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Assessment of the Ellenberg quotient as a practical tool for vertical vegetation zonation

Petr Dujka[1,2]*, Antonín Kusbach[1]

[1]Department of Forest Botany, Dendrology and Geobiocenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic
[2]Forest Management Institute Brandýs nad Labem, Branch Kroměříž, Kroměříž, Czech Republic

*Corresponding author: dujka10@seznam.cz

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Abstract: The Ellenberg quotient (*EQ*) is a climate index defined as a ratio of the hottest month's temperature and the average annual precipitation sum. The quotient indirectly expresses the relationship between climate and vegetation, and its application is related to the ecological niche of *Fagus* sp. Although the quotient was curated on the grounds of field research primarily on German vegetation, the possibilities of its utilisation are not limited to the Central European region. The objective of this study is (*i*) to compare the *EQ* values calculated for the forest vegetation zones in the Czech Republic with the published data using the ecological niche of *Fagus sylvatica*; and (*ii*) to compare the new *EQ*-based vertical model with field empirical mapping. The study area is the Czech Republic, Central Europe. We used climate data from 1970–2000 and the data of the National Forest Inventory, 2nd cycle (2011–2015), representing an objective data design. Geospatial analytic methods, machine learning (boosting), and verification through statistical testing were performed. The results indicate higher *EQ* values between the two most substantial spatial frames – the Hercynicum and Carpaticum regions. By comparing empirical mapped units to their climatic potential (in the *EQ*), a match was found only within the Carpaticum region. The study presents a concretisation of the general climate index for a specific region, adds to the knowledge about the *Fagus* ecological niche in context with the Central European vegetation, and also points to the *EQ*'s potential for evaluating the concept of vertical differentiation of forest communities, as well as a possible prediction tool for the vegetation migration in context with climate change.

Keywords: European beech; *Fagus sylvatica*; forest vegetation zones; national forest inventory; zonal concept

European beech (*Fagus sylvatica*) belongs to the ecologically and commercially most important and widespread broadleaved species in Central Europe (Houston Durrant et al. 2016), being also the subject of a whole series of both local and regional studies (Stojanović et al. 2013; Garamszegi, Kern 2014; Salamon-Albert et al. 2016). Many climate indices have been employed to evaluate the climate change impact on beech, e.g. the Forest Aridity Index – FAI (Führer et al. 2011) or Ellenberg quotient (Ellenberg 2009). For the evaluation of the current state and possible prediction of the impact of climate change on vegetation, the Ellenberg quotient appears as very promising (Mellert et al. 2016; Neniu, Vlăduț 2020).

The Ellenberg quotient is defined as a ratio of the average temperature in the hottest month of a year (July) and the average annual precipitation sum (Ellenberg, Leuschner 2010). In the Czech Republic (CZ), its use is first mentioned by Ambros (1993)

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as a potential tool for defining the dry (xeric) variant of vegetational zonation, within which forest communities of lower altitudes with a natural absence of beech can be found (Buček, Lacina 2007). Hruban (2010) evaluated macroclimate characteristics of the forest vegetation zones (FVZs) on the grounds of the Database of Czech Forest Classification System (DCFCS; Zouhar 2012) data, where the *EQ* value range was calculated for each FVZ. This calculation was then used by Mikeska and Prausová (2013) to characterise FVZs.

The Czech Forest Classification System (ÚHÚL 2023) used for the classification of forest sites in the Czech Republic uses FVZs as a frame for the vertical differentiation of tree vegetation (Zlatník 1976). The FVZs are labelled by their dominant tree species such as oaks (*Quercus* sp.), European beech (*Fagus sylvatica*), silver fir (*Abies alba*), Norway spruce (*Picea abies*) and mountain pine (*Pinus mugo*) (Zlatník 1961, 1963). European beech has a unique status in the system not only for its absence in the hottest (1st) and coldest (9th) FVZs but mostly for its presence from the 2nd (beech-oak) up to the 8th (spruce) FVZs (Plíva 1971). The most important environmental characteristics of FVZs are summarised in Table 1 (the characteristics of Hercynicum and Carpaticum separately were not calculated so far, as the current version of the Czech Forest Ecosystem Classification assumes a uniform unit for the entire study area). Besides the presence of the dominant species, the concept and practical mapping of FVZs have been following their growth/productivity, composition and structure of a tree community since the 1970s. However, the correctness of this approach has not yet been assessed more in-depth (Kusbach et al. 2017, 2018).

The *EQ* values of forest vegetation zones published to this day appear as problematic from a practical perspective: (*i*) intervals of the *EQ* values overlap (Table 1), (*ii*) the values stem merely from macroclimate characteristics with no links to the actual vegetation, (*iii*) more complex, critical assessment of the detected values is missing. For example, in the 4th FVZ of the Czech Forest Classification System (ÚHÚL 2023), where beech is dominant and creates monocenoses, Mikeska and Prausová (2013) established the *EQ* range of 18–27. According to Ellenberg (2009), however, an unmixed beech forest is defined by the *EQ* range of 10–20.

Ellenberg and Leuschner (2010) established value ranges of forest communities in Central Europe (Table 6–7, p. 339). Although the results of their work build mostly on research made in Germany, their concept can be used in other parts of Central Europe as well (Jensen et al. 2004; Mátyás et al. 2010). On the other hand, Stojanović et al. (2013) warned against strictly applying a regional approach for evaluating the *EQ*, as in the case of Serbian beech forests. These values differed widely from those stated in the Ellenberg (2009) model. Due to obvious site-climate-vegetation peculiarities and geographically related pitfalls, we examined the *EQ*'s potential to be a conceptual tool for vertical vegetation differentiation.

