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High resolution predictive modelling of potential natural vegetation under recent site conditions and future climate scenarios: Case study Bavaria

Hochauflösende Modellierung der potentiell natürlichen Vegetation von Bayern unter heutigen Standortbedingungen (h-PNV) und zukünftigen Klimaszenarien (z-PNV): Fallstudie Bayern

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Abstract

Potential natural vegetation (PNV) is a widely used concept to characterise complex site conditions of vegetation types. We developed a model to simulate the distribution of 26 PNV units (forest types) under recent and future climate change conditions (15 scenarios) in the Federal State of Bavaria, SE of Germany (70,550 km^2) with an extraordinarily fine spatial resolution (50 m x 50 m; 28.1 million grid cells). We used MaxEnt and a set of 146 high-resolution site maps. Calibration of the model is based on 7,504 sampling points of the national forest inventory of Germany. Future scenarios include temperature increase only (+1 K, +2 K, +3 K, +4 K, +6 K) and with precipitation increase (+10%) or decrease (-10%).

The model describes the current distribution of natural vegetation types very precisely. For the study area, all future scenarios show drastic changes in site conditions: The constellations of site conditions, which are absent in Bavaria at present, will increase from 36% in the +2 K to 94% in the +4 K scenario. Forestry as well as agriculture and land use management will then find themselves victims of global climate change caused by new site situations.

With the model, we provide a tool that enables politicians at all administrative levels as well as practitioners on their operational level to identify climate change hotspots down to the local level by identifying areas with minor or stronger changes in site conditions to be expected under different climate change scenarios. Moreover, everybody can check how global change will influence his backyard.

Keywords: climate change, conservation management, environment conditions, fine scale modelling, land use management, natural vegetation, predictive vegetation mapping

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Vegetation strongly depends on site conditions. Dating back to BRAUN-BLANQUET (1928), this is why vegetation types or plant communities have been used intensively as proxy indicators for site conditions in ecological based landscape and forest management

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and in land use practice for many decades (e.g. KÜCHLER & ZONNEVELD 1988, FRANKLIN 1995, BREDENKAMP et al. 1998, A. FISCHER 2003, BOHN et al. 2005, KOWARIK 2016). Edaphic, climate and geomorphological factors result in complex site conditions leading to a high diversity of vegetation types (LEUSCHNER & ELLENBERG 2017). Plant communities, not depending on anthropogenic site factors such as mowing, ploughing and fertilising, characterise these complex site conditions in terms of phytosociological units in a very comprehensive way. This concept is called "potential natural vegetation" (PNV). It has been outlined in detail by TÜXEN (1956, title translated: "The today's potential natural vegetation as an object of vegetation mapping"). He explained PNV as the "today's natural growing power under the real existing site conditions" (p. 9, translated), most important climate, relief, bedrock, soil, water, in other words: all naturally occurring soil chemical and physical properties and therefore living conditions at a forest site ("Standortskräfte") (p. 10). Thus, the name of a certain PNV unit (e.g. species-poor oligotrophic beech forest = *Luzulo-Fagetum*) is a proxy label for the corresponding growing conditions of plants.

We understand the concept of PNV according to the meaning postulated by HÄRDTLE (1995), TÜXEN (1956), A. FISCHER (2003), LOIDI & FERNÁNDEZ-GONZÁLEZ (2012) and SOMODI et al. (2012) as a set of abiotic site conditions without any direct influence by man at a certain point in the landscape thus enabling a specific group of plant species (a plant community) to thrive there. In short: PNV is a set of abiotic site conditions, relevant for vegetation patterning, expressed in phytosociological terms (BOHN et al. 2000/2003). MUCINA et al. (2016), referring to this meaning, recently published a list of European natural vegetation types. In the temperate zone of Central Europe, they correspond mostly to forest types, with the exception of the alpine belt and some bogs.

We would like to point out that our approach addresses neither questions of real succession nor climax vegetation nor the question of what vegetation looked like before the appearance of man. Thus, neither the uncertainty related to the influence of invading species during a succession process nor the ability of species to migrate nor the absence of real primeval vegetation in today's landscape is a matter of concern in this concept. Instead, a PNV unit can be rather understood as an umbrella term for proxies of complex site conditions. It reflects the site capability of a site. In reverse, one can conclude from site conditions what corresponding vegetation type could exist there. Therefore, PNV can be constructed for currently forested areas (where it is used to assess naturalness of the actual forest vegetation) as well as for any kind of agricultural or abandoned land, (where it characterises the opportunity for land use).

If a certain stand of a natural plant community is replaced by another and the fundamental set of site conditions (soil properties and macroclimate) remains more or less unchanged, the PNV unit does not change. Furthermore, if, for instance, the former forest is replaced after harvesting by a felled-area vegetation (herbs) for several years or a few decades, and later on, by a pioneer forest (shrubs and trees), or even if it is transformed into agricultural land (grassland or arable land) for long-term use – the fundamental abiotic site conditions remain the same and the PNV unit as well. Although PNV mainly adresses abiotic site conditions, it is conceptional complete different from "site types": PNV is primary based on (natural) vegetation types, site conditions are specified secondarily. "Site types" would be the result of a classification process based on abiotic site conditions, like climate types or soil types. The latter are defined completely independ from vegetation.

In contrast to the previous example, if at a specific location site conditions alter irreversibly (e.g. if top soil was removed or the groundwater table lowered) a new set of site conditions results, and in consequence, the PNV unit changes. Currently, site conditions globally face a fundamental macroclimate change (IPCC 2014), altering all site types everywhere in the landscape resulting in changes in the distribution of PNV units. PNV serves as an essential planning objective (KÖCK 2004, BOHN et al. 2005, LOIDI & FERNÁNDEZ-GONZÁLEZ 2012): in forest management (e.g. Handbook on Forest Communities for Bavaria/Germany; WALENTOWSKI et al. 2013), that aims to practise close-to-nature forest management or to assess the naturalness of existing forests (REIF & WALENTOWSKI 2008) or to support forest restoration (A. FISCHER & H. FISCHER 2012, SOMODI 2017) or conservation management (EUROPEAN COMMISSION 1992, GUTIERRES et al. 2018). Moreover, landscape management and planning processes e.g. application for planning permission, impact and compensation of land use change effects or agriculture like suitability for viticulture (FRAGA & MALHEIRO 2012) use the PNV units for general orientation.

Anticipatory planning, especially in forestry with its very long lasting rotation periods, requires detailed knowledge about future site conditions. H.S. FISCHER (1990), using a Bayes classifier, modelled the occurrence of vegetation types from maps of current climate and soil variables in the "Landscape Davos" (100 km^2) in Switzerland, based on the first attempts in the MaB-projects in Berchtesgaden (Germany) by HEHL & LANGE (1987) and in Davos by BINZ & WILDI (1988). Moreover, H.S. FISCHER (1994) simulated the impact of global warming by increasing the temperature of 2 K on the distribution of vegetation types in the "Landschaft Davos". BRZEZIECKI et al. (1993) applied this approach to construct "*potential natural forest vegetation*" for the whole of Switzerland (41,285 km^2, grid size 250 m x 250 m). Moreover, BRZEZIECKI et al. (1995) and KIENAST et al. (1996, 1998) assessed the impact of climate change on the Swiss forest communities using this model.

FRANKLIN (1995) introduced the term "predictive vegetation mapping" and defined it as "predicting the geographic distribution of the vegetation composition across a landscape from mapped site variables". She stated, "predictive vegetation mapping is founded in ecological niche theory and gradient analysis, and driven by the need to map vegetation patterns over large areas for resource conservation planning, and to predict the effects of site change on vegetation distributions". Since that time, this type of modelling has become a frequently used tool in numerical ecology (ELITH & LEATHMICK 2009, FRANKLIN et al. 2016, 2017).

Furthermore, today much more information on site conditions is available in digital form and in a much higher resolution (smaller grid size, e.g. BECK & KÖLLING 2013). We have already processed a model for formalized PNV construction, using the area of two directly adjacent national parks, the Bavarian Forest National Park in SE Germany and the Šumava National Park in the Czech Republic as a test site, altogether covering an area of about 923 km^2 (H.S. FISCHER et al. 2013). We performed this modelling with polygon data instead of grid data at a scale of 1:25,000. In the present study, we developed a model for the whole Federal State of Bavaria in SE Germany, covering an area of 70,550km^2 with a grid size of 50 m x 50 m, a grid size being on the operational level of landscape management. Thereby, we aim to model the distribution of recent PNV and as well – most importantly – for modified future climate conditions.

Our first goal, therefore, is to develop a model that generates a map of the current PNV based on current site conditions (soil and climate) and on defined algorithms.

In times of climate change (e.g. IPCC 2014), all the single points in a landscape are influenced by changing site conditions such as higher temperatures, longer vegetation periods and increasing or decreasing precipitation levels. "*The future environment will be different from the present*" (MILLAR et al. 2007, NICKL et al. 2015).

Our second goal, therefore, is to model the distribution of the PNV under future climatic conditions. We focussed on temperature increase (+1 K, +2 K, +3 K, +4 K, +6 K) without change in precipitation and decreasing or increasing precipitation by 10%. This allows for visualizing and balancing the change in the distribution of PNV at each point in the landscape all over Bavaria.

2. Material and Methods

2.1 Study area

We conducted the study in the Federal State of Bavaria, SE of Germany as an example. It extends over an area of 70,550 km^2 and ranges from South to North 362 km (47°16′ to 50°34′) and from East to West 384 km (8°58′ to 13°50′). Bavaria geomorphologically consists mainly of uplands between 100 and 500 m a.s.l., with the hook-shaped Franconian Jura in the centre (up to 600 to 700 m a.s.l.), the mountain range named the Bavarian Forest in the east (up to 1,455 m a.s.l., Mt. Arber) and the Northern Calcareous Alps in the south (up to 2,962 m a.s.l. on Mt. Zugspitze).

Geologically, a huge variety of bedrock types exists in Bavaria ranging from calcareous rocks (Alps, Swabian and Franconian Jura) to granite and gneiss (Bavarian Forest). The climate varies from sub-oceanic regimes in the NW to more sub-continental regimes in plains and basins. Cleary distinct from their surroundings are mountain climates with more continental trends in the east and the highland climate of the Alps.

With the exception of the alpine belt and some bog areas, Bavaria – without human interference – under recent site conditions would be totally covered by forests: mainly deciduous (summer-green temperate) forests in the colline-submontane and lower montane belt, mixed deciduous and coniferous forests in the montane and subalpine belts. Therefore, the PNV of Bavaria consists mainly of different forest types. Currently, however, only one third of Bavaria is covered by forests.

2.2 Data

The National Forest Inventory (NFI, POLLEY & SPLETT 1998) of Germany collected data on the state of the forests on a regular grid with a grid size of 4 km (7,504 sampling points in Bavaria). On a subset of the NFI grid within the National Forest Soil Inventory (NFSI, WELLBROCK et al. 2016) detailed information on soil characteristics was recorded as well as phytosociological relevés taken, and the PNV unit determined (349 sampling points). In 2002, the PNV units were recorded at all sampling points of the NFI in Bavaria, following the classification rules set by WALENTOWSKI et al. (2013). The base of this assignment consisted of (1) regional differentiated ecograms for soil water, soil acidity, humus form and base saturation, (2) checklists of indicator species, (3) fact sheets of forest types regarding distribution, habitat, soil, tree species composition and forest management.

WALENTOWSKI et al. (2013) listed 52 forest types (in the sense of PNV units) for Bavaria. 36 of these were identified at the grid points. Those missing occur rarely in the landscape (islands of extrazonal and azonal vegetation of special habitats). Four out of the 36 were excluded from the analyses due to small sample size: *Leucobryo-Pinetum* Matuszkiewicz 1962 (n = 2), *Calamagrostio variae-Pinetum sylvestris* Oberd. (1950) 1957 (n = 8), *Asplenio-Piceetum* Kuoch 1954 (n = 6) and *Alnetum viridis* Br.-Bl. 1918 (n = 2). Two other forest types were removed because they only occur in small spots which lay below the spatial resolution of the models: *Carici elongatae-Alnetum glutinosae* Schwickerath 1933, *Carici remotae-Fraxinetum* W. Koch 1926 ex Faber 1937. Another three rare types

(*Vaccinio-Abietetum* Oberd. 1957, *Pyrolo-Abietetum* Oberd. 1957 and *Adoxo-Aceretum* Passarge 1960 nom. conserv. propos.) could not be modelled because their habitat conditions could not be discriminated with available site factors. In consequence, 26 PNV units remained for modelling (Supplement S1).

In Bavaria site conditions allow forests to grow, mostly dominated by beech (*Fagus sylvatica*), oak (*Quercus robur* and *Q. petraea*) and hornbeam (*Carpinus betulus*), respectively. Beech forests are the most frequent natural forest types in Bavaria, with a clear dominance of the species-poor oligotrophic *Luzulo-Fagetum*. It is subdivided into a colline to submontane form (average annual temperature > 7 °C, 1c) and a montane form (average annual temperature < 7 °C, 1m). According to WALENTOWSKI et al. (2013), the colline to submontane form occurs with precipitation less than 1100 mm only. However, analysing the data we found species-poor oligotrophic, colline to montane beech forests also with higher precipitation. As this resulted in bimodal response curves we added an additional forest type ("1cn"): average annual temperature > 7 °C and precipitation > 1100 mm. Under less oligotroph conditions in the colline to submontane belt, *Galio odorati-Fagetum* and *Hordelymo-Fagetum* occur. Both types are also divided up into a variant with less than 1100 mm precipitation and a variant with higher precipitation. In the montane belt (Alps with very high precipitation), the *Hordelymo-Fagetum* is replaced by the *Aposerido-Fagetum*. On steep south exposed slopes outside the Alps, the *Carici-Fagetum* occurs. This forest type is very rare but hosts many rare and endangered species. The corresponding type in the Alps is the *Seslerio-Fagetum*.

