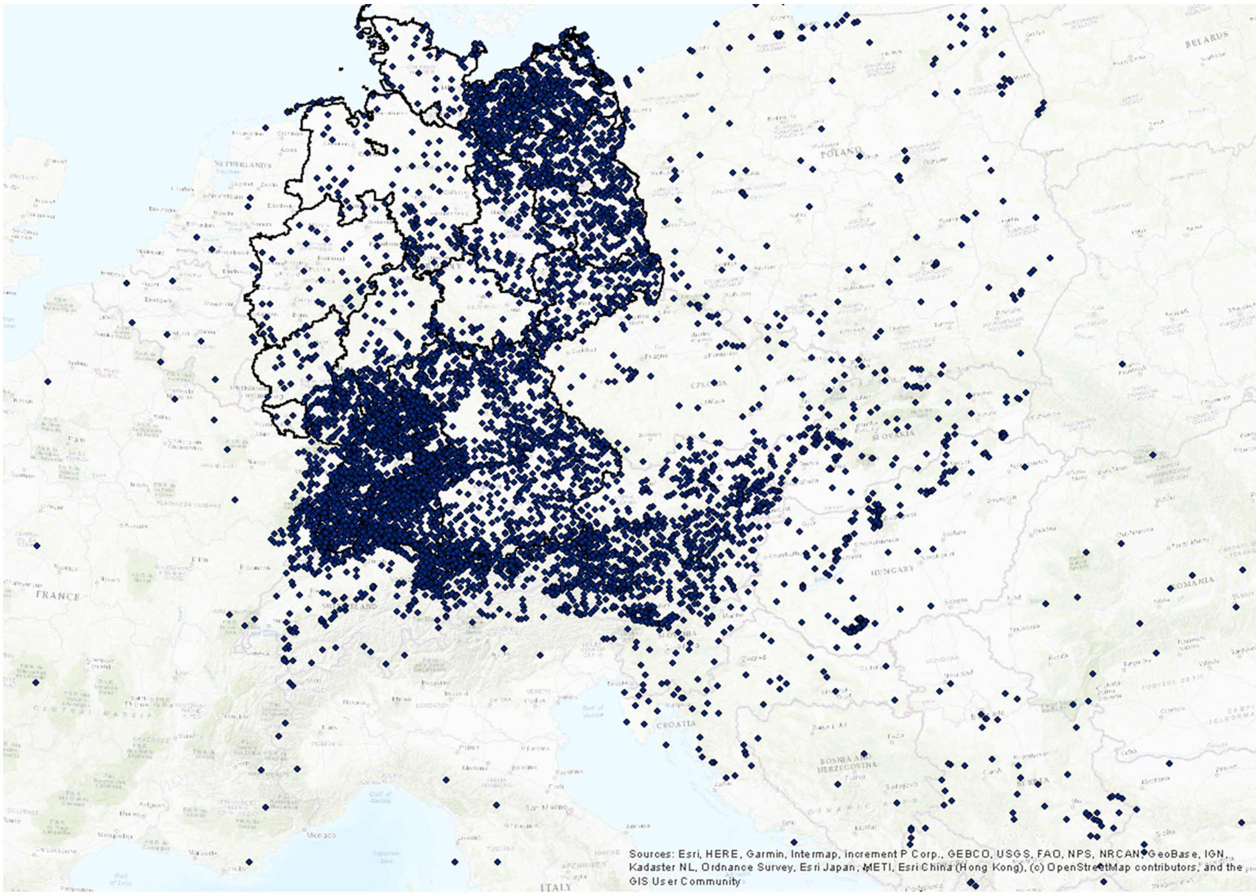

Fig. 1 Distribution of relevés which were evaluated in the BERN5 database (Sources: Authors' own depiction; OpenStreetMap)

thickness. The number of horizons to be considered is determined by the rooting depth of the vegetation. Since plants distribute their main root load over several soil horizons, the respective mean value of most soil parameters of all rooted horizons (weighted according to the horizon thickness) down to the actually rooted depth is of importance. An exception to this is the C/N ratio, which as an average value only from the humus layer + 10 cm mineral topsoil is of importance for the existence of the plants. Thus, different main root lengths of the main tree species(s) or dominant open land species are taken into account when evaluating one and the same profile. For example, to calculate the mean base saturation in the root zone, the horizon values from a forest profile for a pine forest community are included in the averaging up to a depth of 160 cm; for a beech forest community, the base saturation from the same forest profile is averaged only over the horizons up to a depth of 80 cm. For a mixed pine-beech forest, the rooting depth of the deepest rooting mixed tree species (pine) is considered. The average depth rooted by plants is estimated as a function of the potential main root length of the vegetation and the upper depth of a soil horizon that can no longer be rooted. The pH values of the horizons were first de-logarithmized, then averaged, and the result was logarithmized again.

The respective lists of diagnostic plant species are added to the recorded plant communities and their site parameters. That are the species with a high constancy of 70% or more, which were included in the species lists of the plant communities, furthermore the character species if they have a constancy of 40% or more, plus the regional differential species that typically occur in the community, even if not at a high level.

The content of the BERN5 database are the following site factors, which were determined as essential vegetation type-determining parameters and assigned to the plant communities. These parameters form the BERN data basis:

- Soil type, parent material, substrate, humus form.
- Slope inclination [°]
- Exposure [grd:min:sec]

- Wetness Index (Water content at field capacity [m^3 $m.^{-3}$], mean groundwater level, mean backwater stage)
- Base saturation according to Kappen-Adrian [%]
- pH value, measured in $CaCl_2$
- C/N ratio [-]
- Hygric Continentality Index (De Martonne index = precipitation in the vegetation period /mean temperature in the vegetation period + 10)
- Climatic water balance [mm vegetation $month^{-1}$] (precipitation minus evapotranspiration); this parameter is correlated with $R^2 = 1$ with the parameter for humidity (Bowen value = potential evaporation in the vegetation period /precipitation in the vegetation period; this parameter is also correlated with $R^2 = 0.98$ with De Martonne index
- Vegetation period length [d $a.^{-1}$] (mean number of days per year with a daily mean temperature above 10 °C)
- Useful solar radiation [kWh m^{-2} a^{-1})] (sum of light energy in the vegetation period), this parameter includes the temporal course of solar radiation as a function of the angle of incidence according to latitude, the modification of the angle of incidence as a function of slope and exposure, the sunshine probability as an annual average, the overshadowing by overlying vegetation layers as a function of their typical degree of cover in community
- Temperature [°C] from the minimum (frost hardiness) via minimum and maximum of the optimum plateau (start and end of photosynthesis) to the maximum (heat stress).

The parameters soil type, parent material, substrate, humus form, slope, exposure, and temperature are only indirectly included in the BERN database and are not used to determine ecological niches. They are used to derive parameters that are included in the niche determination. The solar radiation can only be determined for the species. The application of the BERN model for the communities is not suitable for this because the species in the forest communities also depend on the cover of higher layers.

The work steps according to which the BERN database was generated are shown in summary form in the following flow chart (Fig. 2). The process of data compilation is explained in more detail in Schlutow [38].