The objective of this study is (*i*) to compare the *EQ* values calculated for the forest vegetation zones in CZ with the published data using the ecological niche of *Fagus sylvatica*; and (*ii*) to compare the new *EQ*-based vertical model with field empirical mapping.

MATERIAL AND METHODS

Study area. The study area includes the territory of the CZ (48°33'–51°03'N, 12°05'–18°51'E). The Natural Forest Areas (NFAs) represent a more detailed division of the territory and are being used

Table 1. Characteristics of forest vegetation zones in the Czech Republic (Mikeska, Prausová 2013)

Forest vegetation zones (Plíva 1971)	Altitude (m a.s.l.)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Ellenberg quotient
1st oak zone	175–400	7.7–9.2	493–665	26–39
2nd oak-beech zone	253–465	7.3–8.5	550–724	24–32
3rd beech-oak zone	280–535	6.8–8.2	585–803	20–30
4th beech zone	395–620	6.4–7.6	618–851	18–27
5th fir-beech zone	480–790	5.4–7.0	677–1 000	15–24
6th spruce-beech zone	600–994	4.3–6.3	736–1 126	12–21
7th beech-spruce zone	810–1 139	3.4–5.3	798–1 158	11–18
8th spruce zone	900–1 275	2.7–4.5	967–1 274	10–13

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in the forestry practice since the late 1980s. In the forestry legislation, NFAs are defined as continuous territories with similar growth conditions for forest growth. The CZ is divided into 41 NFAs (Plíva, Žlábek 1986; Annex 1 of the 298/2018 Decree of the Forest Act). For analytic purposes, we aggregated the NFAs into two spatial frames, resulting from the different geographic, geomorphologic (Bína, Demek 2012; Pánek, Kapustová 2016) and climate conditions: Hercynicum and Carpaticum. The Hercynicum spatial frame represents an area potentially more influenced by oceanic climate (Beck et al. 2018) and, for this study, is represented by NFAs 1–33. The Carpaticum spatial frame presumes a significant influence of continental climate (Hradecký, Brázdil 2016) and consists of the aggregated NFAs 34–41.

Data. The first input data was vector data with the information collected from the ground investigation of the National Forest Inventory, 2nd cycle (NFI II), 2011–2015, representing an objective data design (Kučera, Adolt 2019). The total number of inventory plots in the category 'FOREST' is 6 709. Each plot contains information about the FVZ, edaphic category (ÚHÚL 2023), and tree species present on the inventory site at the time of the investigation (actual vegetation during field survey 2011–2015).

The second input data consisted of raster data with climate characteristics: the average temperature in July (T07) and average annual precipitation sum in 1970–2000 extracted for the CZ (Fick, Hijmans 2017). The size of a raster layer pixel was interpolated from the original 500 m × 500 m to 250 m × 250 m.

Analysis. For the analysis, we considered the complete dataset of 6 709 inventory plots, from which the subset of representative and verification plots (NFI_II_V, Figure 1) labelled as 'zonal sites' was selected. A zonal site is defined by the presence of up to 50% of the rock fragment content (by volume), normal hydric regime, and amount of nutrients that does not radically impact the composition of vegetation communities (Dujka, Kusbach 2022). Additionally, a zonal site is where the prevailing influence of macroclimate is expected to affect the growth/succession of the vegetation. On the other hand, the effect of mesoclimate (topoedaphic conditions) and microclimate is minimal *sensu* Major (1951), regionally verified for the CZ by Macků (2014), or Kusbach et al. (2017, 2018).

For the complete NFI dataset, we calculated the *EQ* from raster climatic data according to the following Equation (1) (Ellenberg, Leuschner 2010, p. 339):

$$EQ = \frac{T07 \times 1\,000}{PREC} \quad (1)$$

where:

EQ – the Ellenberg quotient;

T07 – average temperature in July (°C);

PREC – average annual rainfall (mm).

This calculation resulted in an inventory plots layer NFI_II_*EQ* (Figure 1). Considering that the actual vegetation composition is far from the original outlay due to intensive forest management in the past 200 years (Chytrý et al. 2013), we characterized the composition using a scale of naturalness of a forest stand (percentual naturalness index of 0–100; Macků 2012). From the NFI_II_*EQ* layer, representative plots (NFI_II_R) were chosen based on their degree of naturalness (4–6 was desirable), i.e. zonal sites with the naturalness index above 50%. These selected sites were close-to-natural tree species composition. The presence of European beech in the forest layers, according to Zlatník's classification (Randuška et al. 1986) in the 1st to the 8th FVZs was also crucial (ÚHÚL 2023) in the analysis.

The criteria of plot selection based on the degree of naturalness were met by 32 inventory plots from the 2nd to 6th FVZ range in the Carpaticum spatial frame and by 94 inventory plots from the 2nd to 7th FVZ range in the Hercynicum spatial frame. However, we needed the same foundation in the number of inventory plots.