Oak and oak-hornbean forests grow where beech is suppressed by dry conditions (low precipitation with high temperature) on clayey soils or by water accumulation. We distinguish species-poor acidophilous oak and mixed oak forests from oak-hornbeam forests. Both types are promoted in the actual vegetation by historical coppicing. We aggregated the oak forests *Calamagrostio arundinaceae-Quercetum petraeae* and *Luzulo-Quercetum petraeae* to one PNV unit to increase sample size.

Ravine forests are represented by the *Aceri-Tilietum platyphylli*. Along the flood plains different types of alluvial and wet lowland forests occur, depending on soil water conditions. On peaty soils (typically > 1000 mm precipitation) bog woodland are to be found. Mesophytic and hygromesophytic coniferous and mixed broad-leaved-coniferous forests occur in the submontane, altimontane and subalpine belts. Fir forests characterise submontane to altimontane belt. Above 1600 m, natural spruce forests are found in Bavaria. Subalpine dwarf shrub vegetation occur mainly along the timberline in the Alps subalpine to alpine belt.

The Bavarian Environment Agency (Bayerisches Landesamt für Umwelt, LfU) as the central authority for site protection and nature conservation, geology and water resources management, compiled the Bavarian General Soil Map 1:25,000 ("Übersichtsbodenkarte"). It depicts the distribution of soil types in Bavaria. The Bavarian State Institute of Forestry (Bayerisches Landesamt für Wald und Forstwirtschaft, LWF) extended this map by adding information on soil characteristics, climatic data and information derived from a digital terrain model (HERA et al. 2012, ZIMMERMANN et al. 2013, BECK & KÖLLING 2013, FRANKE 2013, OSENSTETTER et al. 2013, TAEGER & KÖLLING 2016). In total 146 soil and climate variables were available as grid files with a grid size of 50 m x 50 m, suitable for maps in the scale of 1:25,000. The area of Bavaria covers 28.1 million pixels.

In a first step, all 146 variables were tested in a discriminant analysis (n = 7,504 inventory points NFI) to find out which of them separate the forest types (n = 26) significantly. For further analyses we considered only variables with high F-values. Next we performed a correlation analysis with the raster data (n = 28.1 million). Due to the high sample size, most variables were significantly correlated with each other. We decided to build sets of variables representing soil water, soil nutrients and climatic conditions. Within each set, bivariate correlations were calculated, collinear variables were excluded and the most representative (based on F-value in discriminant analyses and ecological importance) predictors were selected for further analysis. In doing so, primary variables were preferred over derivate ones. For climatic variables, annual values were preferred over monthly values as they are more likely obtained for future climatic scenarios.

After this data cleaning process (discriminant and correlation analysis) 24 variables remained (see Table 1) to simulate the PNV units.

Table 1. List of predictors. Map layer: resolution 50 m; Unit: physical unit; Data source: DWD: Deutscher Wetterdienst (Germanys National Meteorological Service); LfU: Bavarian Agency (state institute) of Environment; LWF: Bavarian State Institute of Forestry; LDBV: Bavarian Agency (state institute) for Surveying and Geoinformation; Median and Quartile (Q25, Q75) overall Bavaria (forested and non forested areas).

Tabelle 1. Standortvariablen. Grid files: Auflösung 50 m; Unit: Physikalische Einheit; Daten Quelle: DWD: Deutscher Wetterdienst; LfU: Bayerische Landesamt für Umwelt; LWF: Bayerische Landesanstalt für Wald und Forstwirtschaft; LDBV: Landesamt für Digitalisierung, Breitband und Vermessung; Median and Quartile (Q25, Q75) beziehen sich auf ganz Bayern, bewaldete und unbewaldetet Flächen.

Map layer	Unit	Source	Q_{25}	Median	Q_{75}
Soil					
Total pore volume	mm/m	LFU, LWF	309	396	445
Available water capacity	mm/m	LFU, LWF	116	147	174
Water conductivity coefficient	cm/dm	LFU, LWF	15	26	54
Air capacity	mm/m	LFU, LWF	77	99	121
Hygroscopic water	mm/m	LFU, LWF	77	119	169
Base saturation of the first 30 cm	%	LFU, LWF	10	24	64
Cation exchange capacity (CEC)	cmol/kg	LFU, LWF	5	10	15
Exchangeable calcium (Ca^{2+})	%	LFU, LWF	15	34	63
Exchangeable potassium (K^{+})	%	LFU, LWF	1	1	2
Exchangeable magnesium (Mg^{2+})	%	LFU, LWF	6	10	16
Exchangeable sodium (Na^{+})	%	LFU, LWF	0	0	1
Organic matter	%	LFU, LWF	0.4	0.6	0.9
Soil depth	cm	LFU, LWF	101	110	116
Depth of decalcification	cm	LFU, LWF	100	108	120
Climate					
Average annual potential evapotranspiration	mm	LWF, DWD	44	47	48
Average annual precipitation sum (1971–2000)	mm	LWF, DWD	713	820	999
Average annual solar radiation (1981–2000)	Wh/(m²)	DWD	2879	3007	3116
Average annual temperature (1971–2000)	°C	LWF, DWD	7.53	8.08	8.38
Water balance, May to September	mm	LWF	50	116	221
Aridity-Index (de Martonne)	index	LWF	39	46	56
Growing degree days (threshold: 5 °C)		LWF	1551	1684	1764
Geomorphology					
Floodplain-Index	index	LWF	0.6	0.9	1.2
Aspect-Index	index	LWF, LDBV	0.2	0.9	1.7
Slope	degree	LWF, LDBV	1	4	7

2.3 Software

We applied the software package R (R DEVELOPMENT CORE TEAM 2016), especially packages "raster" (HIJMANS 2016) for data management and data mining, and the package "dismo" version 1.0-15 (HIJMANS et al. 2017, PHILLIPS et al. 2017) for modelling.The simulation was carried out with MaxEnt (PHILLIPS & DUDÍK 2008, ELITH et al. 2011, PHILLIPS et al. 2017).

2.4 Simulation of PNV under recent site conditions

Simulating the PNV of Bavaria comprises two parts. First each PNV unit is simulated separately. This results in probability and distribution maps of a single forest type. Second the PNV map for Bavaria is constructed, each pixel representing the most probable PNV unit.

We started with a series of steps for each individual forest type separately to check the predictors at the level of a single forest type: We calculated descriptive statistics to identify outliers, a Generalised Linear Model (GLM) with confidence bands and a Generalised Additive Model (GAM) to identify bimodal distributed predictors. We determined the Ecological Preference Function (EPF, H.S. FISCHER 1994, Fig. 2, Table 3) to obtain information on the preferred interval of a forest type within the range of a predictor. We calculated bivariate correlations between all predictors and set a high threshold of 0.85 to identify colinear varibles, because they do not contribute additional information but lead to numerical instability of the analysis (DORMANN et al. 2013). For each pair of colinear predictors we selected only one for further analysis.

MaxEnt was set to binomial error distribution and logit link-function with only linear and quadratic feature classes. We did not apply product variables, hinge, threshold and auto-feature. In this way, MaxEnt basically fits a Gaussian response curve by means of Generalised Linear Models. Inventory points of the NFI, a particular forest type was observed were used as presences (training sample, sample size of each forest type see Supplement S1), whereas all other inventory points were treated as absences (background sample) to contrast the site conditions of a specific forest type (MEROW et al. 2013). We choose sampling points of the NFI, that are not sampling points of the NFSI, to calibrate the model. The points of the NFSI served to evaluate the model. Thus, for calibration and evaluation, two independent data sets were applied. This separation was not applicable for rareforest types (n < 20 in NFSI). For them we took the same set of points for calibration and for evaluation.

We run a first MaxEnt simulation with all but no colinear variables to identify the best explaining variables for each forest type based on the statistics “variable contribution” (percent contribution or permutation importance > 5%) and “jack-knife”. After this, we performed a final MaxEnt analysis with the best explaining variables only.

The function “predict” (package “dismo”) calculated probability maps (Fig. 3) for each forest type. These 26 maps show for each grid cells on the map the (continuous) probability of the occurrence of the particular forest type reaching from very high (green) to low (brownish) probability; in the grey marked areas, the probability is close to zero. This set of maps represents a multiple PNV in the sense of SOMODI et al. (2017). Next we applied the threshold that maximises the sum of the true positive rate and the true negative rate to derive a discrete distribution map of the forest type (Fig. 1). Finally, we overlaid the 26 probability maps of the individual forest types, and the most probable unit was determined for each grid and we generated a map that reflects the most probable forest type for each grid (Fig. 7).

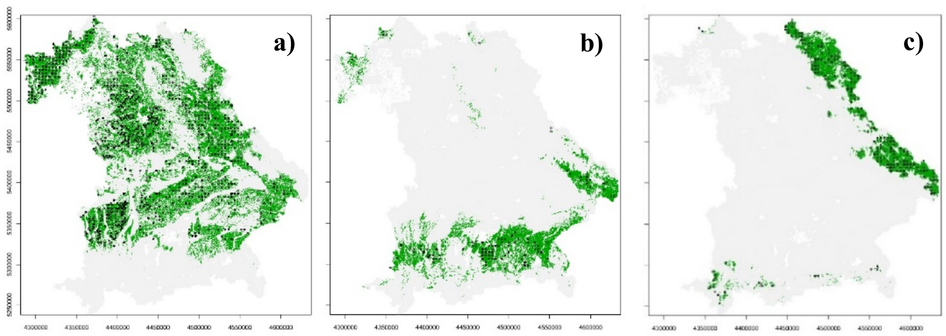

Fig. 1. Predicted distribution of **a)** *Luzulo-Fagetum*, colline-submontane, **b)** *Luzulo-Fagetum*, colline-submontane, precipitation > 1100 mm and **c)** *Luzulo-Fagetum*, montane in Bavaria, derived from the probability map after applying a threshold; black dots represent sampling points of the national forest inventory the forest type was observed in the field.

Abb. 1. Simulierte Verbreitungskarte **a)** des *Luzulo-Fagetum*, collin-submontan, **b)** des *Luzulo-Fagetum*, collin-submontan, Niederschläge > 1100 mm und **c)** des *Luzulo-Fagetum*, montan in Bayern; sie sind anhand eines Schwellwertes von den Wahrscheinlichkeitskarten abgeleitet. Die schwarzen Punkte entsprechen Vorkommen des PNV-Typs an den Inventurpunkten der Bundeswaldinventur (BWI2).

2.5 Simulation of forest types under future site conditions

We simulated future PNV for a series of climate change scenarios. We increased the temperature by 1K, 2K, 3K, 4K and 6K, and either maintained, increased or decreased precipitation by 10%, respectively. This results in 15 future climate scenarios. To carry out the future simulations, the function "predict" was rerun with the parameters of the recent simulation of MaxEnt but with modified layers of temperature, precipitation, potential evapotranspiration, water balance and aridity index. We masked areas with conditions outside the current range in Bavaria (non-analogue climate).

3. Results

3.1 PNV units, based on recent site conditions

First, we identified **predictors that determine the distribution** of the individual forest types. Table 2 lists the predictors used in the final model and their contribution (percent) to the result. AUC (area under the curve) is a measure for the quality of the model. This value

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Table 2. MaxEnt, AUC of the model and variables that contribute to simulate individual forest types (variable contribution or permutation importance > 5%). AUC: Area Under ROC (Receiver Operating Characteristic) Curve; 1c–31 Codes (see below) of forest types; n: absolute frequency the predictor contribute (< 5%) to simulate the distribution of the forest types, n%: relative frequency of n (n/26); the value of a cell in the matrix correspondent to the variable contribution. Dark brown indicates high values, light brown low values. The higher the contribution the more a variable contribute to model the distribution of a forest type.

Tabelle 2. MaxEnt, AUC und Beitrag einzelner Variablen zur Modellierung einzelner Waldgesellschaften. AUC: Area Under ROC (Receiver Operating Characteristic) Curve; 1c–31 Code (siehe unten) der einzelnen Waldgesellschaften, n: absolute Häufigkeit mit der eine variable signifikant zur Modellierung der Waldgesellschaften beiträgt, n%: relative Häufigkeit (n/26); der Wert in den Zellen der Tabelle entspricht dem prozentualen Beitrag einer Variablen zur Modellierung der Verbreitung einer Waldgesellschaft. Hohe Werte sind dunkelbraun, niedrige Werte hellbraun hinterlegt. Desto höher der Wert, desto mehr trägt die Variable zur Simulation der Verbreitung der Waldgesellschaften bei.

Mesophytic deciduous broad-leaved forests: (1c) *Luzulo-Fagetum*, colline-submontane, (1cn) *Luzulo-Fagetum*, colline to submontane, precipitation > 1100 mm, (1m) *Luzulo-Fagetum*, montane, (3c) *Galio odorati-Fagetum*, colline-submontane, (3cn) *Galio odorati-Fagetum*, colline-submontane, precipitation > 1100 mm, (3m) *Galio odorati-Fagetum*, montane, (4) *Hordelymo-Fagetum*, (4n) *Hordelymo-Fagetum*, precipitation > 1100 mm, (6) *Aposerido-Fagetum*, (7c) *Carici-Fagetum*, colline, (7m) *Seslerio-Fagetum*; **Oak and hornbeam forests:** (15) *Luzulo-Quercetum* & *Vaccinio vitis-idaeae-Quercetum*, (18) *Galio sylvatici-Carpinetum*, (17) *Stellario holosteae-Carpinetum*; **Ravine forest:** (24) *Aceri-Tilietum platyphylli*; **Alluvial and wet lowland forests:** (35) *Pruno-Fraxinetum*, (37) *Stellario nemorum-Alnetum glutinosae*, (38) *Alnetum incanae*, (39) *Querco-Ulmetum* & *Salicetum albae*; **Bog woodland:** (33) *Vaccinio uliginosi-Pinetalia sylvestris*, (28) *Bazzanio-Piceetum*; **Mesophytic and hygromesophytic coniferous and mixed broad-leaved-coniferous forests:** (11) *Galio rotundifolii-Abietetum*, (29) *Calamagrostio villosae-Piceetum*, mean annual temperature < 5 °C, (29t) *Calamagrostio villosae-Piceetum*, mean annual temperature > 5 °C, (30) *Adenostylo glabrae-Piceetum*; **Subalpine dwarf shrub vegetation:** (31) *Erico-Mugetum*.