Mathematical method to describe the niche of species and communities

The niche of a species

Plant species adopt to different environmental traits as for instance nutrient supply, acidity, drought and chill. With BERN, we model the potential niche of a plant species as a fuzzy relation between environmental conditions and the plant species occurrence using the "Theory of Possibility" [108]. Optimal conditions for a plant species along an environmental gradient is defined as a range (min/max) where plant growth and reproduction is not hampered by the factor. The upper and lower boundary of the optimum conditions are denoted in the following as x^+_{max}, x^+_{min}, where x is the considered environmental factor. The total range of possible existence is larger (a super set of the optimal conditions) and extends to the pessimum conditions. The plant species should not occur constantly outside of the pessimum conditions. The total range of constant existence is labelled with x^-_{max}, x^-_{min}, accordingly. The existence possibility distribution $\pi(x)$ of the potential niche along an environmental gradient is described with a trapezoid function. In the optimum range, $\pi\left(x^+_{min} > x > x^+_{max}\right) = 1$. Outside the pessimum range the species cannot exist persistent, therefore $\pi\left(x < x^-_{min} \vee x > x^-_{max}\right) = 0$. The rising and falling limbs of the trapezoid function are linear interpolated. For *Luzula luzuloides* (white wood-rush), the potential niches of all traits are shown in Fig. 3:

To calculate the possibility of existence at a site described by multiple traits, the possibilities for the scalar traits are combined using a Fuzzy equivalent of Boolean logic AND operator. The most common Fuzzy AND operator is the minimum of all possibilities and fits together with the traditional minimum Law by Justus Liebig.

$$\pi_{species}(x) = \min(\pi(pH), \pi(BS), \pi(CN)\ldots)$$

The possibility value shows the potential of a species to exist at a site, not the probability in a concurrence- based situation, where bimodal distributions of concurrence weak generalists occur.

The niche of plant communities

A plant community in BERN is defined as group of diagnostic plant species known to grow together constantly at certain environmental conditions. The possibility of a plant community to exist on certain site type is determined by the overlapping possibilities of each constant member species of that community. The theory of possibility differs from frequency related statistics, and is more robust to biased samplings. A classical statistical model is bent to more frequently observed combinations. The possibility value represents the strength of a fuzzy relation between the stie conditions and the occurrence of the community. As a community cannot, per definition, evolve at a site not suitable of one of the constant and therefore defining species, the possibility of the community outside of the overlapping species niches is low.

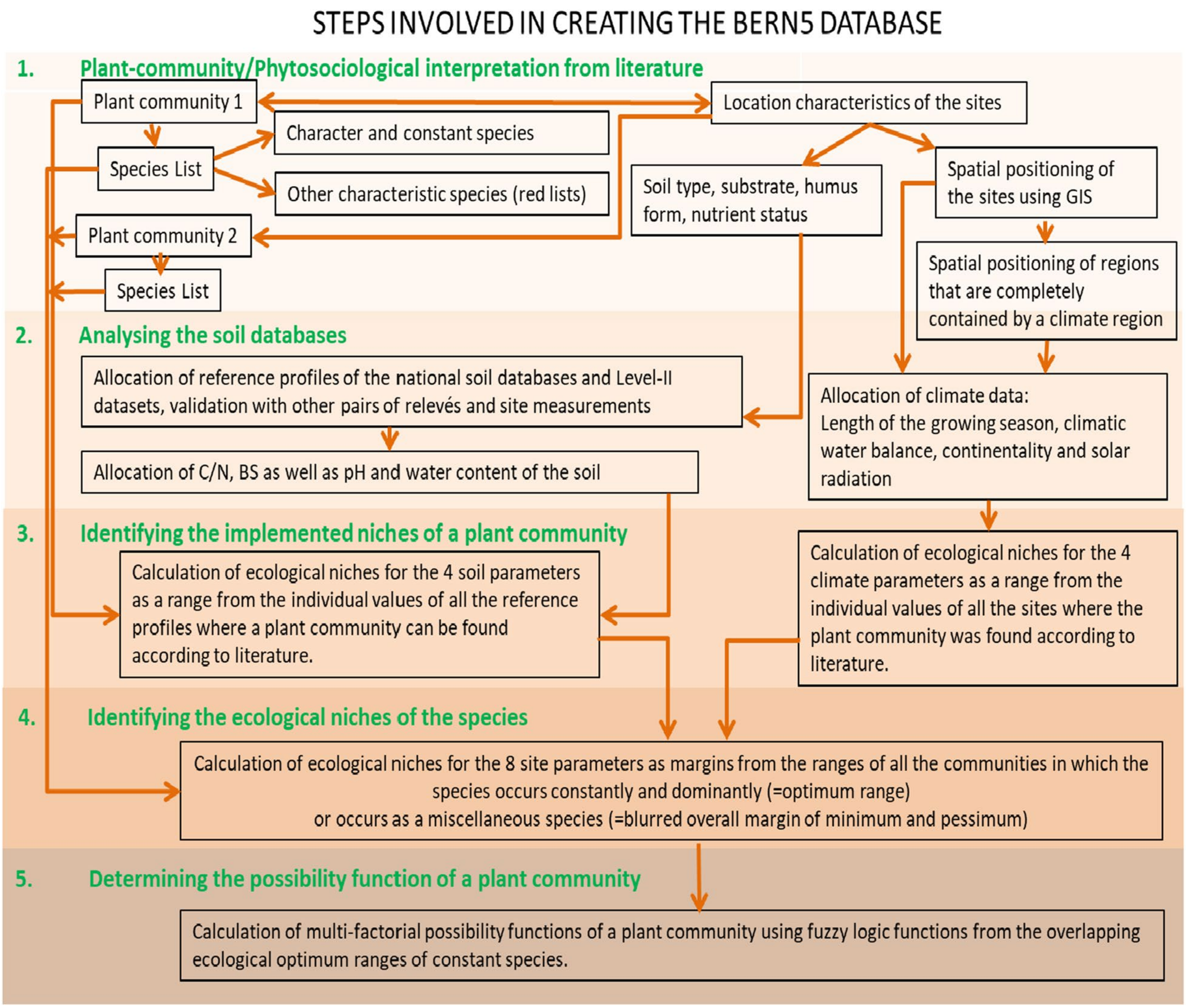

Fig. 2 Flowchart for the generation of the BERN database and the modelling of the possibility function for the existence of plant communities on this basis. (Sources: Authors' own depiction)

It is almost impossible to ever collect all sites of a plant community. But even if this would be possible, there is still no guarantee that this collection of sites would then contain all the site types on which the community could possibly occur. For example, typical sites of a natural deciduous forest community have probably been largely replaced by semi-natural coniferous forests and are therefore no longer identifiable as typical sites of the deciduous forest community. Thus, while the determination of the realized niche of a community only reflects the locational parameters of its already known sites, the range of the community's possibility of existence may go beyond that. Therefore, the possibility function is derived from the occurrence of its constant species with about 70% constancy or more. Since the species mostly occur in several communities, their range of locations is recorded on the basis of many more species-typical sites. Accordingly, their ecological niches determined with the BERN model are broad. Only from the intersection of the ecological niches of their constant species does the possibility function of a plant community emerge approximately.

Because the internal mechanisms of the community can increase the strength of agreement among its members, BERN does not create the overall possibility as the global minimum of all plant species but with a so called γ-Operator from Fuzzy Logic [109]:

$$\pi_{comm}(x) = \left(\prod_{i=1}^{n} \pi(S_i, x)\right)^{\gamma} \cdot \left(1 - \prod_{i=1}^{n} (1 - \pi(S_i, x))\right)^{1-\gamma}$$