The *EQ* values of the representative plots were used for the calculation of confidence intervals (Figure 1). In case of a low number of values (e.g. the 2nd or 7th FVZs) when it was not possible to transform data and reach a normal distribution, we increased the number of data artificially using the boosting method (Frey 2020). Having the same starting point in the amount of modelled *EQ* values for every interval allowed us to set down the confidence intervals more precisely, as the values were normally distributed and did not include extreme cases. The *EQ* confidence interval values were calculated for each FVZ of the Hercynicum and Carpaticum spatial frames using the RStudio software (Version R.4.1.2, 2020), package 'interpretCI', with the significance value $\alpha = 0.05$. Threshold interval values equalled 2.5% and 97.5% of the confidence interval. To create

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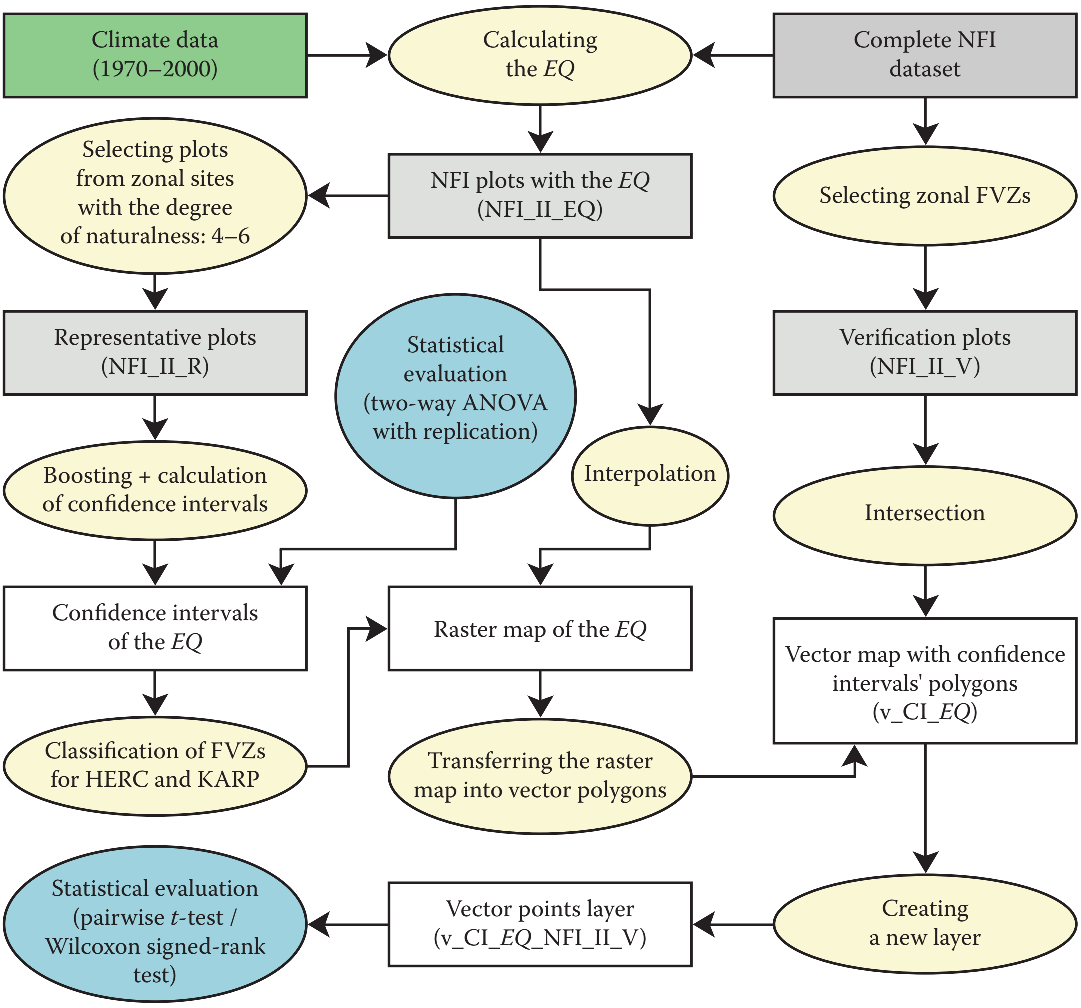

Figure 1. A scheme of the analytical process

Grey rectangles – NFI II input data; green rectangle – climate data; yellow ellipses – processes; white rectangles – outcomes of these processes; blue ellipses – statistical evaluations and methods; *EQ* – Ellenberg quotient; FVZ – forest vegetation zone

a continuous interval of the *EQ* values, which would not create duplex results in the spatial analyses, threshold values of neighbouring FVZs were linearly interpolated, and the resulting value was used for creating a polygon edge. The variability difference of the *EQ* values between the FVZs of the two spatial frames (incl. the differences inside both frames) was tested by a two-way analysis of variance (ANOVA) with replication (level of significance $P = 0.05$).

In the next step, the inventory plots of the NFI_II_*EQ* layer (in the form of vector points) were interpolated using the method of Inverse Distance Weighing into a grid with a pixel size of 100 m × 100 m and then transferred into a raster map.

The values of the raster map were then divided according to (*i*) their spatial frame (Hercynicum and Carpaticum) and (*ii*) the interpolated confidence intervals of each FVZ's *EQ*. It was not possible to include the 1st and 8th FVZs for the lack of relevant data. For better visual output, we calculated their proxy values as a sum of the corresponding *EQ* values, which were higher (in the case of the 1st FVZ) or lower (in the case of the 8th FVZ) than threshold values for the 2nd and 7th FVZ. For further geospatial analysis, the raster layer was transferred into a vector map (v_CI_*EQ*).