Predictor	1c	1cn	1m	3c	3cn	3m	4	4n	6	7c	7m	15	18	17	24	35	37	38	39	33	28	11	29	29t	30	31	Frequ.	
AUC	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.97	1	1	1	1	1	1	1	1	1	1	n	n%
Total pore volume																											0	0
Available water capacity					7										8					46							3	12
Water conductivity coefficient						11					9				6		7					7					5	19
Air capacity												47															1	4
Hygroscopic water				32		11							11								12	11					5	19
Base saturation of the first 30 cm	61	27	30	51	43		62	59	61	45	48	15		12			17	60	39					16	19	38	18	69
Cation exchange capacity																											0	0
Exchangeable calcium (Ca^{2+})	12		6																				23				3	12
Exchangeable potassium (K^{+})					12																9						2	8
Exchangeable magnesium (Mg^{2+})													19						5								2	8
Exchangeable sodium (Na^{+})																											0	0
Organic matter																				51	76						2	8
Soil depth																											0	0
Depth of decalcification							10																				1	4
Average annual potential evapotranspiration		17																									1	4
Average annual precipitation sum (1971-2000)	8	25	7			57		13	25		30	14	33		59				7			66			21		13	50
Average annual solar radiation (1981-2000)												6					13										2	8
Average annual temperature (1971-2000)	8	7	58			17					7		19										72	44	60	32	10	38
Water balance, May to September	8	24		16	29		29	29	8	25			14	20			10										11	42
Floodplain-Index	6							5		21		17	7	58		100	39	40	35			16		37			12	46
Growing degree days (threshold: 5 °C)																			12								1	4
Aridity-Index (de Martonne)																								4		19	2	8
Aspect-Index										9																	1	4
Slope											10	6		10	26		14									11	6	23

is in almost all cases above 0.9, which is generally regarded as "excellent" (PHILLIPS & DUDÍK 2008). The model selected on average four predictors (median) to predict a single PNV unit. Base saturation turned out to be the most frequent, contributing to simulating 69% of the forest types. It is, however, not relevant for the montane *Galio odorati-Fagetum* (3m), the (18), ravine forests (24), alluvial and wet lowland forests (35, 37, 38, 39), bog woodlands (33, 28) and subalpine spruce forests (29). The second most important predictor proved to be annual precipitation, selected to simulate 50% of the forest types. Moreover, flood plain index (46%), water balance (42%) and average annual temperature (38%) played a major role in predicting distribution of the forest types.

Secondly, we quantified the **ecological preference** of all forest types with respect to the predictors they depend on. Ecological optimum and amplitude (Table 3) specify the ecological preference for each forest type. Considering, for example, the base saturation and

Table 3. Ecological optimum and amplitude (minimum – maximum) of predictors selected for modelling forest types (contribution > 5%); n.a. not available. The order of predictors within a single forest type follows the statistic "variable contribution" for each predictor calculated by MaxEnt to simulate the distribution of the forest type. The ecological optimum is the position of the maximum of the bell shaped ecological preference function. The ecological minimum is the intersection of the EPF with the horizontal line at EPF = 1 left of the optimum, the ecological maximum is the intersection right of the optimum, respectively. If the ecological minimum or maximum lies outside the range of values observed in Bavaria, it cannot be determined (centre). If the ecological optimum lies outside the observed range in Bavaria, it cannot be determined likewise. The EPF increases or decreases over the entire range of possible values in these cases (see Fig. 2).

Tabelle 3. Ökologisches Optimum und Amplitude der Standortfaktoren, die zur Modellierung der Waldgesellschaften beitragen (Schwellwert 5 % variable contribution). Das ökologische Optimum des PNV-Typs entspricht der x-Koordinate des Maximums der Glockenkurve der ökologischen Präferenzfunktion (EPF). Das ökologische Minimum ist die x-Koordinate des Schnittpunkt der EPF mit der horizontalen Linie beim Wert = 1, links des Optimum. Das ökologische Maximum entspricht der x-Koordinate des Schnittpunkt der EPF mit der horizontalen Linie beim Wert = 1, rechts des Optimums. Wenn das ökologische Optimum, Minimum oder Maximum außerhalb des in Bayern beobachtbaren Wertebereichs liegt, kann es nicht bestimmt werden (Mitte). In diesem Fall steigt bzw. fällt die EPF über den gesamten Wertebereich (vgl. Abb. 2).

Predictor	Minimum	Optimum	Maximum
Beech forests and mixed beech forests			
1c: *Luzulo-Fagetum*, colline-submontane			
Base saturation of the first 30 cm	2	13	23
Exchangeable calcium (Ca^{2+})	n.a.	11	30
Average annual precipitation sum (1971–2000)	642	794	946
Average annual temperature (1971–2000)	7.5	8.2	8.9
Water balance, May to September	-24	87	199
Floodplain-Index	0.8	1.2	1.5
1cn: *Luzulo-Fagetum*, colline-submontane, precipitation > 1100 mm			
Base saturation of the first 30 cm	6	13	20
Average annual precipitation sum (1971–2000)	928	1182	1435
Water balance, May to September	161	340	518
Average annual potential evapotranspiration	45	n.a.	n.a.
Average annual temperature (1971–2000)	7.1	7.7	8.2

Predictor	Minimum	Optimum	Maximum
1m: *Luzulo-Fagetum*, montane			
Average annual temperature (1971–2000)	5.0	6.1	7.2
Base saturation of the first 30 cm	n.a.	n.a.	13
Average annual precipitation sum (1971–2000)	864	1292	1718
Exchangeable calcium (Ca^{2+})	n.a.	n.a.	18
3c: *Galio odorati-Fagetum*, colline-submontane			
Base saturation of the first 30 cm	27	53	80
Hygroscopic water	145	272	n.a.
Water balance, May to September	-25	65	156
3cn: *Galio odorati-Fagetum*, colline-submontane, precipitation > 1100 mm			
Base saturation of the first 30 cm	29	51	70
Water balance, May to September	223	443	664
Exchangeable potassium (K^{+})	n.a.	n.a.	1.2
Available water capacity	103	133	164
3m: *Galio odorati-Fagetum*, montane			
Average annual precipitation sum (1971–2000)	1119	1980	n.a.
Average annual temperature (1971–2000)	4.1	5.6	7.2
Water conductivity	20	31	42
Hygroscopic water	70	119	169
4: *Hordelymo-Fagetum*			
Base saturation of the first 30 cm	72	88	n.a.
Water balance, May to September	n.a.	n.a.	60
Depth of decalcification	45	70	98
4n: *Hordelymo-Fagetum*, precipitation > 1100 mm			
Base saturation of the first 30 cm	83	100	n.a.
Water balance, May to September	122	315	508
Floodplain-Index	1.2	1.6	2.0
Average annual precipitation sum (1971–2000)	944	1098	1251
6: *Aposerido-Fagetum*			
Base saturation of the first 30 cm	77	100	n.a.
Average annual precipitation sum (1971–2000)	1301	1955	2547
Water balance, May to September	368	690	1006
7c: *Carici-Fagetum*			
Base saturation of the first 30 cm	78	92	n.a.
Water balance, May to September	n.a.	-73	37
Floodplain-Index	1.4	2.1	n.a.
Aspect-Index	1	n.a.	n.a.
7m: *Seslerio-Fagetum*			
Base saturation of the first 30 cm	86	100	n.a.
Average annual precipitation sum (1971–2000)	1617	2269	n.a.
Slope	19	55	n.a.
Water conductivity	n.a.	n.a.	44
Average annual temperature (1971–2000)	n.a.	3.2	6.1
Oak and hornbeam forest			
15: *Calamagrostio arundinaceae-Quercetum petraeae* & *Luzulo-Quercetum petraeae*			
Air capacity	139	292	n.a.
Floodplain-Index	n.a.	n.a.	0.9
Base saturation of the first 30 cm	5	17	29

Predictor	Minimum	Optimum	Maximum
Average annual precipitation sum (1971–2000)	n.a.	646	790
Solar radiation	2704	2853	3002
18: *Galio-Carpinetum*			
Average annual precipitation sum (1971–2000)	n.a.	n.a.	759
Exchangeable magnesium (Mg^{2+})	19	73	n.a.
Water balance, May to September	n.a.	-75	78
Average annual temperature (1971–2000)	8.0	9.7	n.a.
Hygroscopic water	133	272	n.a.
Floodplain-Index	n.a.	0.7	1.1
17: *Stellario-Carpinetum*			
Floodplain-Index	n.a.	n.a.	0.9
Water balance, May to September	-14	76	166
Base saturation of the first 30 cm	11	39	65
Slope	n.a.	n.a.	6
Ravine forest			
24: *Aceri-Tilietum platyphylli*			
Average annual precipitation sum (1971–2000)	1270	1990	n.a.
Slope	16	36	55
Available water capacity	n.a.	n.a.	133
Water conductivity coefficient	16	30	43
Alluvial and wet lowland forests			
35: *Pruno-Fraxinetum*			
Floodplain-Index	n.a.	n.a.	0.6
37: *Stellario nemorum-Alnetum glutinosae*			
Floodplain-Index	n.a.	n.a.	1.0
Base saturation of the first 30 cm	10	31	53
Slope	n.a.	n.a.	9
Solar radiation	2438	2698	2959
Water balance, May to September	93	287	480
Water conductivity coefficient	n.a.	n.a.	42
38: *Alnetum incanae*			
Base saturation of the first 30 cm	100	100	n.a.
Floodplain-Index	0.4	0.5	0.6
39: *Querco-Ulmetum* & *Salicetum albae*			
Base saturation of the first 30 cm	88	100	n.a.
Floodplain-Index	n.a.	n.a.	0.8
Growing degree days	1741	1853	1965
Average annual precipitation sum (1971–2000)	679	789	900
Exchangeable magnesium (Mg^{2+})	7	11	14
Bog woodland			
33: *Piceo-Vaccinienion*			
Organic matter	28	49	n.a.
Available water capacity	514	600	n.a.
28: *Bazzanio-Piceetum*			
Organic matter	12	41	n.a.
Hygroscopic water	139	272	n.a.
Exchangeable potassium (K^+)	0.4	0.4	0.4

Predictor	Minimum	Optimum	Maximum
Mesophytic and hygromesophytic coniferous and mixed broad-leaved-coniferous forests			
11: *Galio rotundifolii-Abietetum*			
Average annual precipitation sum (1971–2000)	1134	1869	2547
Floodplain-Index	n.a.	n.a.	1.0
Hygroscopic water	89	142	192
Water conductivity	11	26	41
29: *Calamagrostio villosae-Piceetum*, T < 5 °C			
Average annual temperature (1971–2000)	3.4	4.2	5.0
Exchangeable calcium (Ca^{2+})	n.a.	n.a.	10
29t: *Calamagrostio villosae-Piceetum*, T > 5 °C			
Average annual temperature (1971–2000)	5.3	6.1	6.9
Floodplain-Index	n.a.	n.a.	0.9
Base saturation of the first 30 cm	n.a.	n.a.	20
30: *Adenostylo glabrae-Piceetum*			
Average annual temperature (1971–2000)	1.9	3.3	4.6
Average annual precipitation sum (1971–2000)	1741	2089	2424
Base saturation of the first 30 cm	66	86	n.a.
Subalpine dwarf shrub vegetation			
31: *Erico-Mugetum*			
Base saturation of the first 30 cm	86	100	n.a.
Average annual temperature (1971–2000)	n.a.	n.a.	5.4
Aridity-Index	107	n.a.	n.a.
Slope	21	49	n.a.

the species-poor oligotrophic *Luzulo-Fagetum*, occurring in the colline-submontane belt (Fig. 2): the minimum is 2%, the optimum 13% and the maximum 30%. Compared with the interval of the range of base saturation all over the forested area in Bavaria (horizontal box-plot), the *Luzulo-Fagetum* colline-submontane occurs at soils with low base saturation.The three most important zonal forest types of the colline-submontane belt in Bavaria – *Luzulo-Fagetum*, *Galio odorati-Fagetum* and *Hordelymo-Fagetum*, clearly follow a gradient of increased base saturation (Fig. 2). Wheras *Luzulo-Fagetum* and *Hordelymo-Fagetum* occupy a small range of the gradient *Galio odorati-Fagetum* and *Galio-Carpinetum* seize a broad intervall.

Thirdly, we present the **probability maps** for selected forest types (Fig. 3). From Table 2, 3 we obtain contribution and ecological preference of variables that were used to calculate the probalitiy of occurrence in each grid cell. Exemplary we focus on the most widespread type, the *Luzulo-Fagetum*. It occurs on soils with low base saturation in colline-submontane forms (Fig. 3a–b) below 23% base saturation, and in a montane form (Fig. 3c), below 13% base saturation; the three typs differ in average annual temperature and in average annual precipitation sum. The colline-submontane forms of the *Luzulo-Fagetum* prefers temperatures between 7.1 °C and 8.9 °C, whereas montane forms occur from 5.0 °C to 7.2 °C. The colline-submontane form can be divided in variants with low and high precipitation, respectively. The water balance of the latter is positive during the vegetation period. It occurs in the foothills of the Alps, the foothills of the Bavarian forests and in the western Spessart hills.