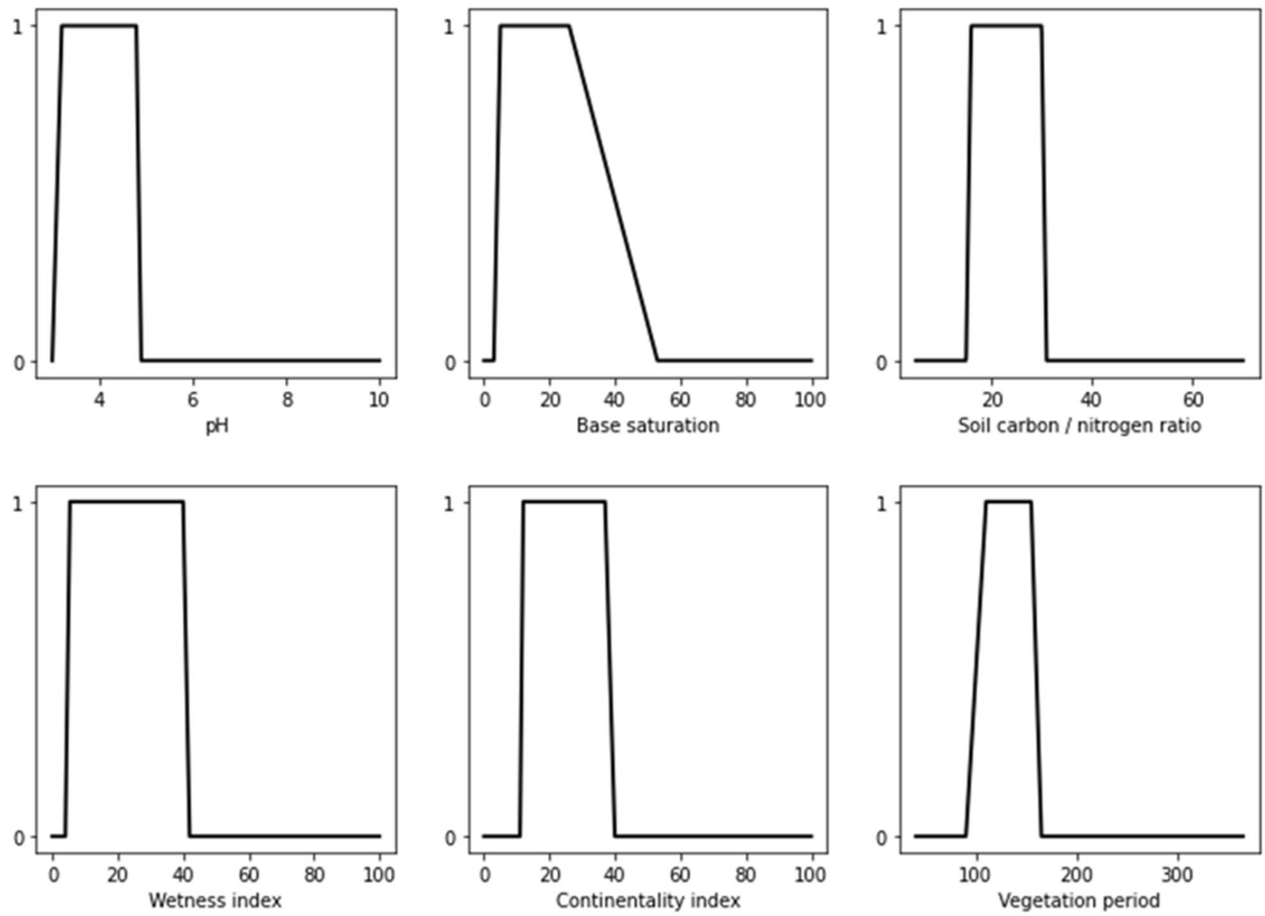

Fig. 3 Potential niches (possibility degree from 0 to 1) of *Luzula luzuloides* for the traits pH, Base saturation, C/N ratio, wetness index, continentality index and length of vegetation period (see explanation in text above) (Source: Authors' own depiction)

– $\pi(S_i, x)$ is the possibility value of species S_i at environmental conditions $\boldsymbol{x} = [\boldsymbol{pH}, \boldsymbol{BS}, \boldsymbol{CN}, \ldots]$
– n is the number of steady species in the community and γ a parameter describing the "community" effect. For the BERN model, we fixed that parameter to 0.2.

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The *Luzulo luzuloides-Fagetum sylvatici caricetosum brizoides* MEUSEL 1937 is a beech forest community adapted to fresh and acidic poor soils and used as an example to show the composition of a community's niche from the potential niches of its constant species. The community is composed by the following highly constant and characteristic species (species ID of the BERN database in parentheses):

– Carex brizoides (3043)
– Fagus sylvatica (123)
– Luzula luzuloides (511)
– Milium effusum (167)
– Polytrichum formosum (174)
– Prenanthes purpurea (445)

Applying the γ-Operator for the species, the niche along the trait pH for the community is shown in Fig. 4.

Exemplary application of the BERN model

Assessment of existence risks in the case of changing site factors

A possible application of the BERN database is shown in the following example. Modelled predictions of developments are determined by the quality of the forecast time series of the drivers. Therefore, the model result from BERN must always be interpreted in the context of the current state of knowledge and requires updating whenever new forecast time series of the input data are made available.

We investigated the impact of acidification, eutrophication and climate change on biodiversity for a intensive

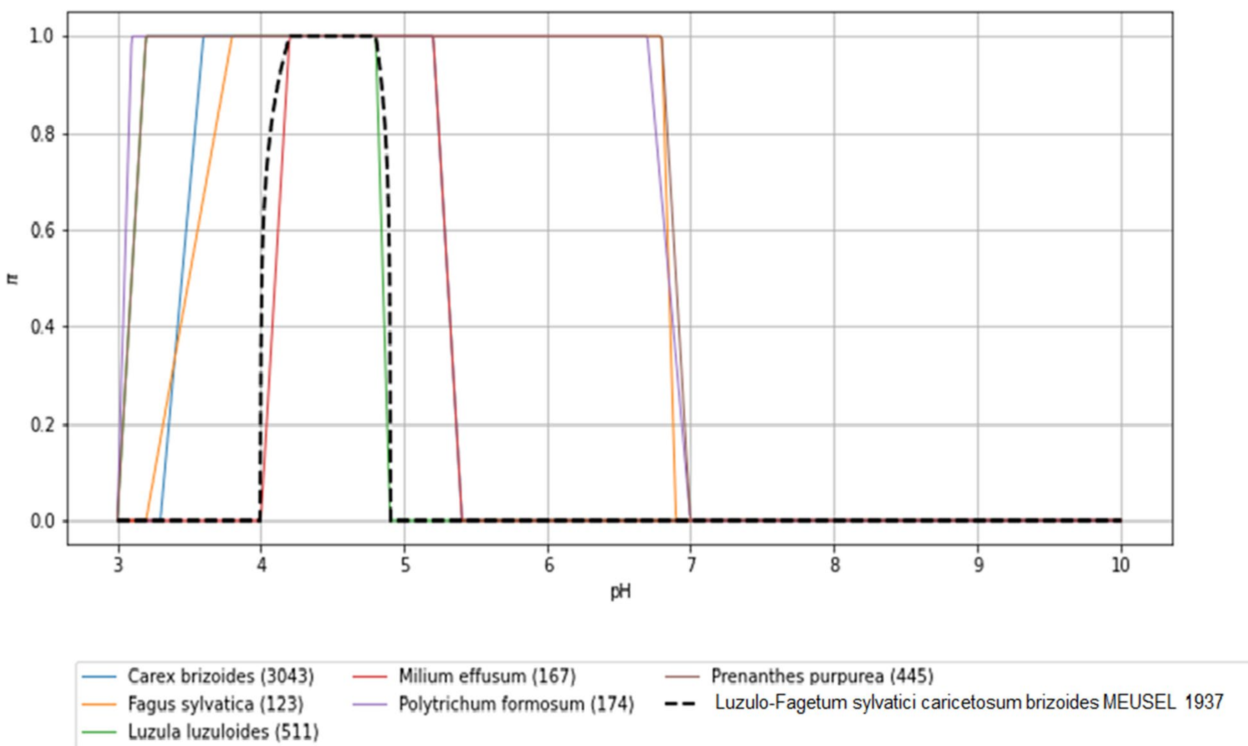

Fig. 4 Resulting possibility distribution of the community *Luzulo luzuloides-Fagetum sylvatici caricetosum brizoides* MEUSEL 1937 over soil pH-Values (Sources: Authors' own depiction)

forest monitoring Level II plot in Brandenburg, (Germany) [110]. As forcing data timeseries of sulphur and nitrogen deposition from year 1880 to year 2000 are taken from EMEP [1]. The deposition data has been scaled to measured deposition data from the Level II plot [111]. The future climate is estimated on the basis of the greenhouse gas scenario RCP 8.5 which assumes only a slight reduction in current greenhouse gas current greenhouse gas emissions. Based on this the mean run of three different global models (ECHAM6, ACCESS models (ECHAM6, ACCESS 1.0 and INM-CM4) as the basis for global climate basis for global climate development, which was then modeled with the STARS II model [112] for the regionalized for the northern German lowlands. The driving data are fed into the geochemical model VSD + [113]. The result of VSD + are timelines of soil pH, base saturation and carbon to nitrogen ratio (C/N). The climatic conditions from the STAR II dataset ranges from 1900 until 2070 under different emission scenarios. As an exemplary application in this study, only the RCP 8.5 scenario has been used.