In the QGIS (QGIS Development Team 2023) software interface (Version 3.28.0, 2022), an intersection (using the *Intersection* command) of the v_CI_*EQ* layer with the verification layer NFI_II_V was made. A new vector layer (v_CI_*EQ*_NFI_II_V) was thus created, consisting of points with the attributes of FVZs according to *i*) confidence interval values of representative plots and *ii*) NFI field survey of the verification plots (Figure 1).

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Table 2. Forest community type and the corresponding *EQ* values (modified from Ellenberg and Leuschner, 2010, p. 339)

Forest community type	*EQ*
Oak forest (± no beech)	> 30
Beech forest with oaks	20–30
Beech forest	10–20
Beech-fir forest	~ 10
Subalpine beech forest	< 10

EQ – Ellenberg quotient

In the next step, a statistical evaluation was performed to see the match/difference rate between the confidence intervals of the *EQ* and the verification plots. The *EQ* confidence intervals of each FVZ represent the climatic potential for the succession of communities with the presence/absence of European beech according to potential natural spreading of climax tree species (Zlatník 1976). To verify the normality of the v_CI_*EQ*_NFI_II_V attribute table values, we used the Shapiro-Wilk normality test (level of significance $P = 0.05$). In case the normal distribution was detected, a paired *t*-test was performed. If normal distribution was not found, a non-parametric Wilcoxon signed-rank test (Wilcoxon 1945) was performed (level of significance $P = 0.05$). The calculations were done in the R Studio software using the 'tidyverse' package; the graphic output was made using the 'ggstatplot' package. To evaluate the power of the test's statistical significance, the package 'effectsize' was used. We employed a verbal scale to describe the *rank biserial* indicator (Funder and Ozer 2019). We used the 'qqwithinstats' function for displaying the results as it is capable of creating a user-friendly output based on the probability density function. This innovative approach (Patil 2021) uses box/violin plot methods of display (Hintze, Nelson 1998) which can help to easily interpret the results of the Wilcoxon signed-rank test and is more comprehensible than a long-winded text description.

The detected *EQ* interval values were compared to those stated in the literature (Ellenberg, Leuschner 2010, p. 339; or Table 2). The suitability of dividing the study area into spatial frames was then evaluated.

RESULTS

Revision of the *EQ* values. In the first step, *EQ* threshold values were calculated for those FVZs which can be compared with the so-far published values (Table 1), as the definition of an FVZ is identical in both cases.

The confidence intervals for the Hercynicum and Carpaticum FVZs are listed in Table 3 and graphically in Figure 2.

The *EQ* confidence intervals calculated for the individual FVZs in both spatial frames were more or less continuous and, after interpolating their threshold values, created mostly continuous polygons. For example, an interpolated confidence interval for the 2nd FVZ in the Carpaticum frame is shown: The newly interpolated confidence interval ranges between 31.1 and 26.4. The spatial distribution of values in the modelled FVZs (Figure 3) points out the diffusive character of the borders between neighbouring polygons (intervals). Higher *EQ* values (shades of red) represent a transition towards the 1st FVZ, which is warmer and drier. Meanwhile, lower values (shades of blue) point to a transition towards the colder and moister 3rd FVZ (Figure 3).

Two-way analysis of variance denied the null hypothesis of the *EQ* confidence intervals' match in both Hercynicum and Carpaticum, and their respective FVZs. A statistically significant difference was found between the two frames: $F(1,5) = 10\,715$; $P < 0.05$. The Tukey's HSD post-hoc test then revealed statistically significant differences between (*i*) confidence intervals in each spatial frame individually, and (*ii*) confidence intervals when comparing the two frames. An exception was found

Table 3. The calculated confidence intervals and mean values of the *EQ* for the Hercynicum and Carpaticum FVZs

FVZ (Plíva 1971)	Hercynicum			Carpaticum		
	2.5%	50.0%	97.5%	2.5%	50.0%	97.5%
2nd beech-oak zone	33.6	31.9	30.3	31.1	28.7	26.1
3rd oak-beech zone	29.7	28.9	28.0	26.6	25.6	24.5
4th beech zone	26.8	25.5	24.3	22.8	21.1	19.5
5th fir-beech zone	23.8	22.3	20.9	19.0	17.2	15.7
6th spruce-beech zone	18.7	16.8	15.1	13.3	12.6	12.0
7th beech-spruce zone	15.2	13.5	11.7	–	–	–