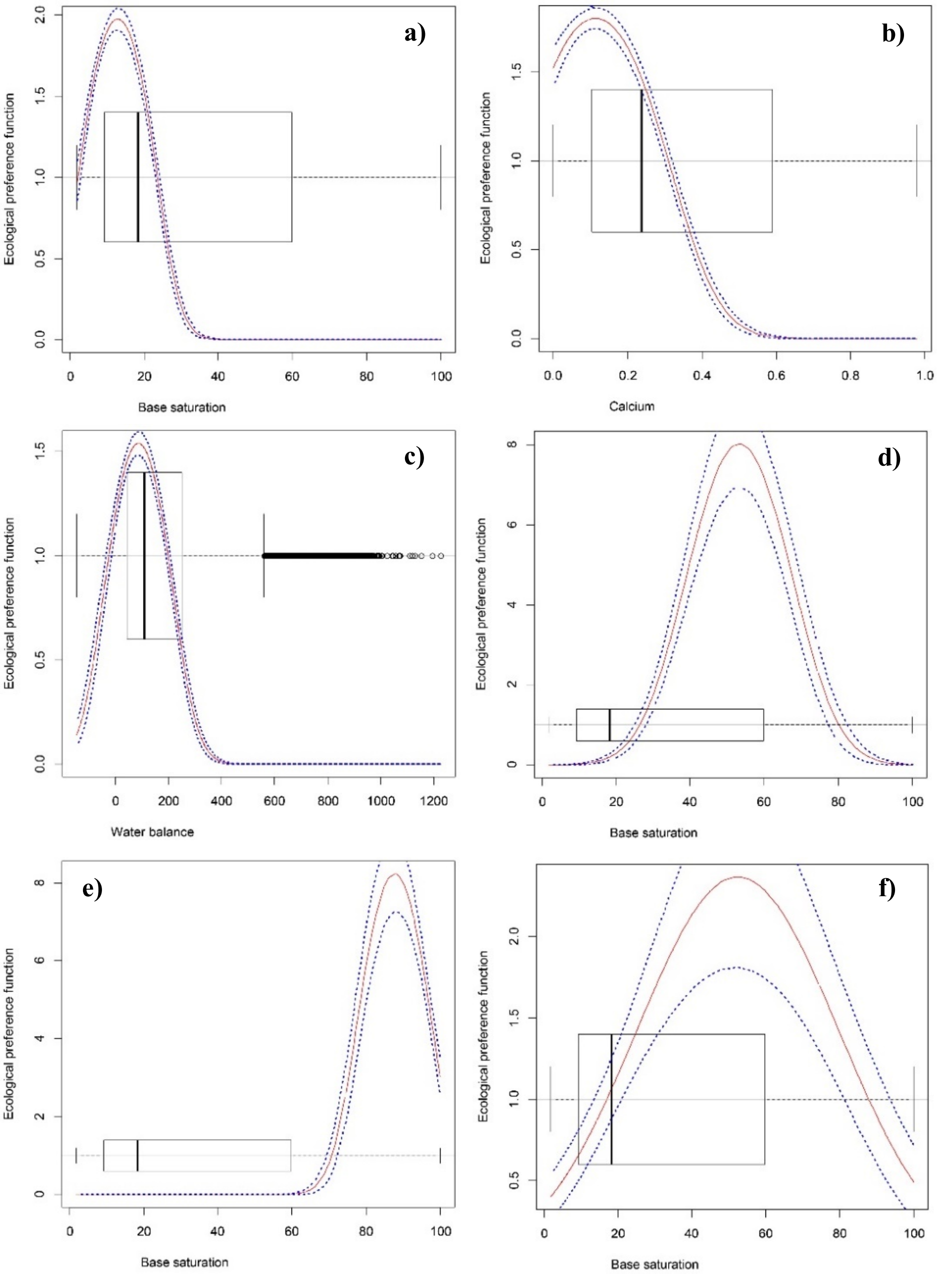

Fig. 2. Examples of Ecological Preference Function (EPF, red curve), most contributing predictors used to simulate *Luzulo-Fagetum*, colline-submontane: **a)** base saturation, **b)** calcium, **c)** water balance and EPF of **d)** *Galio odorati*- and **e)** *Hordelymo-Fagetum*, colline to submontane forms and **f)** *Galio-Carpinetum* regarding base saturation. The box-plot describes the range and quartiles of the predictor overall Bavaria (forested area). The ecological optimum is the position of the maximum of the bell shaped ecological preference function. The ecological minimum is the intersection of the EPF with the horizontal line at EPF = 1 left of the optimum, the ecological maximum is the intersection right of the optimum, respectively. If the ecological minimum or maximum lies outside the range of values

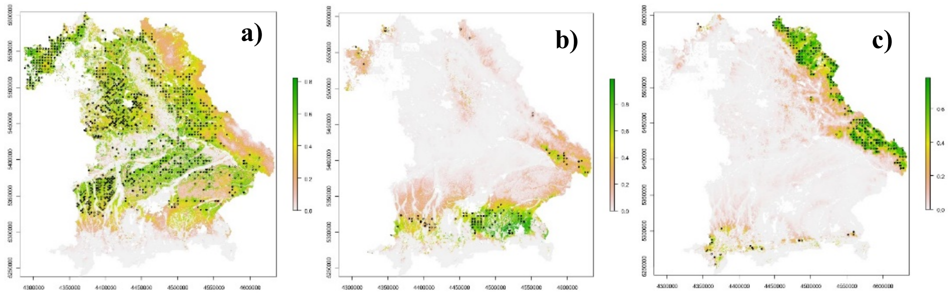

Fig. 3. Probability map of **a)** *Luzulo-Fagetum*, colline-submontane, **b)** *Luzulo-Fagetum*, colline-submontane, precipitation > 1100 mm and **c)** *Luzulo-Fagetum*, montane in Bavaria; black dots represent sampling points of the national forest inventory the forest type was observed in the field.

Abb. 3. Wahrscheinlichkeitskarte für **a)** das *Luzulo-Fagetum*, collin, **b)** *Luzulo-Fagetum*, collin bis submontan, Niederschläge > 1100 mm und **c)** das *Luzulo Fagetum*, montan in Bayern; die schwarzen Punkte entsprechen Vorkommen der Waldgesellschaft an den Inventurpunkten der BWI2.

Mesotrophic to eutrophic beech forests of the colline-submontane belt are represented by the *Hordelymo-Fagetum* (Fig. 4a–b) in 2 variants. Whereas the optimum of the first lies below zero the type occurring in the foothills of the Alps show a positive water balance. The corresponding pre-Alpine type is the *Aposerido-Fagetum*, which extends from the lower montane to the altimontane belt of the Alps (Fig. 4c). Positive water balance characterises it.

Under dry and nutrient-poor conditions, i.e. sandy soils indicated by high air capicity, low precipitation and low base saturation, species-poor acidophilous oak forests occur (Fig. 4d). Dry conditions, negative water balance based on low precipitation and high evapotranspiration rates as well as Mg-rich, clayey (high values of hygroscopic water) soils induce the emergence of *Galio-Carpinetum,* oak-hornbeam-forests (Fig. 4f) whereas the *Stellario-Carpinetum* occurs on the brink of the floodplain (Fig. 4e).

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observed in Bavaria, it cannot be determined (2b and e). If the ecological optimum lies outside the observed range in Bavaria, it cannot be determined likewise. The EPF increases or decreases over the entire range of possible values in these cases.

Abb. 2. Beispiele zur ökologischen Präferenzfunktion (rote Kurve), Umweltvariablen, die maßgeblich zur Simulation des *Luzulo-Fagetum*, collin-submontan beitragen: **a)** Basensättigung, **b)** Ca-Gehalt, **c)** Wasserbilanz; EPF **d)** *Galio odorati-* und **e)** *Hordelymo-Fagetum*, colline bis submontane Formen und **f)** *Galio-Carpinetum* hinsichtlich der Basensättigung. Der Boxplot beschreibt die Spannweite und die Quartilen der Standortvariablen für die bewaldete Fläche Bayerns. Das ökologische Optimum des PNV-Typs entspricht der x-Koordinate des Maximums der Glockenkurve der ökologischen Präferenzfunktion. Das ökologische Minimum ist die x-Koordinate des Schnittpunkt der EPF mit der horizontalen Linie beim Wert = 1, links des Optimums. Das ökologische Maximum entspricht der x-Koordinate des Schnittpunkt der EPF mit der horizontalen Linie rechts des Optimums. Wenn das ökologische Optimum, Minimum oder Maximum außerhalb des in Bayern beobachtbaren Wertebereichs liegt, kann es nicht bestimmt werden (2b und e). In diesem Fall steigt bzw. fällt die EPF über den gesamten Wertebereich.

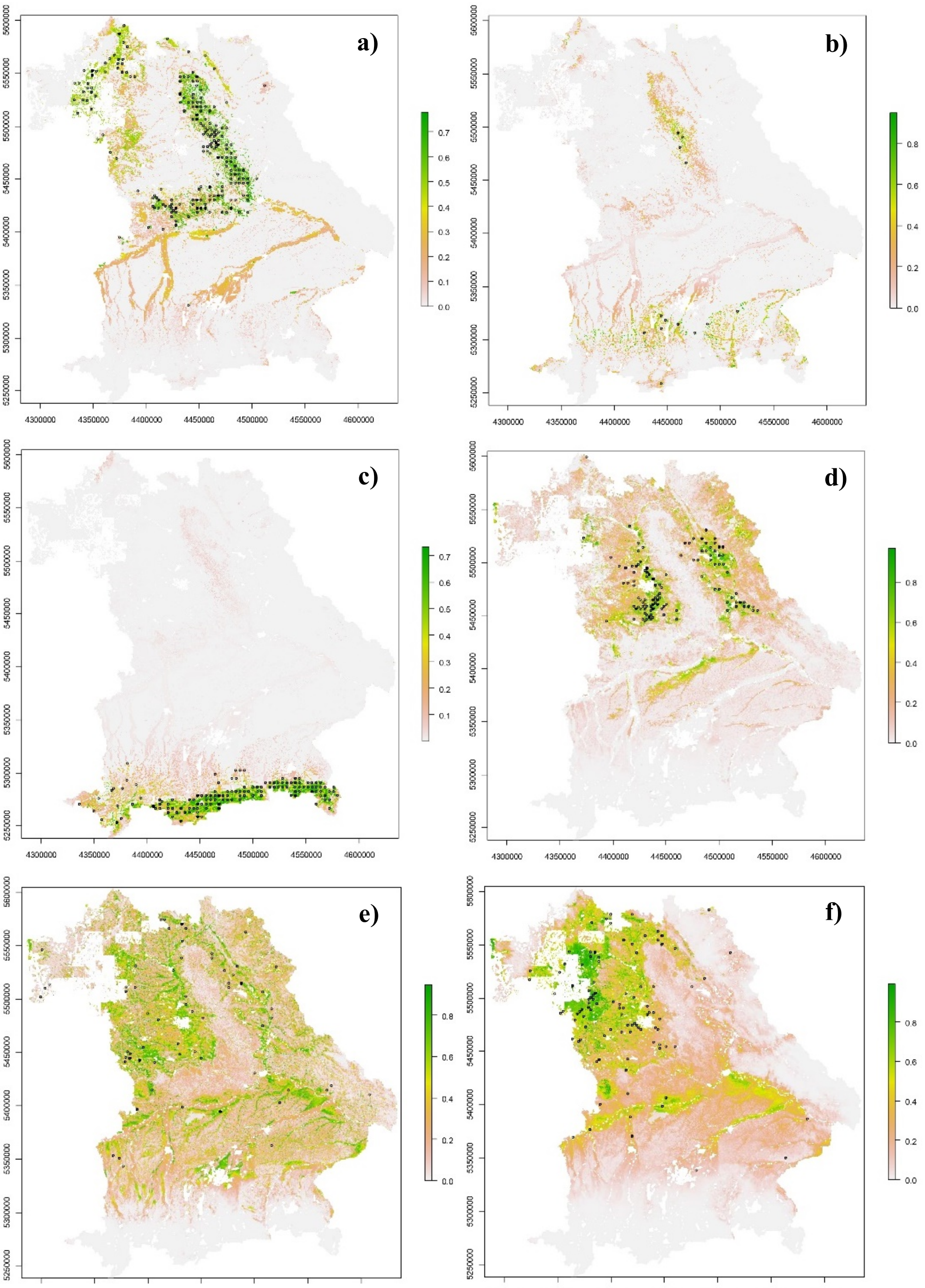

Fig. 4. Examples for probability maps of forest types in Bavaria: **a)** *Hordelymo-Fagetum,* colline-submontane, **b)** *Hordelymo-Fagetum*, colline-submontane, average annual precipitation sum > 1100 mm, **c)** *Aposerido-Fagetum*, **d)** *Calamagrostio arundinaceae-Quercetum petraeae* & *Luzulo-Quercetum petraeae* colline-submontane, **e)** *Stellario-Carpinetum*, colline (to submontane), **f)** *Galio-Carpinetum*, colline-submontane; black dots represent sampling points of the national forest inventory the forest type was observed in the field.

3.2 PNV units, future climate scenarios

The changes in distribution of forest types in Bavaria under one (out of 15 modelled) climate change scenarios (as an example: +2 K, without change in precipitation) is outlined for four different PNV units (Fig. 5a–d). Areas marked in green indicate that the conditions correspond to the same PNV unit today and in the respective future scenario, being an area without major change. Blue colour indicates areas the distribution of the PNV unit expands to whereas the PNV unit vanishes in red-labelled regions. As the MaxEnt-method cannot make reliable predictions in regions with site conditions lying outside the recent range of values, these regions are coloured in vanilla in the current version of the model – an extended version is currently developed (see discussion); mostly the temperature value exceeds the highest one actually observed. The mountain mixed forest on calcareous soils (*Aposerido-Fagetum*, Fig. 5a) will retreat from the Alpine foreland towards higher elevations of the Alps. The mountainous *Luzulo-Fagetum* (Fig. 5b) will almost totally disappear, the colline-submontane *Carici-Fagetum* (Fig. 5c) will hold its status in the Franconian Alb, and the *Galio-Carpinetum* oak-hornbeam forests (Fig. 5d) will spread intensively.