The resulting timeline from 1900 to 2070 for soil chemical and climatic drivers is shown in Fig. 5.

As a result of the predominantly acidifying effect of the very high S and N input, the pH value decreased from 5.6 to 5.0 and the base saturation from 66 to 48% between 1920 and 1985. The loss of bases through exchange at the soil colloids and their leaching with the percolation water goes hand in hand with the drop in pH and base saturation. The N input caused only a slight increase in the N stock, because the demand of the vegetation is just covered by the input. However, the decrease in C stock caused a decrease in the C/N ratio from 26.5 to 21 in the period 1920 to 1985. From 1985 to 2009, S deposition decreased to 0.31 keq S ha^{-1} a^{-1}, while nitrogen input decreased only to 0.9 keq N ha^{-1} a^{-1} during this period. The modelled pH value rose again significantly to 5.5. The base saturation fell further to 43%, and the C/N ratio fell to 19.6.

From 2010 to 2070, the temperature in the RCP 8.5 scenario will increase from approx. 8.6 °C to approx. 11.8 °C. The seepage rate will then decrease drastically. The S deposition is expected to remain constant at the low level of 2009. It can be assumed that the N deposition will remain stable at about 15 kg N ha^{-1} a^{-1} until 2070. This N deposition scenario results from a trend of further increase in ammonia deposition after 2010 with decreasing NOx inputs. According to this deposition scenario, the C pool will continue to decrease and, accordingly, the C/N ratio will fall further to 16.7.

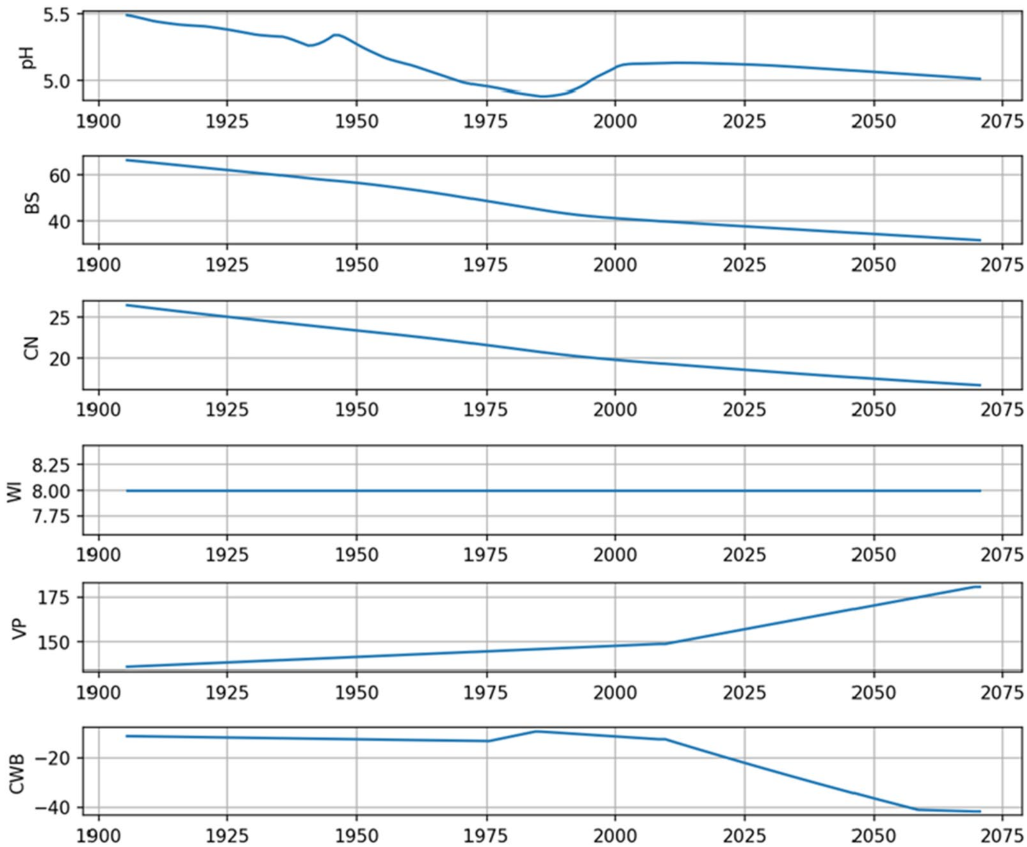

Fig. 5 Climatic and soil chemistry driver variables for the Level II Site (*pH* pH measured in H_2O, *BS* base saturation in %, *CN* C/N ratio in g/g, *WI* Soil Water Index m^3/m^3, *VP* Vegetation Period length in d/a with ≥ 10 °C, *CWB* = Climatic Water Balance in mm/vegetation month) [110]) (Sources: Authors' own depiction based on results from Schlutow et al.

The effect of these drastic change of abiotic habitat properties results in a change of the natural vegetation (Fig. 6).

The selected climatic drivers are from an extreme, yet realistic scenario to demonstrate the ability of BERN to predict impacts of climate change on biodiversity targets. In a full study, we recommend the use of ensemble predictions and uncertainty bands. Using the BERN model and BERN5 dataset, the possibility of population changes for plant communities will be investigated (Table 3).

As the possibility degree of a species, the possibility value of a community shows the potential sites where this community can occur newly. However, it should be noted, that in a changing environment, change from one community to another is often triggered by singular extreme events, like the drought 2018–2021. Hence, established communities may exist outside the modelled niche as a result of different conditions in the past. The BERN model does not predict the timing of change.

Determination of forest conversion targets under predicted climate change

The following application example shows one possibility for using the BERN database to describe forest development trends in relation to (currently!) projected climate change. With this project, development trends are recorded according to the current state of knowledge.

Since the goals of Germany's national sustainability strategy are very closely linked to the concerns of sustainable forest management, forestry and the timber industry are particularly well suited to helping shape the guiding principle of the sustainability strategy.

The already started forest conversion towards site-appropriate vital mixed forests was intensified again in the Free State of Saxony to reduce the negative effects of decreasing vegetation's resistance doe to climate change. The identification of near-natural forest communities for all existing or expected climatic conditions in Saxony