EQ – Ellenberg quotient; FVZ – forest vegetation zone

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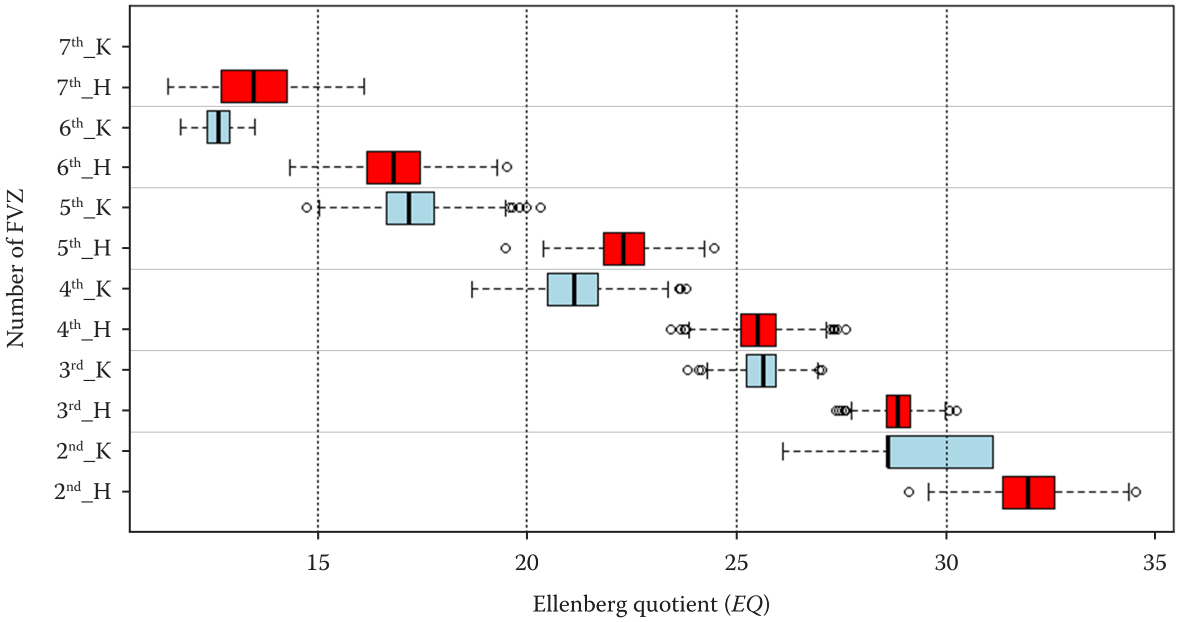

Figure 2. Diagram of the Ellenberg quotient (*EQ*) values distribution for each FVZ (2nd–7th) of Hercynicum (labelled with the letter H, boxplots in red) and Carpaticum (labelled with the letter K, boxplots in blue)

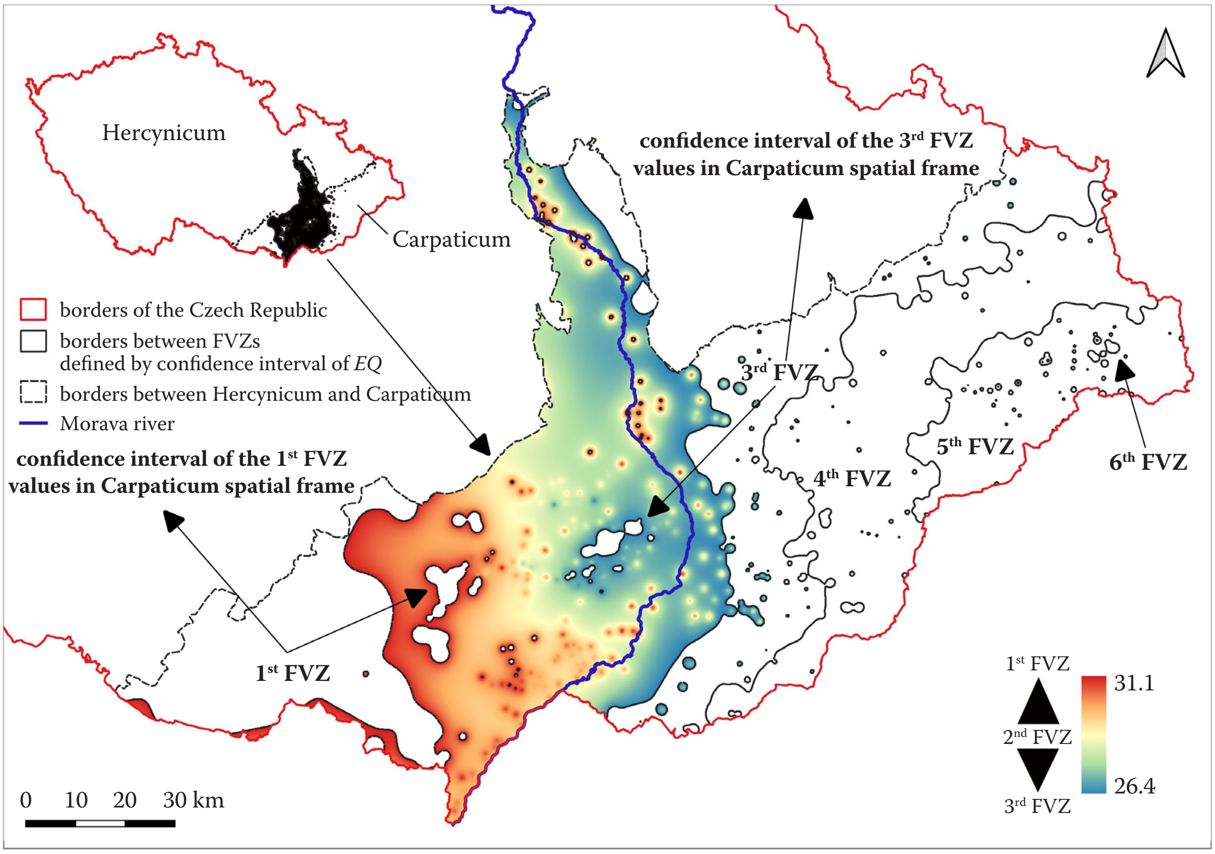

Figure 3. Schematic visualisation of *EQ* values distribution by confidence interval, calculated on the grounds of ecological *Fagus sylvatica* niche, defined by close-to-nature communities of the 2nd FVZ in the Carpaticum frame

Red shades – the highest values of the interval that can be found in the transition towards the lower (1st) FVZ; blue shades – transition to the higher (3rd) FVZ; *EQ* – Ellenberg quotient; FVZ – forest vegetation zone

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in the confidence interval of the 4th FVZ in Hercynicum and the 3rd FVZ in Carpaticum. In this one case only, the difference between the two FVZ values was found statistically insignificant (P = 0.63). The study area can be labelled, from the point of the *EQ*, as consisting of two heterogenous frames.