Alternatively, Figure 6 shows what will happen to the currently most widespread PNV unit in Bavaria, the colline-submontane type of the species-poor oligotrophic beech forests (*Luzulo-Fagetum*, Fig. 6a) under different climate scenarios (Fig. 6b–f). Rising temperature (precipitation not modified) changes the distribution step by step: *Luzulo-Fagetum*, colline-submontane will still be widespread under the +1 K scenario (Fig. 6b) and is even starting to conquer areas in the higher mountains in the Northeast and South of Bavaria. While with more increasing temperature (Fig. 6c–f), it will retreat more and more to mountain regions, while in a +6 K scenario it will almost totally disappear from Bavaria. If the temperature increases strongly, such site conditions, which do not yet exist in Bavaria, will arise in large parts of Bavaria (coloured in vanilla). No reliable prediction of PNV unit in the model is possible at these places to date.

3.3 Present day PNV map of Bavaria and future PNV-scenarios maps

As a major first result, we compiled the map of potential natural vegetation for Bavaria with a resolution of 50 m to 50 m pixels (Fig. 7), by assembling the single probability maps of the forest types together into one map. The map shows the distribution of the PNV units under recent site conditions. Shades of green highlight site conditions characteristic for different types of beech forests. The light green in the NW indicates beech forests on acidic soils in the colline-submontane belt, dark green symbolises the mountain mixed forest along the northern fringe of the Alps, and the blue-green hook in the centre of Bavaria represents the colline-submontane beech forest on calcareous soils. The yellow to reddish marked areas in the Bavarian uplands correspond to mixed oak-hornbeam and species-poor acidophilous oak

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Abb. 4. Exemplarische Darstellung der Wahrscheinlichkeitskarten verschiedener PNV-Typen in Bayern: **a)** *Hordelymo-Fagetum*, **b)** *Hordelymo-Fagetum*, Niederschläge > 1100 mm, **c)** *Aposerido-Fagetum*, **d)** *Calamagrostio arundinaceae-Quercetum petraeae* & *Luzulo-Quercetum petraeae*, **e)** *Stellario-Carpinetum*, **f)** *Galio-Carpinetum*. Die schwarzen Punkte entsprechen Vorkommen des PNV-typs an den Inventurpunkten der Bundeswaldinventur (BWI2).

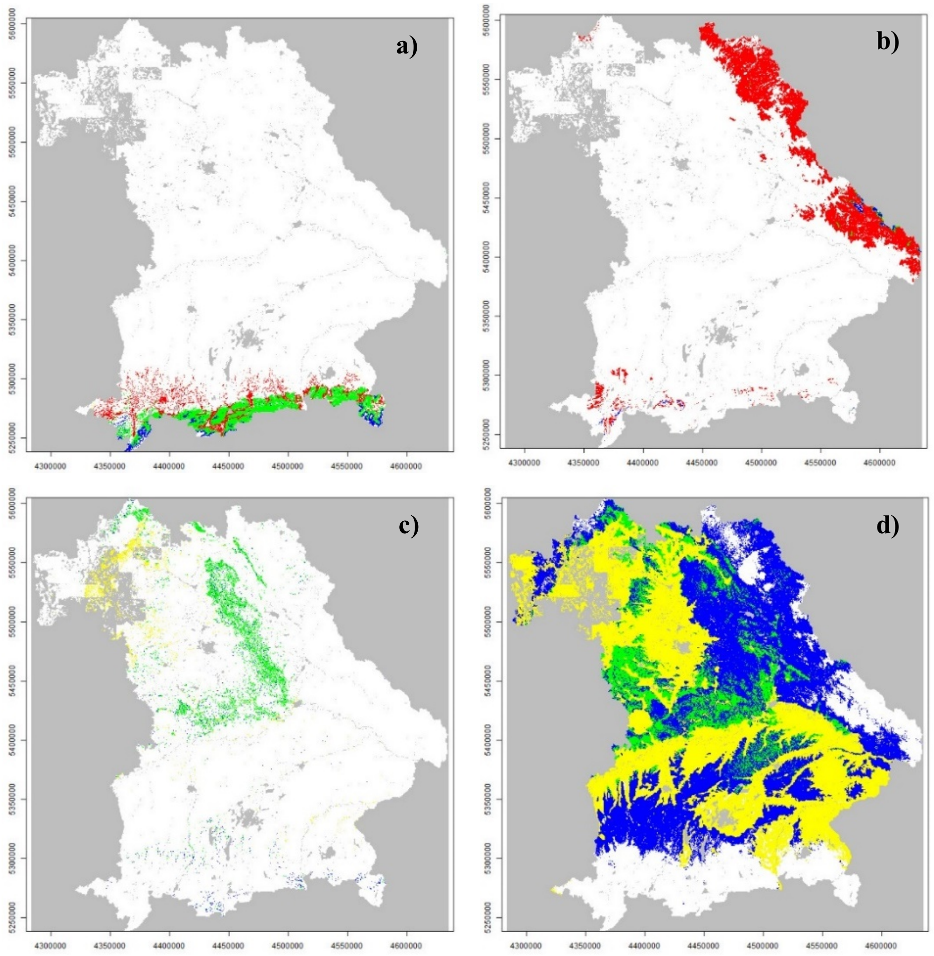

Fig. 5. Distribution of different forest types in Bavaria in one selected scenario: +2 K (change2T): **a)** *Aposerido-Fagetum*; **b)** *Luzulo-Fagetum*, montane; **c)** *Carici-Fagetum*; **d)** *Galio-Carpinetum*. White: Absence in present PNV and in scenario; green: Occurrence in present PNV and in scenario; blue: Gain in scenario; red: Loss in scenario; vanilla: site conditions in scenario lay beyond the current range of site conditions in Bavaria regarding the forest type.

Abb. 5. Vorkommen verschiedener PNV-Typen in Bayern in einem ausgewählten Szenarium: +2 K (change2T): **a)** *Aposerido-Fagetum*; **b)** *Luzulo-Fagetum*, montane; **c)** *Carici-Fagetum*; **d)** *Galio-Carpinetum*. Weiß: Kommt **nicht** in der heutigen PNV und auch nicht im Szenarium vor; grün: Kommt in der heutigen PNV und im Szenarium vor (unverändert); blau: Zugewinn im Szenarium; rot: Verlust im Szenarium; vanille: Standortbedingungen im Szenarium liegen außerhalb des heutigen Wertebereichs der Standortbedingungen des PNV Typs in Bayern.

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Abb. 6. Aktuelle Verbreitung des häufigsten PNV-Typs, *Luzulo-Fagetum*, colline-submontane **a)** und dessen Verbreitung in verschiedenen Szenarien **b)** +1 K, **c)** +2 K, **d)** +3 K, **e)** +4 K, **f)** +6 K; ohne Veränderung der Niederschläge. Farberklärung siehe Abbildung 5.

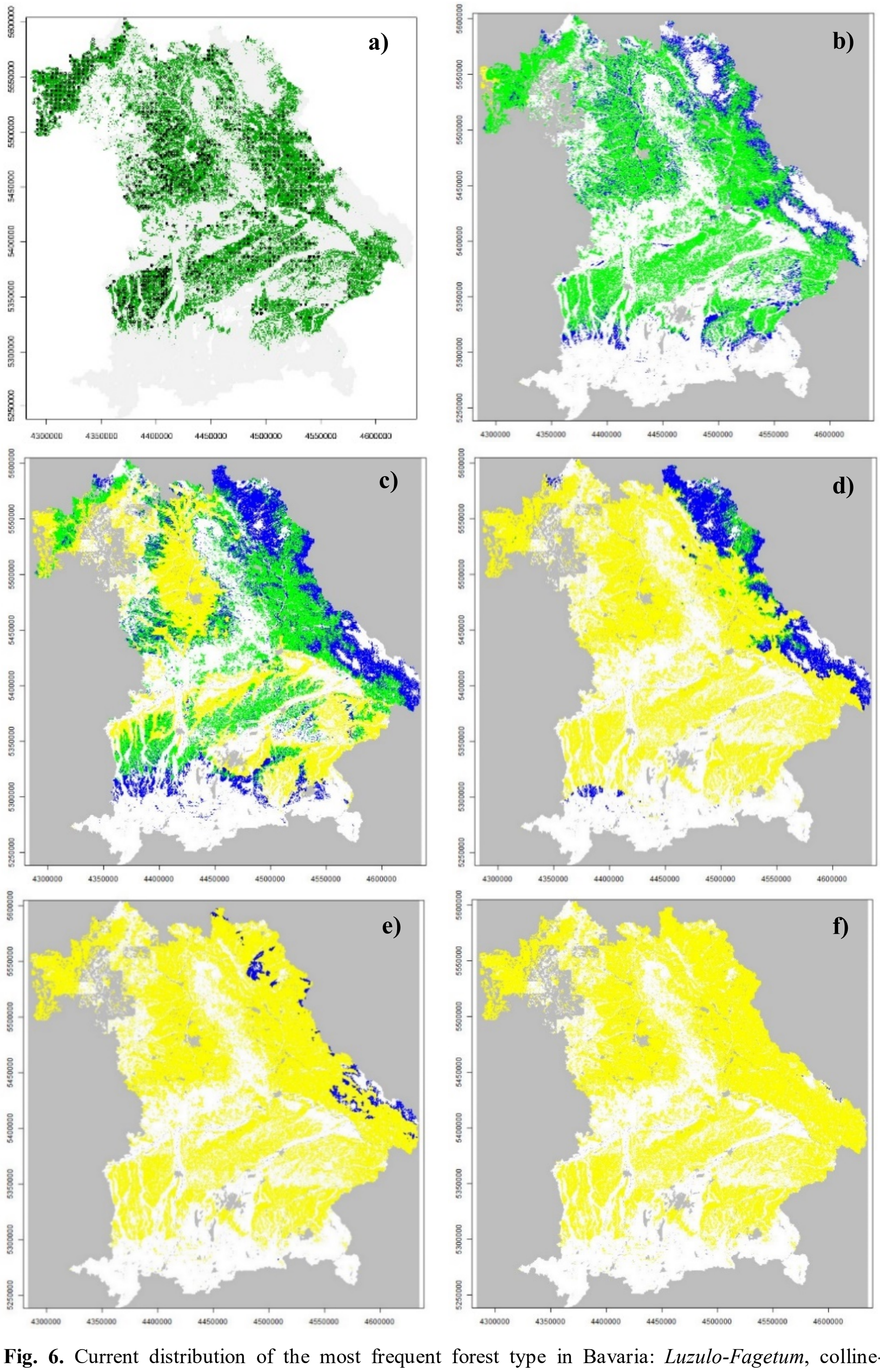

Fig. 6. Current distribution of the most frequent forest type in Bavaria: *Luzulo-Fagetum*, colline-submontane: **a)** and its distribution in different scenarios: **b)** +1 K, **c)** +2 K, **d)** +3 K, **e)** +4 K, **f)** +6 K; without any change in precipitation. Colour explanation: see Figure 5.

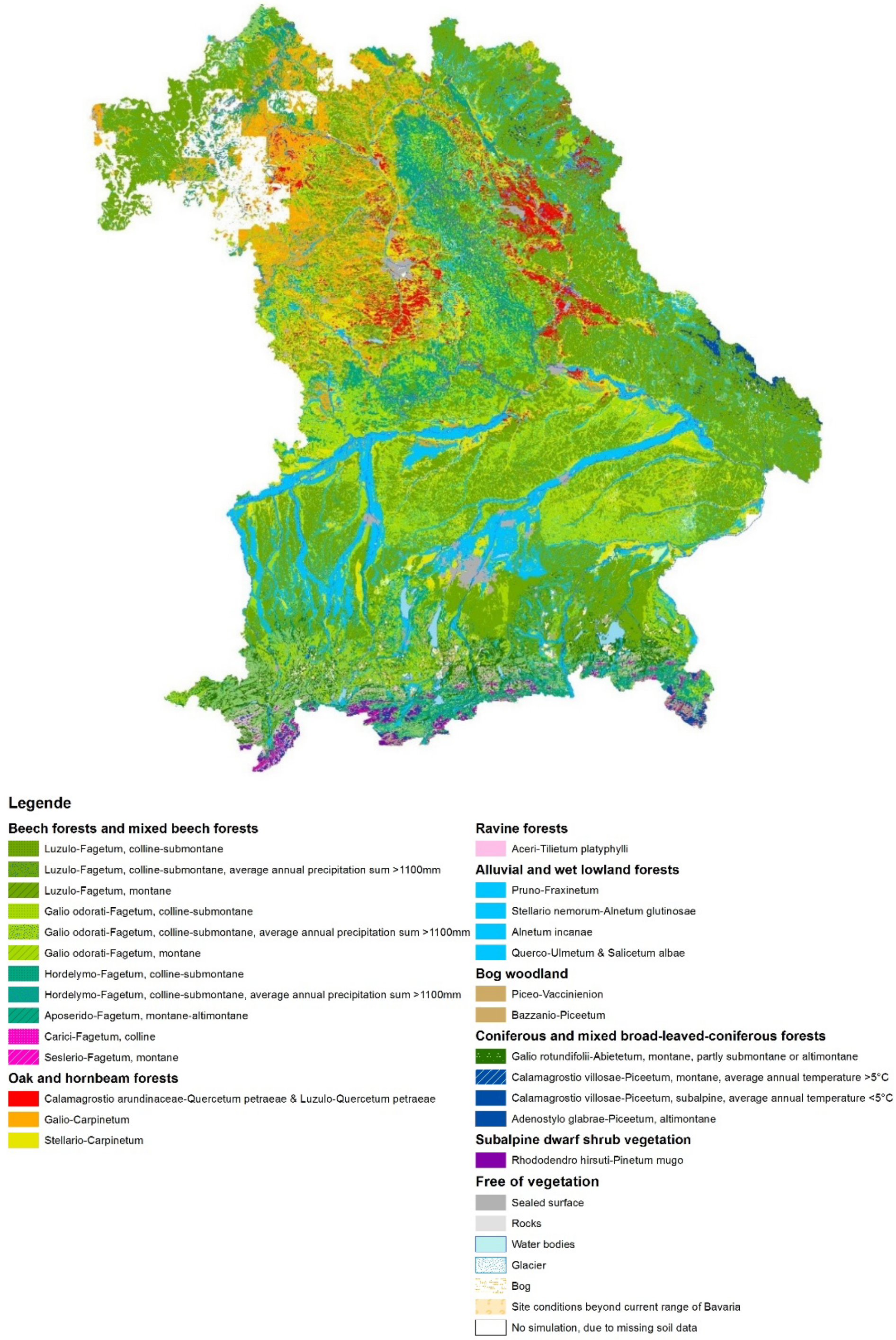

Fig. 7. Map of simulated potential natural vegetation of Bavaria under recent site conditions.