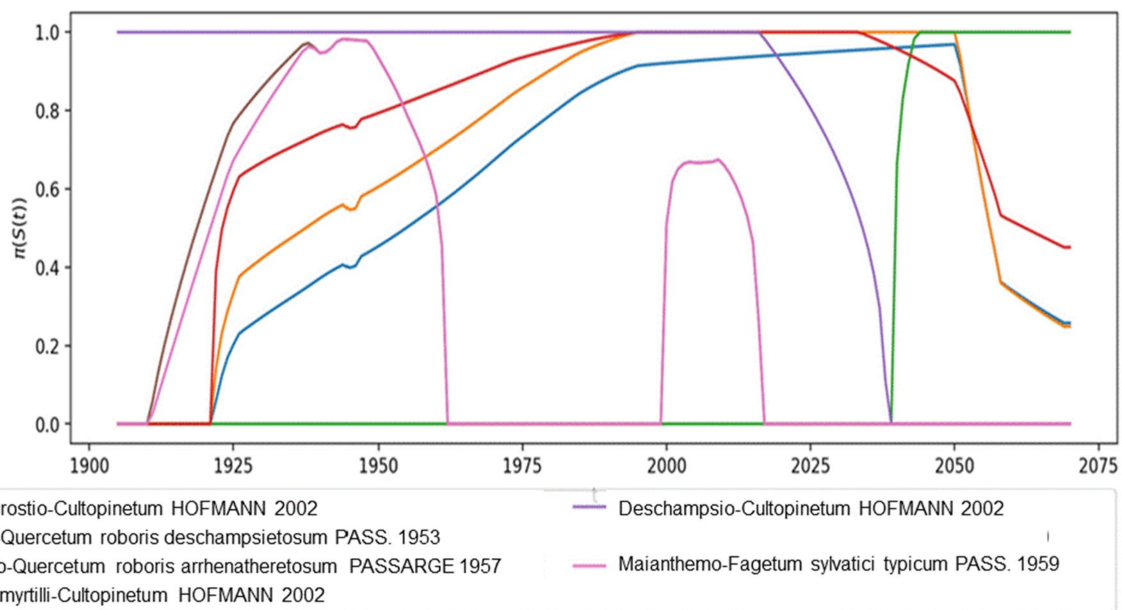

Fig. 6 Results of the BERN modelling of the degree of possibility [π(S(t))] of the forest communities at the Level II plot (Source: Author´s own depiction)

Table 3 Time table of the historic wood, current forest and future potential wood community at the Level II plot

Year	Site properties at the time	forest community
< 1920	Sub-oceanic, moderately dry to fresh, nutrient-poor beech wood	Maianthemo-Fagetum sylvatici typicum PASS. 1959
1950	Sub-oceanic, moderately dry to fresh, nutrient-poor pine forest after reforestation	Vaccinio myrtilli-Cultopinetum HOFMANN 2002
1990	sub-continental, dry, nutrient-poor pine forest resulting from acidifying impacts	Deschampsio-Cultopinetum HOFMANN 2002
2010	sub-continental, dry, vigorous nutritious pine forest resulting from eutrophying impacts	Calamagrostio-Cultopinetum HOFMANN 2002
> 2040	sub-continental, dry, vigorous nutritious wood after natural forest conversion taking climate change into account	Agrostio-Quercetum roboris deschampsietosum PASS. 1953 em. SCHUB. 1995
> 2070	sub-continental, dry, vigorous nutritious wood under progressive global warming	Cynancho-Quercetum roboris arrhenatheretosum PASSARGE 1957

serves as a planning basis [114] (Figs. 7, 8). The influence of air pollutant inputs is not considered in this example.

The determination of the vegetation period length and climatic water balance per vegetation month to the climatic classes and stages in Saxony is derived from the measurement data of the German Weather Service of the period 1991–2020 [115] or from the forecast data according to the RCP 8.5 scenario with the model WEREX VI [116] in a 1 × 1 km^2 raster [114]. A direct coupling to the typical parameter ranges for the plant communities in the BERN5 database is thus easily possible. Daily mean temperature values are included in the calculation of the length of the vegetation period if they were > 10 °C for 5 days in a row.

The Forest Site Map of Saxony at a scale of 1:10,000 [117] is the basis for the regional distribution of the soil forms. For the assignment of the C/N and base saturation value ranges for the plant communities of the BERN5 database to the forest site forms based on the mapped nutrient power level, the scheme from the forest site mapping according to SEA95 [118] is applied.

The 1555 different site types of the Saxon forests are combined with the relief and exposure variants in question (plain, shady and sunny slopes). The 2724 combination types that were created are then combined with the climate classes that currently prevail or are expected to prevail until 2070 according to the forecasts. For these 22,000 actual site combination types in Saxony, the

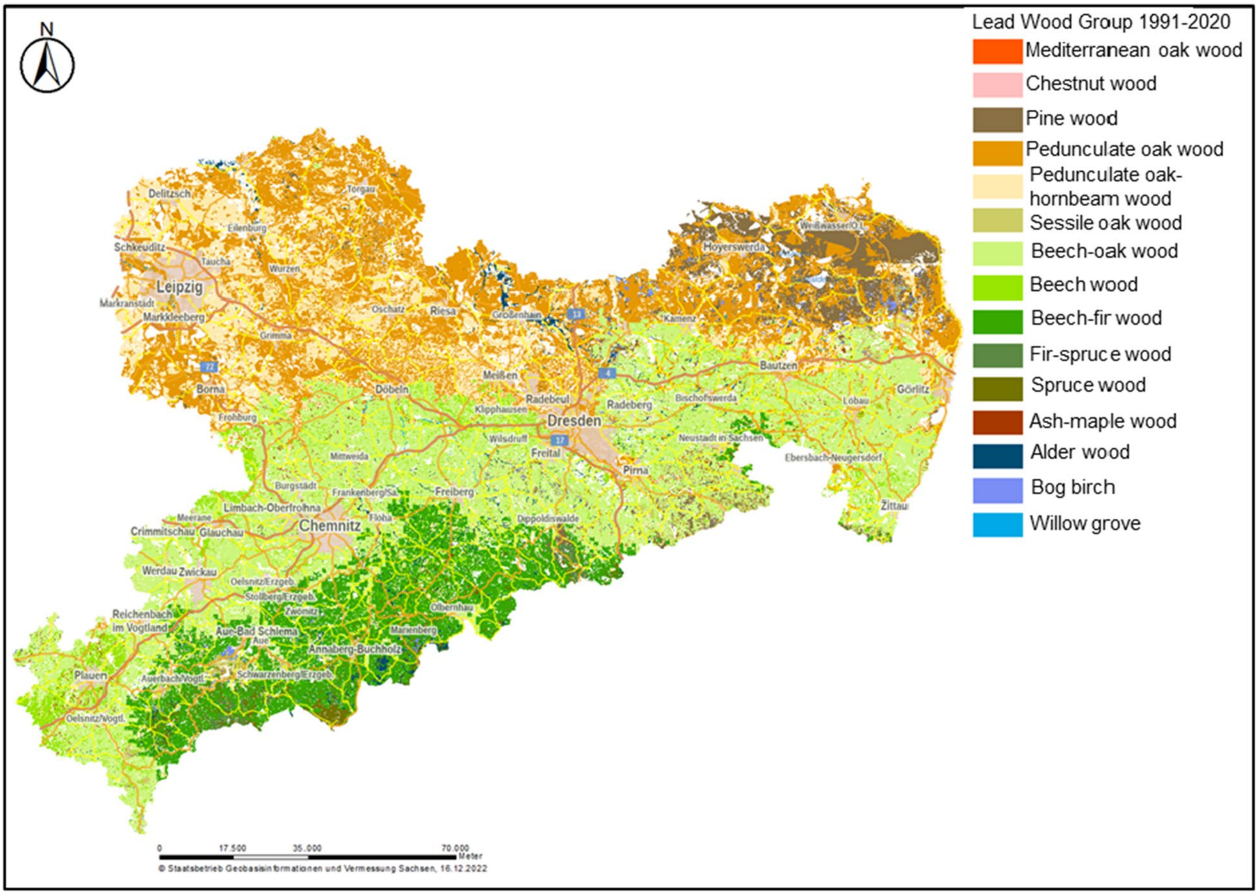

Fig. 7 Regional distribution of the possible lead wood groups in the period 1991–2020 (Sources: Authors' own depiction)

reference forest communities are now assigned whose community-typical reference value ranges for climate and site parameters largely correspond to the value ranges of the site and climate types of the Saxon forest site mapping. The 123 reference forest communities selected for this purpose, each with the highest degrees of viability under current and future site conditions in Saxony, are to serve as a recommendation for deriving the stocking target types for ecological forest conversion. These 123 reference forest communities are summarized into 15 lead wood groups.

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The reference forest community should correspond to a plant community that is as natural as possible, because only an ecologically site-adapted and competitively stable biocoenosis can meet the forestry objectives of forest conversion. Only a self-regenerating biocenosis can withstand biotic or abiotic damaging and disturbing factors and constantly restore itself to homeostasic equilibrium. The production risk is thus minimised for the forester and at the same time he can help himself to nature's free services.