Evaluation of the FVZs. In Carpaticum, a statistical assessment of the FVZs was carried out based on the *EQ* confidence intervals and the NFI II field survey on 532 inventory plots that met the conditions of a zonal site (verification plots, Figure 1). In Hercynicum, the number of plots was notably higher – 3 046 in total. However, in both cases, the Shapiro-Wilk test did not prove the data file's distribution normality. Therefore, it was undesirable to use the paired t-test, and the non-parametric Wilcoxon signed-rank test was performed instead.

In the case of Carpaticum, the test did not deny the null hypothesis (Z = 11 336; P = 0.54), and the zonal FVZs of the NFI II survey do match the climate characteristics based on the calculated *EQ* confidence intervals. The rank biserial correlation = 0.04 [confidence interval $CI_{95\%}$ (–0.05; 0.14)], effect size verbally rated as 'tiny'. The positive effect points to a positive correlation between the two compared approaches (*EQ* and NFI II survey). The correlation between the FVZs modelled by using the *EQ* confidence intervals and the FVZs from the NFI II survey, although it may be 'tiny', points to the trend of either increase or decrease of density in both columns (*EQ*_K and NFI_II_K) respectively (Figure 4A). While the inventory zonal plots of the 1st–6th could have been used from the survey data, we needed to calculate the *EQ* interval even for the 7th FVZ. The graphic comparison points to a more balanced distribution trend of the *EQ*_K column, while the NFI_II_K column presents an uneven value distribution (Figure 4A). Most notably, the representation of values is higher in the 3rd FVZ and lower in the 2nd FVZ.

In the case of Hercynicum, the test did deny the null hypothesis (Z = 1 162 096; P = 0.02), and the zonal FVZs of the NFI II field survey mostly do not match the climate characteristics based on the calculated *EQ* confidence intervals. The rank biserial correlation = –0.05 [confidence in-

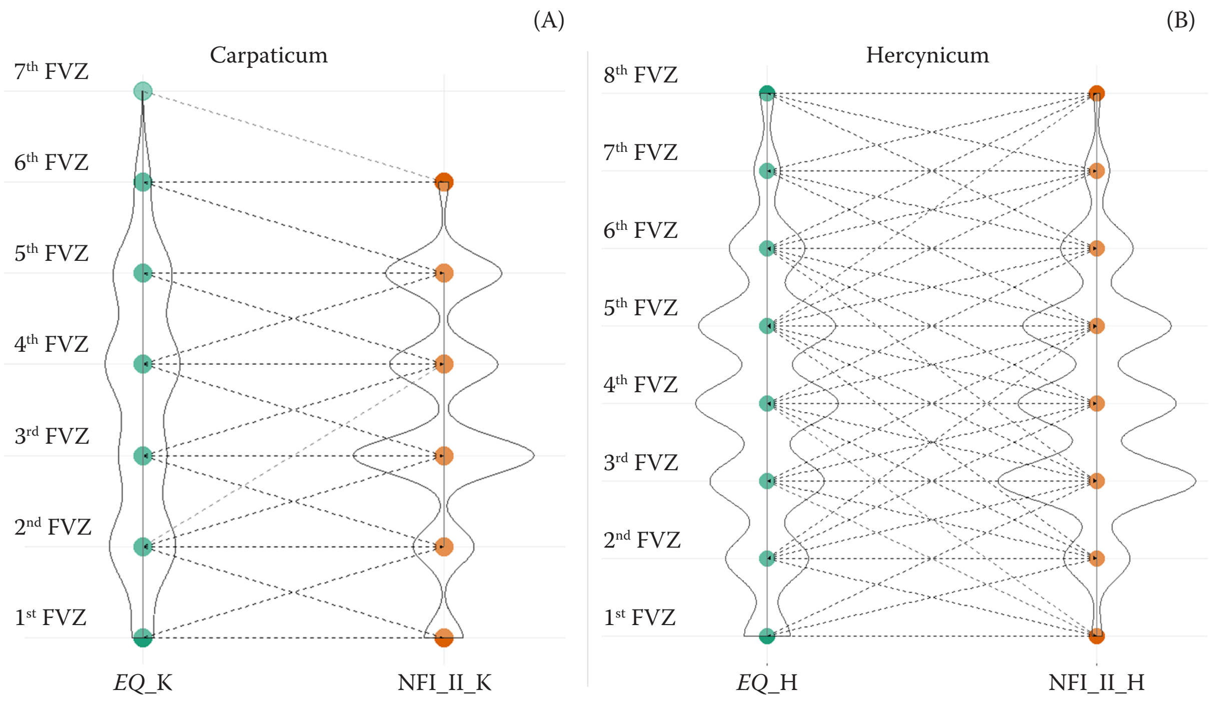

Figure 4. Diagram of the non-parametric Wilcoxon signed-rank test results for (A) Carpaticum and (B) Hercynicum