Abb. 7. Karte der simulierten heutigen potentiell natürlichen Vegetation von Bayern.

forests, respectively, and the blue colour symbolize forests connected to riverbeds. Altogether the map reflects the topography, soil characteristics, temperature and precipitation of Bavaria very well. In detail, each PNV unit indicates the site factors it depends on (Table 2–3).

Determining the most probable PNV unit for each pixel, synoptic maps for different climate scenarios can be constructed (Fig. 8b–e) and be compared to the one under recent climate conditions (Fig. 8a). The +1 K scenario (Fig. 8b) shows a moderate change in the distribution of PNV units, respectively, site conditions in the study area, but for almost the whole of Bavaria, constellations of site conditions appear, which also exist at present (may be at other localities). Starting with the +2 K scenario, the area with constellations of site conditions, which do not exist in Bavaria at present, will increase from 36% in the +2 K scenario to 94% in the +4 K scenario.

The results cannot only be represented on small-scale outline maps as in Figure 8, but also it is possible to zoom in to 50 m x 50 m pixels, which can be seen separately Figure 9.

Figure 10 displays the proportions of forest types and the proportion of areas out of the recent range of site conditions (non-analogue climate, FITZPATRICK & HANGROVE 2009) within Bavaria (recent vegetation) and in different scenarios (+1 K, +2 K, +3 K, +4 K, +6 K and modified precipitation). The vanilla area increases drastically, indicating an enormous change in site conditions towards conditions that do not exist at present in the study area. Comparing the scenarios with and without change in precipitation, an increasing precipitation leads to a higher proportion of beech forests, whereas decreasing precipitation gives an advantage to oak and hornbeam forests.

4. Discussion

With the model presented above we achieved our two goals to (1) develop a model to generate maps of the current PNV and (2) predict future PNV under different climate change scenarios.

Our approach to assess the impact of climate change on land use capability focuses on changing site conditions. PNV is a concept to characterise complex site conditions composed of edaphic, geomorphological and climatic factors in phytosociological terms. Most of the vegetation maps of today are static (EUROPEAN ENVIRONMENT AGENCY 2014), in the sense of referring to one fixed point in time (usually: the present day). This holds not only for maps of today's potential vegetation (e.g. BOHN et al. 2000/2003), but as well for any kind of vegetation maps developed for management planning in Natura 2000 or assessment of protected areas and landscape planning in general.

However, in times of global change, a dynamic concept is required, being able not only to display the current site conditions, but as well as to predict the spatial distribution of future site conditions at a local level. Therefore, maps of future site constellations are necessary in a detailed resolution to meet requirements of any kind of landscape planning and landscape management including forestry, agriculture and nature conservation.

Two maps of PNV in Bavaria already exist: One compiled by SEIBERT (1968) and another one by SUCK & BUSHART (2012). They display the site conditions at the times when or before they were compiled. Even more: differences between the two maps might not only reflect changes in site conditions, but also, different expert based perception of natural vegetation (cf. WILDI 2013). In practice, PNV maps are required for the respective management level. However, the existing (static) PNV maps have a fixed coarse scale of 1:500,000. They are hardly helpful if applied to a fine scale.

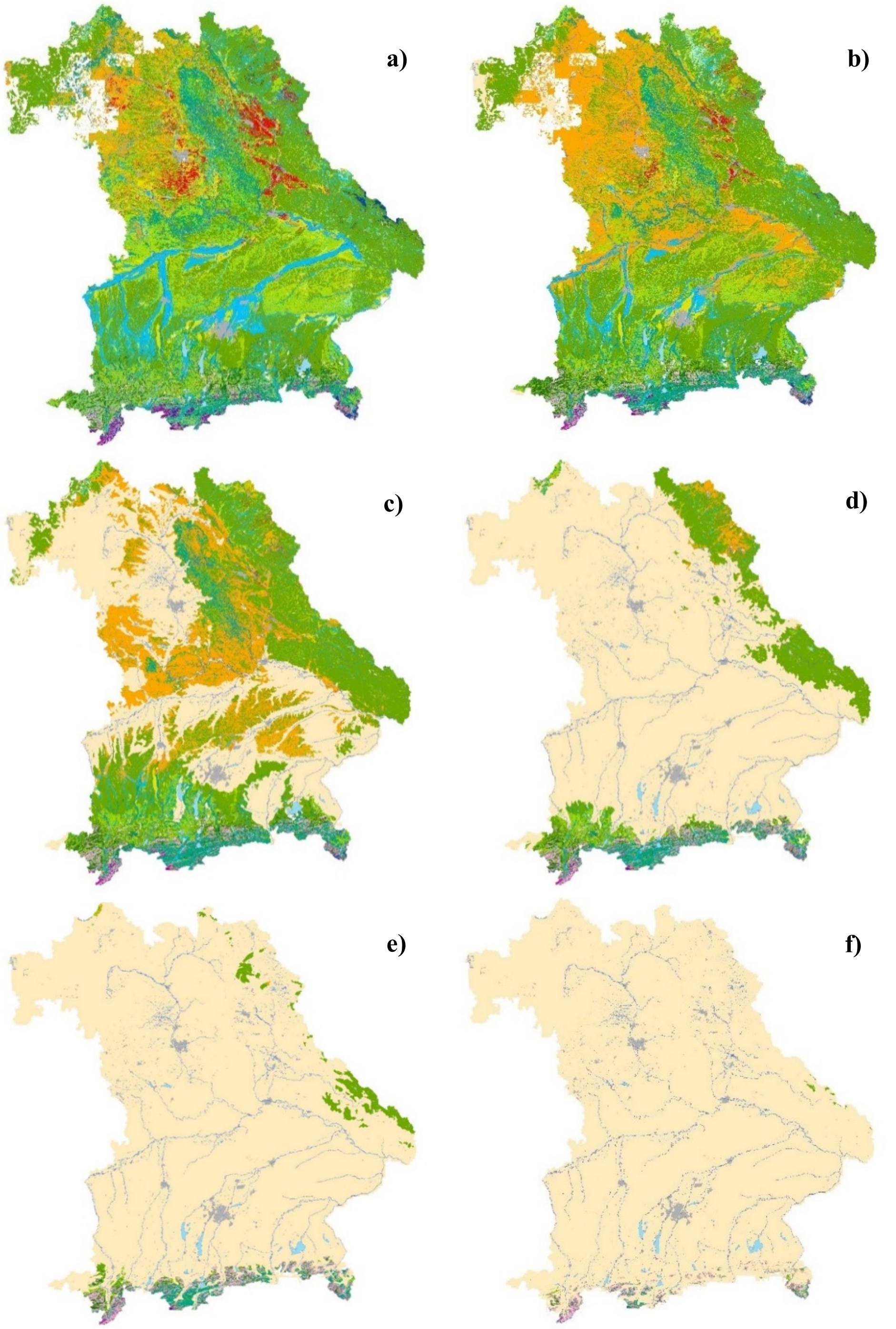

Fig. 8. Map of present PNV **a)** and future PNV in scenario **b)** +1 K, **c)** +2 K, **d)** +3 K, **e)** +4 K, **f)** +6 K; legend see Figure 7.

Abb. 8. Karte der heutigen PNV **a)** und der zukünftigen PNV im Szenarium **b)** +1 K, **c)** +2 K, **d)** +3 K, **e)** +4 K, **f)** +6 K; Legende siehe Abbildung 7.

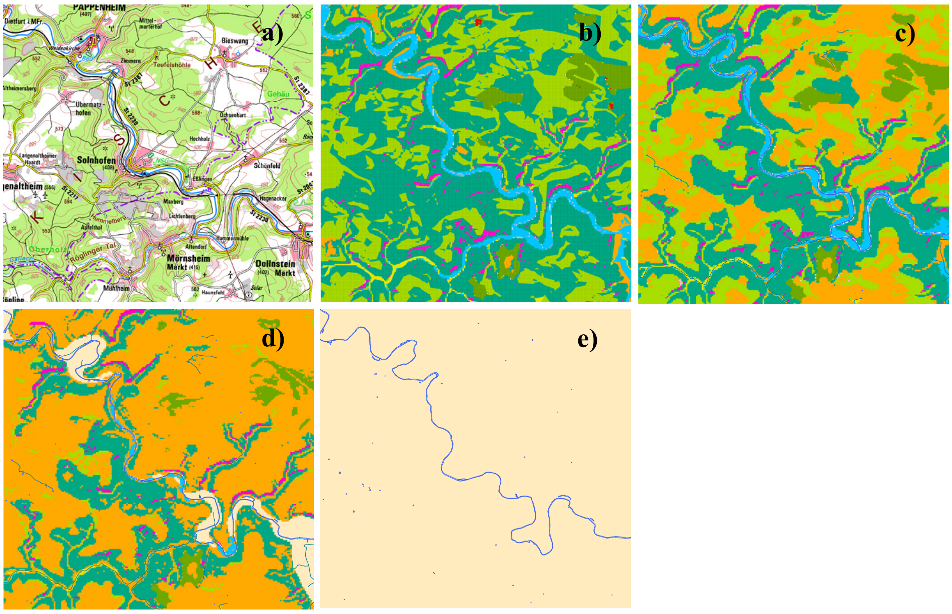

Fig. 9. Details of simulation, Altmühl valley; recent and future distribution of PNV. **a)** Topographic map (10 x 10 km sample; source Geobasisdaten: © Bayerische Vermessungsverwaltung; www.geodaten.bayern.de); **b)** recent PNV; scenarios: **c)** +1 K, **d)** +2 K, **e)** +3 K, Legend see Figure 7.

Abb. 9. Kartenausschnitt Altmühltal; heutige und zukünftige PNV. **a)** Topographische Karte (10 x 10 km; Quelle Geobasisdaten: © Bayerische Vermessungsverwaltung; www.geodaten.bayern.de); **b)** heutige-PNV; Szenarien: **c)** +1 K, **d)** +2 K, **e)** +3 K; Legende siehe Abbildung 7.

We generated maps of the PNV based on algorithms (MaxEnt) with high spatial resolution of 50 m x 50 m. This approach allows for predicting its distribution under current and different future site conditions. The model predicts a certain PNV unit at a specific point in the landscape as an expression of the site conditions that correspond today to this PNV unit in modified climate scenarios. It does not address the future real vegetation.

HICKLER et al. (2012) used a generalised dynamic vegetation model to simulate the growth of 20 species and plant functional types. From these 12 formations are derived for whole Europe. They used a very coarse grid of approximately 18.5 km x 12 km. The model predicted at the level of vegetation formation a moderate change of 31% of the surface of Europe in a +2.9 K scenario and of 42% in a +4.9 K scenario, respectively. This small rate of change seems to be due to the coarse classification. MÜCHER et al. (2015) used MaxEnt to generate habitat suitability maps with 1 km spatial resolution for 28 EUNIS forest habitat types (EUROPEAN ENVIRONMENT AGENCY 2018) of Europe. The authors used, like HICKLER et al. (2012), a coarse thematic resolution (only level 2 of EUNIS classification system), whereas our simulation is mainly based on a detailed classification at the level of phytosociological associations.