The BERN database offers the possibility to identify the natural forest communities that have already existed for centuries under climatic conditions that are to be expected in Saxony in the future in the course of climate change. These are usually forest communities from

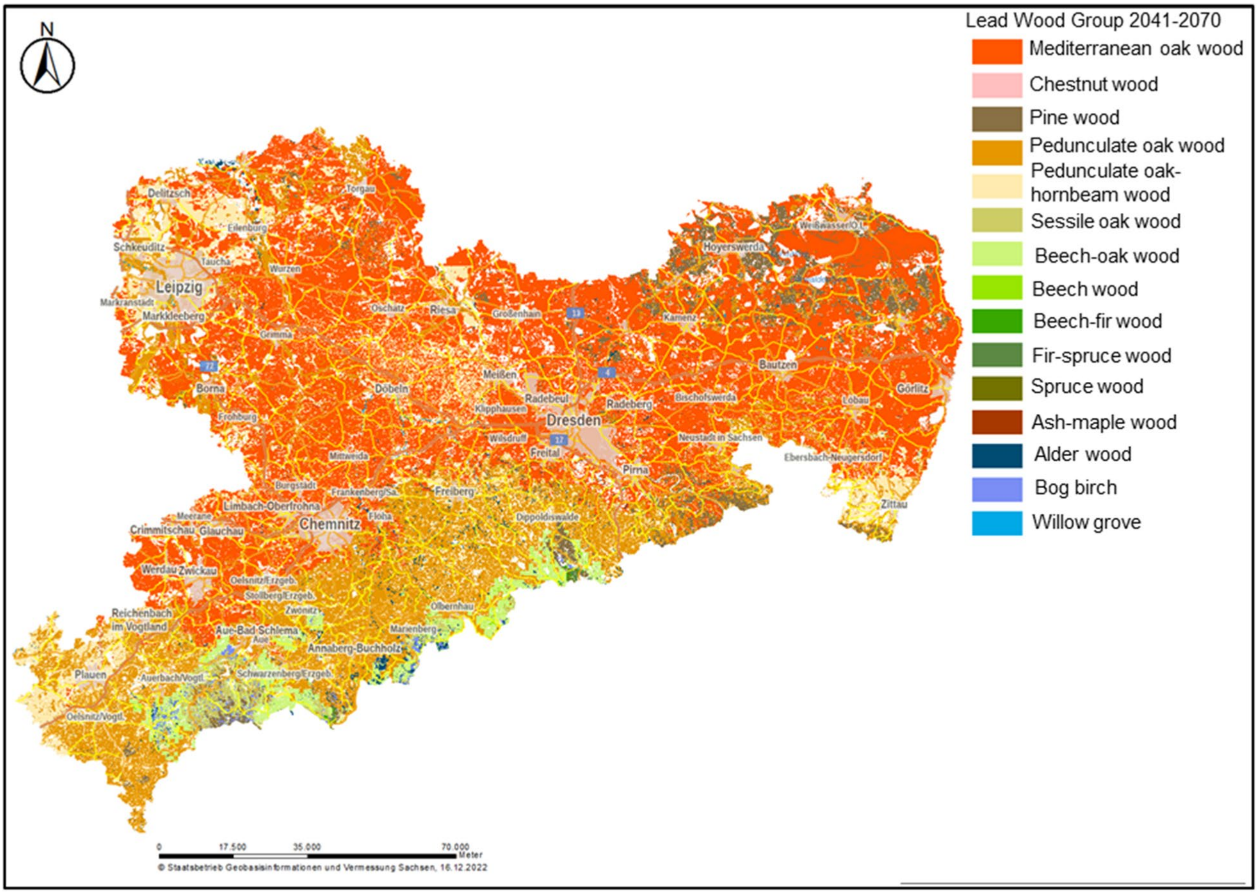

Fig. 8 Regional distribution of the possible lead wood groups in the period 2041–2070 after RCP8.5 scenario (Sources: Authors' own depiction)

regions southeast of Germany. These communities could theoretically migrate to Saxony on their own, bringing with them more or less all associated animal and plant species. However, this would take too long, especially as the Alps are an obstacle. However, some of the characteristic animal species are often already here.

Modelling of future possible communities in response to climate change can only be as realistic as the climate projections are realistic. As soon as new findings lead to more refined climate models, the modelling with BERN must also be updated. For full studies, the results should be presented with uncertainties. Therefore, ecograms were additionally developed for all climate stages, as shown in the following example, to facilitate subsequent adjustment of stocking targets to updated forecasts. In particular, forest communities with the broadest possible climatic-ecological niche were considered in order to minimize possible effects of wrong decisions.

The resulting ecograms of modelling with the BERN model is shown using the example of a fresh cambisol from granite (Fig. 9).

Modelling of future possible communities in response to climate change can only be as realistic as the climate projections are realistic. As soon as new findings lead to more refined climate models, the modelling with BERN must also be updated. Of course, the BERN model cannot replace a critical interpretation of the results, but can only provide the trend of development for further planning approaches. For example, it was sometimes necessary to choose among several possible communities. Therefore, other criteria are also taken into account and assessed by experts: Resilience to heavy rain and drought, to diseases and pests, and fire risk [114].

Discussion

Comparison with historical observations

To evaluate the model predicted ecological niches of plant communities a comparison was made with the available historical measurement data at the locations where the vegetation was recorded.

Therefore, the ecological niches of the communities determined on the basis of the reference soil profile data of the German soil map BÜK1000N and the Europe-wide

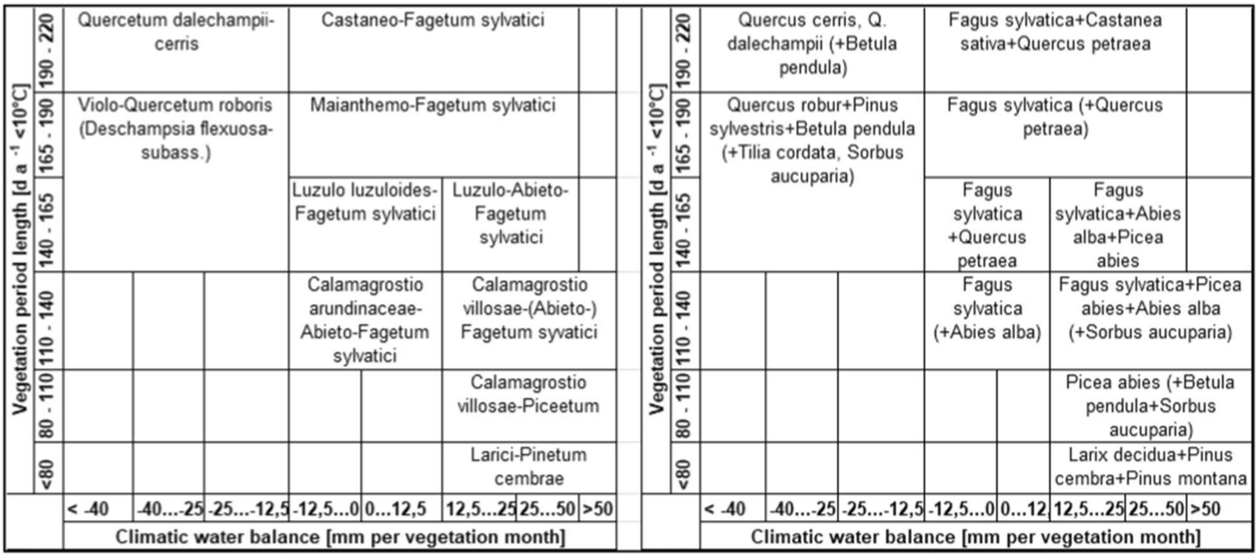

Fig. 9 Climate classes in Saxony with the best possible forest communities (left) and their main, mixed (and secondary) tree species (right) on a fresh cambisol from granite with C/N of 16 to 22, base saturation of 15% to 30% and a water content in the soil of 6% to 23%. (Sources: Authors´ own depiction)

Level II soil datasets were compared with 193 site-plant community pairs from historical surveys [19, 39, 45, 52, 53, 57, 71, 75, 76, 81, 82]. These observations have been compared with the BERN-modelled ranges in the Supplementary Materials. The soil parameters of these site-plant community pairs are not fed into the BERN model database for determining ecological niches because their number is too small to be representative. Rather, they should serve to validate the model results of the BERN5 database.