Green points – median value of the *EQ* confidence intervals of each FVZ (based on representative plots); orange points – median value of the zonal FVZs based on the NFI II field survey (verification plots); dashed black lines connect and compare the green and orange points (in an ideal case, a green point would correspond with an orange one on the same level; connection on different levels presents a misalliance); dashed grey lines depict isolated incidents; *EQ* – Ellenberg quotient; FVZ – forest vegetation zone; NFI – National Forest Inventory

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terval $CI_{95\%}$ (–0.09; –0.01)], effect size verbally rated as 'very small'. The difference between the FVZs modelled by using the *EQ* confidence intervals and the FVZs from the NFI II survey is very small, and the negative effect points to a negative correlation. The correlation between the FVZs modelled by using the *EQ* confidence intervals and the FVZs from the NFI II survey is very small, and the increase/decrease of density in both columns (*EQ*_H and NFI_II_H) respectively does not show a unified trend (a decreasein density of the *EQ* column can mean an increase in density for the NFI II column and vice versa). The comparison points to a more balanced density distribution of the (modelled) *EQ* column, while the NFI II column is unevenly distributed (Figure 4B).

DISCUSSION

Interval values of the *EQ*, defining natural forest communities with the presence/absence of beech, originate from studies performed on German and Alpine vegetation and can differ depending on geographic location and climatic data range, similarly to the widely used Ellenberg indicator value (Chytrý et al. 2018). The applicability of the *EQ*, however, exceeds the Central European region (Fang, Lechowicz 2006; Mátyás et al. 2010; Stojanović et al. 2013; Hohnwald et al. 2020). The *EQ*, in this study applied to the region of Central Europe, is purely a climate index/factor, and its assertion should have its regional limits, as is the case of the regional climate (Stojanović et al. 2013) or macroclimate (Major 1951). The modification of the *EQ* value intervals of the study area using the degree of naturalness of the sites (Macků 2012) appears as a promising approach, as the *EQ* values link with forest communities with relatively intact special composition. Those, when found on the zonal sites (Dujka, Kusbach 2022), in the long term reflect the effects of the macroclimate as the dominant environmental gradient (Kusbach et al. 2017, 2018). Boosting is a common method of ecological data analysis (De'ath 2007; Hastie et al. 2009), appropriate where the amount of data is limited. The compactness of the original dataset, combined with a carefully chosen algorithm for selecting sites that are 'typical' for each FVZ, proved to be sufficient for employing the boosting method, which is based on the principles of machine learning (Frey 2020).

For the 1st FVZ, the absence of beech is typical except for wetter locations (Průša 2001). This completely matches the Ellenberg and Leuschner's (2010) definition with a threshold value of *EQ* > 30. Ambros (1993) stated the possibility of defining the dry (xeric) plot variant with a natural absence of beech for the *EQ* > 30. Similar beech threshold values were defined by Czúcz et al. (2011) and Garamszegi and Kern (2014); in those cases, the threshold value of beech was even lower, the *EQ* = 29. Mellert et al. (2016) listed the *EQ* = 30 value as the 'maximal value of the intermediate' in which beech is consecutively present. However, the maximal value for its marginal occurrence equalled 40.4. Interestingly though, Miletić et al. (2021) listed the occurrence of beech even for the *EQ* = 38.26 in some locations in Serbia. Similarly, Stojanović et al. (2013) stated that the *EQ* values of the Serbian beech forests commonly surpass a threshold value of 30. It is, however, necessary to remind that Serbian *Fagus* forests grow upon a mostly basic substrate derived from limestone in contrast with generally acidic soils weathering from a crystalline parent material of Central Europe. High *EQ* values, which in Central Europe indicate a remarkable absence of European beech, do not necessarily indicate the same in Serbia – growth of the *Fagus* trees is controlled by different factors there, probably due to topoedaphic factors. The results of this study point to a divergence between the values stated by Ellenberg and Leuschner (2010) and Czúcz et al. (2011). Values for Hercynicum and Carpaticum hover slightly above the *EQ* > 30. The range of values published by Mikeska and Prausová (2013) seems to be significantly imprecise (*EQ* = 26–39), namely due to the lower interval boundary in the transition towards the 2nd FVZ. A lower elevation line of natural presence/absence of beech is difficult to identify in the field because of intensive human activities and the alteration of the natural special composition (Chytrý 2012).

In the 2nd FVZ, beech can be found as a minor species (Průša 2001), i.e. 10–30%. In the 3rd FVZ, beech is majorly represented, i.e. > 50%. Oak becomes a minor species, which finds its production optimum here contrary to its ecological optimum in the 1st FVZ (Vacek, Simon 2009). The division of mixed stands of beech and oak species into the two FVZ in the Czech Forest Classification System contrasts the concept of Central European

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vegetation (Ellenberg 2009). The difference in the division of both communities in the Czech system is justified by the different social status of *Fagus* and *Quercus* and the production demands of forest management. In anthropogenically influenced forests of mid-altitudinal locations, however, cannot be uncritically accepted because of (*i*) a lack of original natural communities (Culek et al. 2005), and (*ii*) past forest management influencing the composition and structure of forest stands (Maleki et al. 2020). Lower *EQ* values of both FVZs were detected in Carpaticum, where they fall into a range of 31.1–24.5 and do correspond more to the values by Ellenberg and Leuschner (2010). They also match the values for the 2nd FVZ (Mikeska, Prausová 2013). In Hercynicum, both zones' values are generally higher (33.6–28.0), here we can also find a parallel to the basic Serbian forests, e.g. in the Bohemian Karst region. Although the *EQ* values in this instance range from 29–33, the 2nd FVZ is prevalent in Hercynicum. However, due to the influence of mesoclimate, conditions for both the 1st and 3rd FVZ can emerge (Šamonil, Viewegh 2005; Šamonil et al. 2009).