Modelling PNV under different climate change scenarios leads to certain constellations of site conditions disappearing at one place and getting realized at another, but as well completely new constellations may appear. Planning landscape management e.g. selection of tree

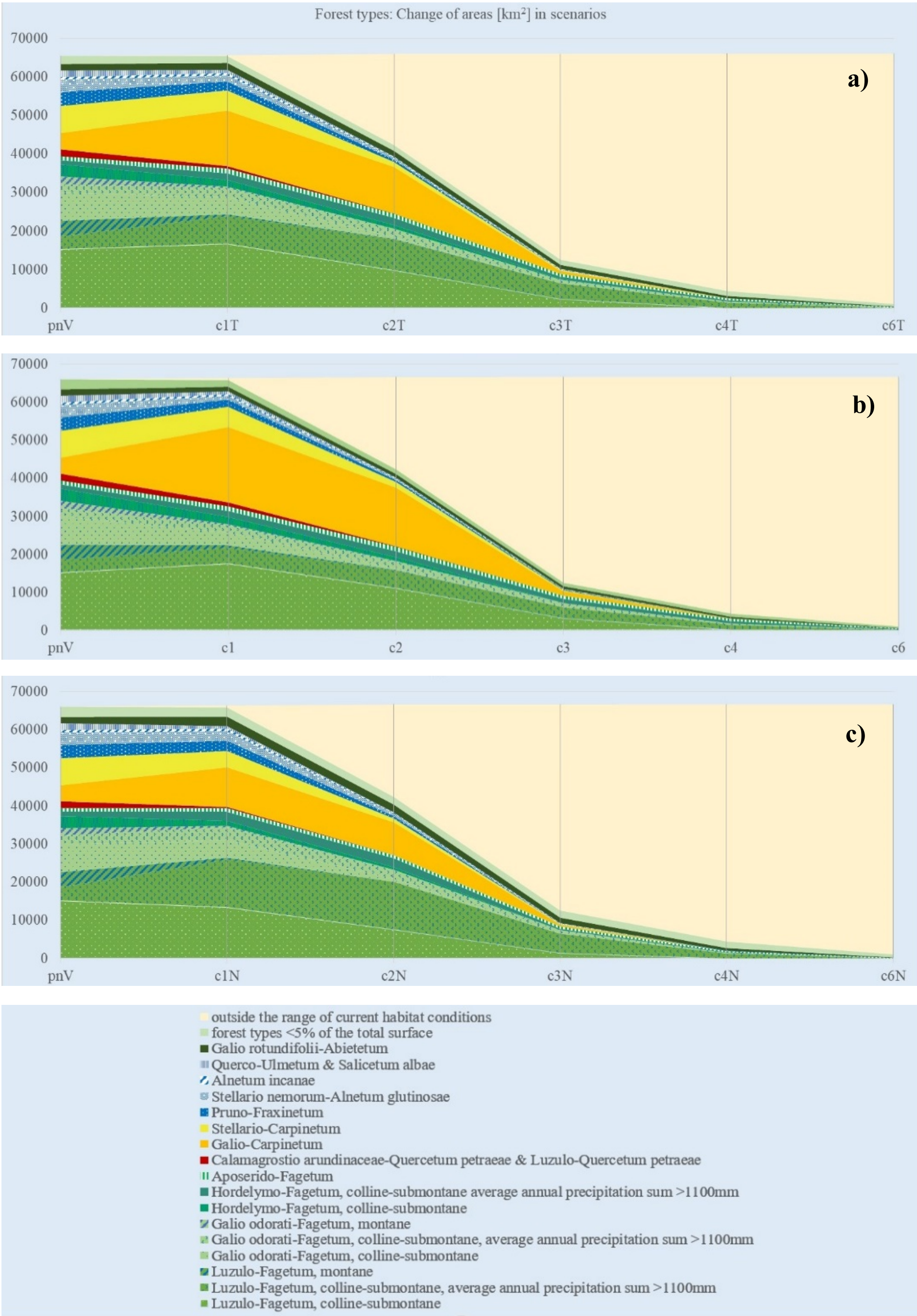

Fig. 10. Surface areas of PNV of Bavaria under current situation (pnV) and in scenarios with increasing temperature (+1 K, +2 K, +3 K, +4 K +6 K) and changing precipitation **a)** only temperature increase (c1T–c6T): +1 K to +6 K; **b)** temperature increase and precipitation decrease (c1T–c6): +1 K, -10% precipitation to +6 K, -10% precipitation; **c)** temperature increase and precipitation increase (c1N–c6N): +1 K, +10% precipitation to +6 K, +10% precipitation.

species for forestry, managing of protected areas or habitats of endangered species, essentially relies on knowledge of how climate change will impact the future site conditions. It is imperative to have a certain idea of what the site conditions could look like in the future, of which alternatives exist, and of which kind of vegetation patterning could be realized under different scenarios.

Previously unknown constellations of site conditions may appear in a landscape. In this case, the sample used to calibrate the model should be extended by observations outside the region under observation. Only regions outside the landscape under observation can contribute to gain knowledge about the PNV corresponding to the new constellation, thus requiring a "space-for-time substitution" approach (not included in this case study). This can be done by subsequent analysis of the interactive version of the vegetation map of Europe (BOHN et al. 2000/2003).

In order to describe the dependence of vegetation types on site factors, we started with 146 predictors. Discriminant analysis showed that all but three available site factors significantly contribute to the differentiation of forest types. However, many of them have only a minor influence as their small F-value indicates; their significance is only due to the large sample size (n = 7,504). Moreover, many of them are highly correlated. With the help of 24 of them, site characteristics of 26 different forest types in Bavaria can be determined, all together covering nearly the total area of Bavaria.

WALENTOWSKI et al. (2013) compiled characteristics of plant communities. However, until to date these descriptions are based on experts' opinions or local studies in small areas. Our results revealed several new findings and specifications. We added the EPF of particular site variables. The EPF describes, based on the statistical distribution of the predictors and on probabilistic foundation, sound and evidence based, quantitatively the ecological amplitude and optimum regarding a specific plant community (Table 3). Furthermore, WALENTOWSKI et al. (2013) gave a fixed set of site factors for all plant communities. The results of the model enable us to select the most relevant predictor that affect significantly a specific forest type.

Base saturation affects 69% of all forest types. Typically *Luzulo-Fagetum* (1c, 1cn, 1m) on soils with low base saturation (below 30%) and *Hordelymo-Fagetum* (4, 4n) occurs on soils with very high (above 80%) base saturation. But some like types of *Galio odorati-Fagetum,* montane and *Galio-Carpinetum* (18) occupy a wide intermediate range of the base saturation gradient. *Galio odorati-Fagetum*, colline-submontane is influenced by negative water balance whereas the *Galio odorati-Fagetum, colline-submontane,* precipitation > 1100 mm in the foothills of the Alps faces shortage of potassimum. The NFSI confirms the later result (WELLBROCK et al. 2016). The montane form occur on loamy soils (intermediate range of water conductivity and hygoscopic water, positive water balance) and *Galio-Carpinetum* (18) depends on other site factors such as magnesium- rich, clayey soil and low

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Abb. 10. Flächenbilanz der PNV-Typen der heutigen PNV und Szenarien der zukünftigen PNV in Bayern; mit steigender Temperatur (+1 K, +2 K, +3 K, +4 K, +6 K) und veränderten Niederschlägen **a)** nur Temperaturanstieg (c1T–c6T): +1 K bis +6 K; **b)** Temperaturanstieg und Niederschlagsreduzierung (c1–c6): +1 K, -10 % Niederschläge bis +6 K, -10% Niederschläge; **c)** Temperaturanstieg und Niederschlagsanstieg (c1N–c6N): +1 K, +10 % Niederschläge bis +6 K, +10 % Niederschläge.

water balance. Ravine forests occure in our model only on steep slopes in the Alpine region. We could improve the model by adding the sky view. Alluvial and wet lowland forests depend mainly on the flood plain index. For subalpine spruce forests on acid soils (29), the model selected Ca^{2+} as a site factor, which is very low and correlated, but not collinear, with base saturation.

Climatic parameters are the next important predictors. This conforms to H.S. FISCHER et al. (2014) who analysed vegetation, soil and climatic data from mountain forests of the Bavarian Alps. They found that in the understorey, edaphic and climatic variables contributed almost equally to explain species composition. ZICHE et al. (2016) analysed vegetation and soil data (n = 1,838 plots) that were recorded in the national forest soil inventory (NFSI II, WELLBROCK et al. 2016) and pointed out that base saturation explains the species composition of the understorey best. Moreover, base saturation is positively correlated with Ca^{2+}, Mg^{2+}, K^{+}, P-nutrition and pH. Climatic conditions appeared as the second independent gradient in the ordination.

We generated a probability map for each of the 26 modelled forest types for each scenario. It displays the spatial distribution of the probability of the occurrence of the forest type. Unlike a traditional map, the probability map has fuzzy boundaries, rather than crisp ones. Therefore, this approach is close to reality: If site conditions in the field change gradually, vegetation likewise changes gradually; transitions are visible that have properties of both adjacent types. Nevertheless, traditional crisp maps can be derived by applying a threshold to the probability or by selecting the most probable type.

The overall view of the recent PNV map for Bavaria reflects site characteristics of the different parts of Bavaria perfectly: Base saturation, temperature and precipitation are the basic site factors that determine the distribution of the forest types and influence the tipping points for a change.

Compared to species distribution models (SDM, e.g. HIJMANS et al. 2017), PNV models provide much more detailed information on habitat conditions since single species usually show a broader ecological amplitude than plant communities. The latter are composed of a variety of species respresenting the intersection of the habitat requirements of the different species occurring together. A single tree species, like beech e.g. occurs in very different habitats from very dry soils on limestone (*Carici-Fagetum*), over intermediate conditions (*Galio odorati-Fagetum*) to forests on acidic soils (*Luzulo-Fagetum*), under warm and cold climate. The plant communities, beech is occurring in, differentiate climate and soil conditions much more detailed than beech only.

Based on the simulated map of recent PNV, it is possible to change site factors: increase temperature or increase/decrease precipitation. Under these scenarios, many colline-submontane PNV units, e.g. *Luzulo-Fagetum*, shift to the montane regions. This is what is to be expected. The montane vegetation types, on the other hand, cannot shift further to higher altitudes either because there is no space above the summits (e.g. Bavarian Forest) or because the soil conditions are not favourable above the timberline. This corresponds to the results of H.S. FISCHER (1994). However, the model also identifies types that are relatively insensitive to climatic warming like alluvial and wet lowland forests. Beside the upward shift, we observe a remarkable shift in the surface balance: under moderate temperature increase the *Galio-Carpinetum* type increases in area. This coincides to findings in WALENTOWSKI et al. (2017).

In Bavaria between 1881 and 2014 the mean annual temperature raised by 1.4 K (BSTUV 2015), not far below the level of the modelled +2 K scenario. Our simulations demonstrate that even this “moderate” change will have a dramatic impact on the site conditions. The latest results of research in Switzerland show that an increase of 3.4 K is most probable by the year 2100 (PLUESS et al. 2016). This would lead to completely new constellations of site conditions in large parts of Bavaria. Moreover, IPCC (2014) scenarios show that even an increase of +6 K could be possible. Even if “only” the +2 K scenario becomes reality, in 36% of the area throughout Bavaria constellations of site conditions springs up, which currently do not exist. This area extends to 81% in the +3 K scenario and more than 93% in the +4 K. This means that site conditions will completely change almost throughout Bavaria. Forestry as well as agriculture, and generally, to all kinds of land use management will then find themselves victims of global climate change in form of new site situations.

5. Conclusions

We do not know how climate will actually change in the next few decades. However, with the PNV model we provide a valuable tool to find out how and where site conditions change if certain scenarios of climate change come true. The PNV model allows pointing out changes in the distribution of site conditions on a regional or landscape scale, but also reaches the local scale, where land-users are working (50 m x 50 m cells). If drastic scenarios come true, the model makes perfectly clear that everybody’s backyard will be affected.

Erweiterte deutsche Zusammenfassung

Einleitung – Die potentielle natürliche Vegetation (PNV) ist ein bewährtes Konzept, um die komplexen Standortbedingungen der Vegetation zu charakterisieren. Ziel der vorliegenden Arbeit ist es, auf Basis der existierenden Standortdaten und der Informationen über die Verbreitung von Waldgesellschaften (Datenquelle Bundeswaldinventur, BWI2) eine auf definierten Algorithmen basierende dynamisierte Karte der heutigen potentiell natürlichen Vegetation (h-PNV) Bayerns im Maßstab 1:25.000 (50 m-Raster, 28,1 Mio. Rasterzellen) zu generieren. Des Weiteren wollen wir vor dem Hintergrund von „climate change“ die zukünftige Standortsituation in Bayerns modellieren: zukünftige PNV („z-PNV“). Zukünftige Klimaszenarien umfassen eine Temperaturzunahme um +1 K, +2 K, +3 K, +4 K und +6 K ohne oder mit Zu- bzw. Abnahme der Niederschläge (15 Szenarien).

Methode – Wir benutzen die Methode MaxEnt und 146 hochauflösende digitale Standortkarten. Anhand von Diskriminanz- und Korrelationsanalysen identifizierten wir 24 Standortfaktoren (Tab. 1), die die Waldgesellschaften (Beilage S1) signifikant differenzieren. Die Kalibrierung des Modells basiert auf den 7.504 Rasterpunkten der Bundewaldinventur (BWI2) in Bayern. Wir modellierten die potentielle Verbreitung von 26 Waldgesellschaften (Beilage S1) in Bayern mit 24 Standortvariablen (Bayerisches Standortinformationssystem, LWF), die die Bodenchemie, den Luft- und Wasserhaushalt und die Profileigenschaften des Bodens, das Klima und das Relief beschreiben (Tab. 1). Verschiedene Modelle wurden getestet, z. B. GLM, MaxEnt. Es zeigt sich, dass die Modellierungen nach der Methode MaxEnt die aktuellen Verbreitungen der Pflanzengesellschaften am besten wiedergibt. Jede Waldgesellschaft wurde separat modelliert und die sie determinierenden Standortfaktoren wurden individuell ermittelt. Die Abhängigkeit der Waldgesellschaften von diesen Standortfaktoren wird mit den Ökologischen Präferenzfunktionen (EPF) beschrieben und grafisch (Abb. 1, 4) dargestellt. Als Ergebnis der Modellierung erhält man für jede einzelne Waldgesellschaft eine Wahrscheinlichkeitskarte (Abb. 2) des Auftretens. Aus den Wahrscheinlichkeitskarten wird in einem weiteren Schritt durch das Setzen eines geeigneten Schwellenwerts eine Karte der Verbreitung der Waldgesellschaft abgeleitet (Abb. 3). Eine Karte der aktuellen PNV entsteht, indem für jeden Punkt der Karte von Bayern die wahrscheinlichste Waldgesellschaft genommen wird.

Karten der zukünftigen PNV werden erstellt, indem man die Simulation wiederholt, nachdem man einzelne Standortkarten modifiziert hat. Wir haben dabei zum einen die mittlere Jahrestemperatur um 1, 2, 3, 4 bzw. 6 K erhöht und zudem für jede Temperaturstufe die Jahresniederschlagssummen entweder wie heute belassen oder um 10 % erhöht bzw. erniedrigt. Insgesamt wurden somit 15 Szenarien gerechnet. Verbreitungs- und Wahrscheinlichkeitskarten für jede Waldgesellschaft wurden für alle 15 Szenarien erstellt. Des Weiteren wurde für jedes Szenarium für jede Waldgesellschaft eine Änderungskarte (Zugewinn- und Verlustflächen) angefertigt. Für jedes Szenarium wurden die einzelnen Karten zu einer Gesamtkarte der zukünftigen PNV zusammengefügt und eine Flächenbilanz für die am weitesten verbreiteten Waldgesellschaften berechnet.