The comparison of minima, maxima and mean/median values shows a relatively wide variance for both the pH values and the C/N ratios. This is mainly due to the fact that some authors [19, 39, 75], have already stratified their measured values, and thus only classes are given which can now no longer be clearly assigned to the minima, maxima and mean/median values (Fig. 10).

The statistics of the value pairs show a good and significant correlation of the pH and C/N minima and maxima (Table 4).

However, the significance of these comparisons is limited. Much more important is the question of whether the measured values lie within the modelled ecological niches, because the number of measured values is far too small to be representative of all potential sites of a community.

Of 130 communities, the ranges of measured values and the modelled niche ranges of pH values overlap completely or more than 60% in 110 communities (85%), as shown in Table 5. The ranges of C/N ratios overlap completely or more than 60% in 113 of 150 communities (75%).

It should be noted that the measured C/N values in the wet open land communities according to Succow [75] and Succow and Joosten [19] are somewhat lower than the BERN results (mostly 10–17 instead of 12–22). It would have to be checked whether in 1974 the wetland sites were already significantly eutrophic, possibly due to drainage and the associated mineralisation surge.

Adjustment of species niches from the BERN database to measured values was performed whenever a constant species showed extremely deviant niches compared to the other constant species in the community. In these cases the information on associations units on the EVA website [29] were used when ambiguities or contradictions arose in the evaluation of historical surveys and measurement data.

Comparison of the ecological niches from the BERN database with Ellenberg indicator values

The indicator values for mineral nitrogen supply during the vegetation period (hereafter: "N indicator value") and for soil reaction (hereafter: "R indicator value") according to Ellenberg et al. [18] are given for plant species, not for plant communities. Therefore, the constant and character species of the plant communities had to be included in this comparison. However, not all of these species have specific N indicator value or R indicator value. The remaining species are assigned an X by Ellenberg et al.

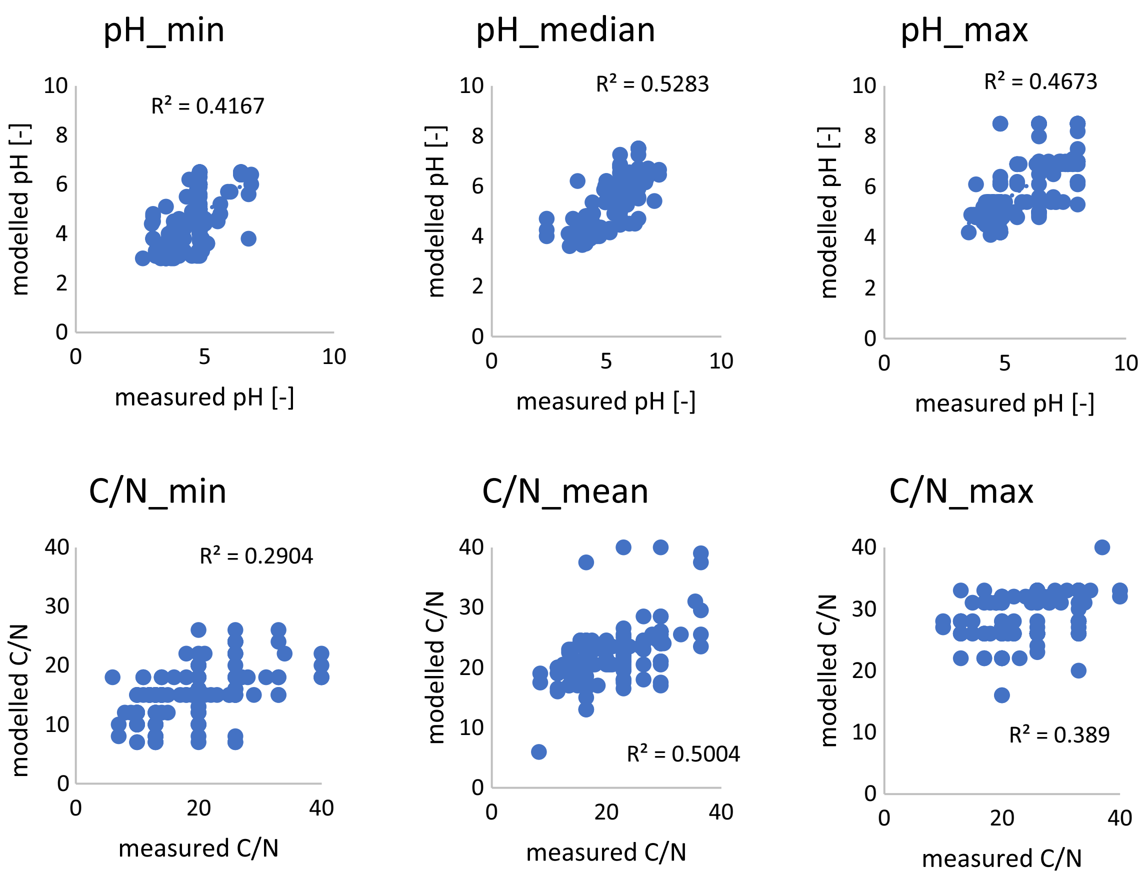

Fig. 10 Comparison of the lower and upper range limits as well as the mean/median values of the measured value ranges for pH values, base saturation and C/N ratio and the corresponding modelled ecological niches (Sources: Authors' own depiction)

Table 4 Statistical evaluation of the comparison of the lower and upper range limits, and the mean values of the measured value ranges for C/N ratio (CN) and the median values of pH and the corresponding modelled niches

	n	Pearson-correlation coefficient	*t*-Value	*p*-value (ANOVA)
pH_min_measured	153	0.65	63,47	< 0.05
pH_min_modelled				
pH_median_measured	131	0.72	− 1,39	0.17
pH_ median modelled				
pH_max_measured	161	0.68	54,89	< 0.05
pH_max_modelled				
C/N_min_measured	160	0.54	32,22	< 0.05
C/N_min_modelled				
C/N_Mean_measured	151	0.70	− 0,35	0.72
C/N_Mean_modelled				
C/N_max_measured	151	0.62	34,78	< 0.05
C/N_max_modelled				

Table 5 Number of communities whose measured and modelled parameter ranges match completely, partially or not at all

	pH	C/N
The range of measured values overlaps completely with the modelled ecological niche	58	91
The measured value range lies completely outside the modelled ecological niche	0	0
The range of measured values is partly within the modelled ecological niche, partly below it	39	30
The range of measured values is partly within the modelled ecological niche, partly above it	32	29

[18], which means "indifferent", so that these species could not be included in the comparison. The Ellenberg numbers represent the occurrence focus of a species within the ecological niche of the species, not the niche width.