Ergebnisse – Für jeden PNV-Typ liegt eine Liste der für die Simulation bedeutsamen (variable contribution) Standortfaktoren (Tab. 2), deren ökologisches Optimum und Amplitude (Tab. 3) vor. Basensättigung, die Wasserbilanz und die Lufttemperatur sind für die meisten Waldgesellschaften maßgebliche Standortfaktoren.

Wahrscheinlichkeitskarten (Abb. 3, 4) und daraus abgeleitete Verbreitungskarten (Abb. 1) des heutigen Vorkommens und des zukünftigen Vorkommens (Abb. 5, 6) in ausgewählten Szenarien zeigen exemplarisch für ausgewählte PNV-Typen die potentielle aktuelle und die zukünftige Verbreitung. Zugewinne und Verluste sind farblich hervorgehoben.

Basierend auf klar definierten Algorithmen konnten wir eine Karte der heutigen PNV (Abb. 7) für Bayern erstellen. Sie zeigt die Verbreitung der PNV-Typen im dynamischen Maßstab 1:25.000 (lokaler Ausschnitt) bis zu 1: 2,5 Mio. (ganz Bayern). Für 15 Szenarien lässt sich in gleicher Weise die zukünftige PNV Bayerns darstellen (Abb. 8–10). Alle zukünftigen Szenarien zeigen eine drastische Veränderung der Umweltbedingungen (Abb. 10). Schon bei dem relativ moderaten +2 K Szenarium finden sich auf 36 % der Fläche Bayerns Bedingungen, wie sie aktuell nirgends in Bayern vorkommen, bei dem +4 K Szenarium sind es bereits 94 %. Die Karten ermöglichen (sowohl im Überblick als auch pixelgenau) abzuschätzen, wo in Bayern welche Änderungen der Standortfaktoren-Konstellationen in den verschiedenen Klima-Szenarien zu erwarten sind.

Diskussion – Vegetationskarten bilden meist die aktuellen Standortbedingungen ab. Der Klimawandel verändert die aktuellen Standortbedingungen. Für aktuelle Planungen, sei es in der Forstwirtschaft, der Landwirtschaft oder im Naturschutz, ist ein Konzept, das zukünftige Standortbedingungen berücksichtigt, notwendig. Für Bayern existieren bereits zwei unterschiedliche Vegetationskarten (SEIBERT 1968, SUCK & BUSHART 2012). Sie repräsentieren jedoch nicht nur etwaige unterschiedliche Standortbedingungen zum Zeitpunkt ihrer Erhebung sondern vielmehr auch die unterschiedliche Einschätzungen der Experten. Unser Ansatz ist es, die heutigen und zukünftige PNV objektiv auf der Grundlage definierter Algorithmen und einer statistisch repräsentativen Stichprobe (BWI) zu modellieren. Das Vorkommen der Waldgesellschaften wird anhand der heutigen und zukünftigen Standortfaktoren ermittelt.

Planungen basieren auf unterschiedlichen Maßstäben (z. B. Raumordnungsplanung, Grünordnungsplan) und benötigen daher auch Planungsgrundlagen auf unterschiedlichem Maßstab. Die modellierte PNV stellt diese Grundlagen dynamisch im erforderlichen Maßstab zur Verfügung.

Zudem leben wir in einem Zeitalter beschleunigten Wandels. Heute zu treffende Entscheidungen dürfen nicht nur die heutigen Bedingungen berücksichtigen, sondern müssen auch zukünftige Veränderungen einbeziehen. Deshalb haben wir die Verbreitung der PNV-Einheiten unter zukünftigen Szenarien berechnet.

Die Veränderung der Verbreitung der PNV-Typen mit zunehmender Temperatur zeigt grundsätzlich den zu erwartenden Trend der Aufwärtsverlagerung im Gebirge, wobei die verschiedenen PNV-Typen unterschiedlich stark reagieren. Neben einer Verschiebung der Areale sind auch gravierende Änderungen in der Flächenbilanz zu beobachten.

Im Zeitraum von 1881 bis 2014 hat sich in Bayern die Jahresdurchschnittstemperatur um +1,4 K (BSTUV 2015) erhöht. Unsere Simulationen zeigen, dass schon bei einem moderaten Temperaturanstieg von +2 K etwa auf einem Drittel der Fläche Bayerns Bedingungen herrschen werden, die es heutzutage in Bayern nicht gibt. Steigt die Jahresdurchschnittstemperatur um +3 K, sind 81 % der Fläche und bei einem Anstieg von +4 K 93 % der Fläche betroffen. Das bedeutet, dass sich die Standortbedingungen für die Forstwirtschaft, die Landwirtschaft und alle Formen der Landnutzung gravierend ändern.

Schlussfolgerung – Die Modellierung zeigt drastische Standortveränderungen für die Zukunft. Mit diesem Modell stellen wir ein Werkzeug bereit, das es Politikern auf allen administrativen Ebenen, aber auch den Praktikern in Forst- und Landwirtschaft oder im Naturschutz ermöglicht, Brennpunkte der Auswirkungen der Klimaänderungen zu identifizieren, die unter den zukünftigen Klimabedingungen zu erwarten sind – im Landesüberblick, aber auch bis auf jedes einzelne 50 m x 50 m-Pixel in Bayern hinab.

Damit erhält das von Tüxen stark geprägte und entwickelte Konzept der PNV eine ganz neue Anwendungsebene, nämlich im Sinne der Erkundung möglicher Zukünfte.

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Author contribution statement

A. Fischer and H.S. Fischer conceived the idea of the research; defined the aim and questions of the study. H.S. Fischer and B. Michler determined methods to perform the simulations. B. Michler tested variables and performed the simulations. All three authors discussed the results and contributed to write the manuscript.

Supplements

Supplement S1. List of forest types.

Beilage S1. Liste der PNV-Typen bzw. Waldgesellschaften.

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Supplement S1. List of forest types
IC: **i**dentification code in plots and tables; [#] simulation current site conditions (h-PNV); [##]simulation future climate scenarios (z-PNV); n: **s**ample size of forest types in simulations; forest types, code according to WALENTOWSKI et al. (2013); vertical zonation of forest types, additional differentiation due to bimodal distribution of temperature and precipitation values; temperature: average annual temperature (1971-2000); precipitation: average annual precipitation sum (1971-2000) forest types assigned to the code of natural vegetation of Europe (BOHN et al. 2000/2003); HCode: NATURA 2000-habitatcode of the simulated forest types; HCode*: priority habitat type; oft: other but no Natura 2000 forest type.

Beilage S1. Liste der PNV-Typen bzw. Waldgesellschaften)
IC: Identifizierungscode in Abbildungen und Tabellen; [#] Simulation der Waldgesellschaft unter heutigen Standortbedingungen (h-PNV); [##] Simulation unter zukünftigen Klimabedingungen (z-PNV); n: Stichprobenumfang der Waldgesellschaft in den Simulationen; Waldgesellschaft codiert nach WALENTOWSKI et al. (2013); vertikale Zonierung der Waldgesellschaften und zusätzliche Differenzierung durch Temperatur und Niederschlägen; Zuordnung der Waldgesellschaften zu den Vegetationseinheiten nach BOHN et al. (2000/2003); HCode: Zuordnung der Waldgesellschaften zu NATURA 2000-Lebensraumtypen; HCode*: Prioritärer Lebensraumtyp; oft: Sonstiger Waldtyp, kein Natura 2000 Lebensraumtyp.

ICode	n	Forest types of Bavaria (WALENTOWSKI et al. 2013)	Forest type (RENNWALD 2000)	Vertical zonation	Code Natural Vegetation of Europe (BOHN et al. 2000/2003)			HCode
Mesophytic deciduous broad-leaved and mixed coniferous-broad-leaved forests								
Beech forests and mixed beech forests								
1c[#;##]	2194	1.1.1	*Luzulo-Fagetum* Meusel 1937	Colline to submontane; average annual temperature > 7 °C	F5.1.2	F83, F85, F86	Species-poor oligotrophic to mesotrophic beech and mixed beech forests, colline-submontane type	9110
1cn[#;##]	273	1.1.1	*Luzulo-Fagetum* Meusel 1937	Colline to submontane; average temperature > 7 °C, average annual precipitation sum > 1100 mm				
1m[#;##]	558	1.1.2	*Luzulo-Fagetum* Meusel 1937	Montane, average annual temperature < 7 °C	F5.1.3	F90, F96, F97	Species-poor oligotrophic to mesotrophic beech and mixed beech forests, montane-altimontane type	
3c[#;##]	237	1.2.1	*Galio odorati-Fagetum* Sougnez et Thill 1959 nom. conserv. propos.	Colline to submontane; average annual temperature > 7 °C	F5.2.2	F110, F115	Species-rich eutrophic and eu-mesotrophic beech and mixed beech forests, colline-submontane type	9130
3cn[#;##]	28	1.2.1	*Galio odorati-Fagetum* Sougnez et Thill 1959 nom. conserv. propos.	Colline to submontane; average annual temperature > 7 °C, average annual precipitation sum > 1100 mm				
3m[#;##]	53	1.2.2	*Galio odorati-Fagetum* Sougnez et Thill 1959 nom. conserv. propos.	Montane, average annual temperature < 7 °C			Species-rich eutrophic and eu-mesotrophic beech and mixed beech forests, montane-altimontane type	
4[#;##]	403	1.3.1	*Hordelymo-Fagetum* Kuhn 1937	Colline to submontane; average annual temperature > 7 °C		F113, F114	Species-rich eutrophic and eu-mesotrophic beech and mixed beech forests, colline-submontane type	
4n[#;##]	25	1.3.1	*Hordelymo-Fagetum* Kuhn 1937	Colline to submontane; average annual temperature > 7 °C, average annual precipitation sum > 1100 mm				
6[#;##]	338	1.3.2	*Aposerido-Fagetum* Oberd. 1950 ex Oberd. 1957	Montane	F5.2.3	F133	Species-rich eutrophic and eu-mesotrophic beech and mixed beech forests, montane-altimontane type	
7c[#;##]	30	1.5.1	*Carici-Fagetum* Moor 1952	Colline to submontane	F5.2.2	F113, F114, F118	Species-rich eutrophic and eu-mesotrophic beech and mixed beech forests, colline-submontane type	9150
7m[#;##]	27	1.5.2	*Seslerio-Fagetum* Moor 1952	Montane		F118	Species-rich eutrophic and eu-mesotrophic beech and mixed beech forests, montane-altimontane type	
Oak and hornbeam forests								
15[#;##]	242	2.1.1	*Calamagrostio arundinaceae-Quercetum petraeae* (Hartmann 1934) Scamoni et Passarge 1959	Colline	F1.2	F20	Species-poor acidophilous oak and mixed oak forests, colline-submontane type	9190
		2.1.2	*Luzulo-Quercetum petraeae* Hilitzer 1932 nom. invers. propos.	Colline		F20		oft
18[#;##]	183	2.3.1	*Galio-Carpinetum* Oberd. 1957	Colline	F3.2	F50, F51	Colline-submontane sessile oak-hornbeam forests	9170
17[#;##]	81	2.3.2	*Stellario-Carpinetum* Oberd. 1957	Colline	F3.1		Colline (to submontane) pedunculate oak-hornbeam forests	9160
Ravine forests								
24[#]	38	3.1.1	*Aceri-Tilietum platyphylli* Faber 1936 nom. conserv. propos.	Up to submontane			Forests of slopes and ravines and on scree	9180*
Alluvial and wet lowland forests								
35[#]	55	4.2.2	*Pruno-Fraxinetum* Oberd. 1953	Up to montane	U3.2	U24, U27	Alluvial and wet lowland forests, alder-ash forests	91E0*
37[#;##]	30	4.3.1	*Stellario nemorum-Alnetum glutinosae* Lohmeyer 1957					
38[#]	22	4.3.2	*Alnetum incanae* Lüdi 1921	Up to altimontane				
39[#]	43	4.3.3 5.1.1	*Querco-Ulmetum* Issler 1924 *Salicetum albae* Issler 1926	Planar to colline	U.3.1	U9	Hardwood and softwood alluvial forests	91F0 91E0*
Bog woodland								
33[#;##]	50	6.3.1	*Vaccinio uliginosi-Pinetalia sylvestris* Passarge et Hofmann 1968		T		Fen forests	91D0*
28[#;##]	29	6.4.1	*Bazzanio-Piceetum* Br.-Bl. et Sissingh in Br.-Bl. et al. 1939				Fen forests	91D4
Mesophytic and hygromesophytic coniferous and mixed broad-leaved-coniferous forests								
11[#;##]	58	8.2.1	*Galio rotundifolii-Abietetum* Wraber (1955) 1959 nom. conserv. propos.	Submontane to altimontane	D4.1	D28	Montane, partly submontane or altimontane fir and mixed fir forests	9130
29t[#;##]	10	9.1.1	*Calamagrostio villosae-Piceetum* (Tx. 1937) Hartmann et Schlüter 1966 nom. conserv. propos.	Subalpine; average annual temperature > 5 °C	D4.2	D34	Montane spruce and mixed spruce forests	9410
29[#;##]	29	9.1.1	*Calamagrostio villosae-Piceetum* (Tx. 1937) Hartmann et Schlüter 1966 nom. conserv. propos.	Subalpine; average annual temperature < 5 °C			Altimontane, partly montane spruce and mixed spruce forests	
28[#;##]	28	9.2.2	*Adenostylo glabrae-Piceetum* M. Wraber ex Zukrigl 1973	Subalpine				
Subalpine dwarf shrub vegetation								
31[#;##]	81	10.2.2	*Rhododendro hirsuti-Pinetum mugo* Br.-Bl. et al. 1939 nom. invers. propos.	Subalpine to alpine	C3	C20	Rhododendron-mountain pine scrub	4070*