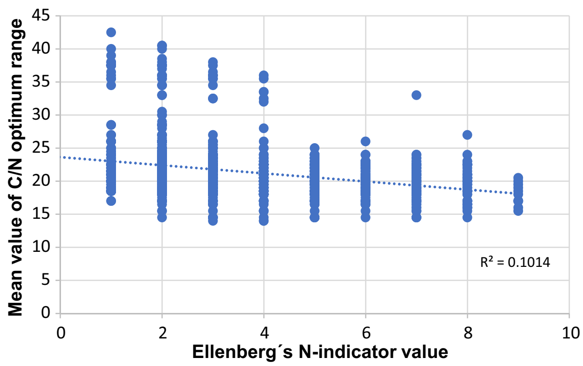

Fig. 11 C/N mean value of the optimum plateau of the ecological niche of the species ($n_{paired}=1307$ from BERN5) versus N indicator value [18]. (Sources: Authors' own depiction)

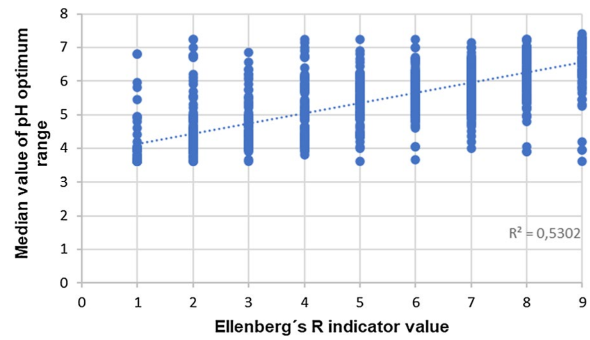

Fig. 12 pH median of the species' ecological niche optimum plateau ($n_{paired}=1454$ from BERN5) versus R indicator value [18]. (Sources: Authors' own depiction)

The comparison of N indicator value and the mean values of the optimum range of the ecological niche with regard to the C/N ratio of the comparable species shows a wide dispersion (Fig. 11). A trend of increasing N indicator values with decreasing $C/N_{opt(mean)}$ is recognisable.

This result was to be expected and is confirmed by a large number of comparative studies in this regard. Ellenberg et al. [18] regarded the assignment of nitrogen indicator values as an "experiment". The comparison of R indicator value with the mean values of the ecological niches with regard to pH is clearly significant (cf. Fig. 12).

De Vries et al. [119] tested the correlation of measured pH with R indicator value ($n=2759$) and found a coefficient of determination of 0.54. Figure 13 shows the comparison of the moisture indicator value F according to Ellenberg et al. [18] with the mean value of the optimum range of the water content in the effectively rooted soil (WI) of the corresponding species in the BERN5 database.

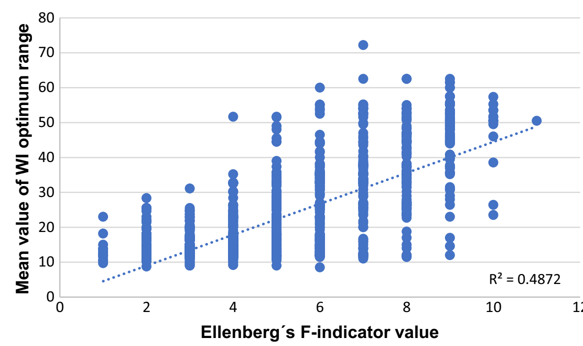

Fig. 13 Water Index mean of the species' ecological niche optimum plateau ($n_{paired}=1457$ from BERN5) versus F indicator value [18]. (Sources: Authors' own depiction)

Conclusion

With its publication in github (https://github.com/bern-model/BERN), the BERN database of ecological niches for plant species and plant communities becomes generally available for use by anyone for the first time. The publication of the database now is intended to open the possibility for all interested parties to use it, to develop it further and to modify the model for new applications.

The BERN database provides data of site parameter spans for the possibility of existence of plant communities in a good ecological status, and additional information on anthropogenically influenced communities.

The database requires further additions. According to the latest climate forecasts, it must also be expected that some regions of Germany may become wetter. As a result, analyses of vegetation in France and Italy, for example, are becoming increasingly interesting. However, warmer regions further east of Germany (e.g. Ukraine) must also be considered.

The BERN model was developed for some applications of dynamic modelling of vegetation changes as a function of changes in site conditions (pollutant inputs and removals, climate change). The BERN model is used to determine the degree of existence´s possibility of plant communities as a function of given or predicted site parameters, but not their probable occurrence at a given point in time.

Two examples demonstrate application possibilities of the BERN database.

The necessary requirement for the determination of dynamic vegetation change is the implementation of corresponding time series of geochemical or climate-ecological parameters in the BERN model. The BERN model can be used as an "add-on" for dynamic models such as VSD+and ForSAFE [120] or SMART2 [121] and LandscapeDNDC [122] for the integrated assessment of impacts on biodiversity due to acidification, eutrophication and climate change. In this way, the current regeneration potentials of ecosystems can be read from the results of the BERN coupling, a target state in the natural equilibrium of the site factors can be determined, and the degree of deviation of the current state from this target state can be depicted.

For example, the ranges of possible existence for forest communities under the conditions of climate change resulting from the BERN model can provide foresters with clues if they are pursuing the goal of establishing near-natural forests. How and with which forestry methods they achieve this on site is another question that only they can answerBut the results are to be evaluated with caution. Modelling of future possible communities in response to climate change and/or pollution impacts can only be as realistic as the climate and deposition projections are realistic. As soon as new findings lead to more refined climate and deposition models, the modelling with BERN must also be updated.

The application of the BERN model for the dynamic modelling of the existence of communities cannot make any predictions about the temporal development of vegetation.

Of course, the BERN model cannot replace a critical interpretation of the results, but can only provide the trend of development for further planning approaches. For example, it is sometimes necessary to choose among several modelled possible communities. Therefore, other criteria are also taken into account and assessed by experts: Resilience to heavy rain and drought, to diseases and pests, fire risk and others.

The mathematical basis used to describe the relationship between the occurrence of plant communities and their requirements for environmental conditions is an aid to better understand ecological relationships. A further need for research arises from the experience that the biogenic compartments of ecosystems (especially vegetation) usually react with a time lag to changes in biochemical or climate-ecological site factors. The BERN model results have so far taken neither the so-called damage delay time nor the recovery delay time into account. In principle, the programmatic implementation of this aspect in the BERN model is intended to determine the response time of species and plant communities as a function of the duration and intensity of exposure to changes in one or more site factors. The age of a plant to reach the reproductive maturity has a decisive influence on the delay time until lethal damage or recovery.

This approach should be pursued further in order to be able to simulate the effects of air pollutant inputs and climate change even more realistically. This is the only way to achieve increasing political acceptance of the proposed reduction targets.

Abbreviations

BERN	Model and database "Bioindication for Ecosystem Regeneration towards Natural conditions"
BÜK1000N	Reference soil profile of the land use-specified soil map 1:1,000,000 Germany
C/N	Carbon/nitrogen ratio
CLC	Corine Landcover [123]
CLRTAP	Convention on long-range transboundary air pollution
DWD	German Weather Service
EMEP	European Co-operative programme for monitoring and evaluation of the long-range Transmissions of air pollutants in Europe
eq	Equivalent of hydrogen ions
EU	European Union
IMS	Intensive monitoring site
N	Nitrogen
NH3_dep	Atmospheric deposition rate of ammonia [eq m^{-2} a^{-1}]
NOx_dep	Atmospheric deposition rate of oxidized nitrogen compounds [eq m^{-2} a^{-1}]
pH value	Value of the negative decadic logarithm of hydrogen concentration measured in water
RCP	Representative concentration pathways
S_dep	Atmospheric deposition rate of sulphur compounds [eq m^{-2} a^{-1}]
STAR	Statistical regional climate model
VSD+	Very simple dynamics soil model, version 5.3.1 [113, 124]

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12302-023-00826-0.

Additional file 1: Table S1. Comparison of measured and modelled value ranges for pH-values (pH), and C/N ratio (CN).

Author contributions

AS—conceptualization, methodology, investigation, writing—original draft, visualization. PK—conceptualization, methodology, software, writing—original draft, visualization. TS—investigation, validation, writing—review and editing. MS—investigation, methodology, software. WS—writing—review and editing.

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Data Availability

All data has been compiled by the authors themselves. They are hereby made freely available.

Declarations

Competing interests

The authors declare no competing interests.

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