The beech (4th) FVZ is characterized by Průša (2001) as an unmixed beech forest where a slight occurrence of sessile oak or silver fir is possible. While Ellenberg and Leuschner (2010) state the value range of *EQ* = 20–30 for beech communities, Mellert et al. (2016) listed values of 11.8–22.6 for optimal beech growth conditions. According to this, the beech FVZ would be above this interval's upper border (26.8–24.3) in Hercynicum. In Carpaticum, the values are lower (22.8–19.5). The *EQ* value range published by Mikeska and Prausová (2013) (18–27) is too wide, with the upper border too high. Matějka (2012) adds that around the turn of the 20th and 21st century, field survey of the 4th FVZ was either suppressed, or this zone was not recorded at all. Kubošová et al. (2011) also point out the need to revise the surface representation of the 3rd and 5th FVZs, as the mapped area of the 4th FVZ seems to be smaller than that of the 3rd and 5th FVZs. This problem is also noticeable in comparing the employed *EQ* method and the NFI II field survey in Hercynicum (Figure 4B). Inventory plots of the 4th FVZ correspond to up to four intervals of the *EQ* values, revealing the unequivocal delimitation of beech communities in relation to macroclimate.

Ellenberg and Leuschner (2011) list the occurrence of beech-fir stands in the *EQ* value range ~ 10. Průša (2001) characterizes the corresponding 5th FVZ as a community with the prevalence of either beech or silver fir with a potential addition of spruce and absence of oak. Mikeska and Prausová (2013) list the value range of *EQ* = 15–24, which would match the results of this study. However, the values differ substantially for Hercynicum, where the values' interval range is more expansive than that of Carpaticum, ranging from 19–24 from the average to the upper border of the interval. In Carpaticum, it is the opposite (15–19). The comparison of the *EQ* method and the NFI II field survey in Hercynicum seems considerably problematic, as the zonal 5th FVZ range corresponds to up to six confidence interval values, which suggests that the mapping of the 5th FVZ has been done in macroclimate conditions of the 2nd–6th FVZs. This can be due to overestimating the actual tree composition (Zlatník 1955), given the fact that the recent representation of silver fir in the actual tree composition (including zonal sites) is very low in comparison with the site's vegetation potential (Novák, Dušek 2021; Remeš 2022).

Evaluation of the Hercynicum and Carpaticum spatial frames is fully justified in case of higher altitudes, defined by forest communities of the 6th and 7th FVZs. The potential natural tree composition consists of a mixture of spruce, fir and beech, which on the transition to the 8th (spruce) FVZ recedes into the understory (Průša 2001). Ellenberg and Leuschner (2010) label the presence of beech under the *EQ* = 10 (Table 1) as a subalpine beech forest. The intervals' values, set in the autochthonic stands with the presence of beech in both Hercynicum and Carpaticum, are generally higher and do not fall under the *EQ* = 10. A disproportion can be caused by the different ecological *Fagus* niche in the Alps (Ellenberg, Leuschner 2010). Mellert et al. (2016) list *EQ* = 9.5 as the minimal value of the intermediate value range, in which beech is consecutively present. However, the value for beech marginal occurrence is 7.7. Mikeska and Prausová (2013) state the values in the range of 21–10 for both FVZs, with the 8th FVZ's *EQ* < 10. According to this study, the growth of beech on zonal sites can only be reliably defined for the 6th FVZ in Carpaticum. The occurrence of higher FVZs is only marginal in Carpaticum, and only azonal sites with other than a production/commercial purpose are carefully mapped (Holuša, Holuša st. 2011). In Hercynicum, however, the occurrence of close-to-natural

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communities with beech has been monitored even in the 7th FVZ, which is generally caused by higher mountains (e.g. Jeseníky Mts., the Giant Mts., the Bohemian Forest).

Although beech can sporadically occur in the 8th FVZ as well (Průša 2001), in a field mapping practice, the presence of beech is used as a determinator for differentiating between the 7th and 8th FVZs.

The calculated intervals of the *EQ* values do, in our opinion, better correspond to the reality than the values listed in the work published by Mikeska and Prausová (2013), based on Hruban (2010). The value misalliance probably does not stem from a different nature of the climate data (the climatic normal of 1961–1990) as much as from an uncritical interpretation of the calculated values as well as a missing method for the *EQ* calculation. It is necessary to stress that the comparisons of the calculated FVZ values with those by Ellenberg and Leuschner (2010) are tentative, based on differently defined communities of two different classification systems. Therefore, we list them for the completeness of information but make no effort to evaluate the relevance of both classifications in relation to the study area.

The Ellenberg quotient could also be used for predicting the composition of communities with *Fagus* in connection to rapidly changing climate conditions, as was done in Serbia (Stojanović et al. 2013), Denmark (Jensen et al. 2004), Hungary (Mátyás et al. 2010), or southern Germany (Mellert, Šeho 2022).

CONCLUSION

The Ellenberg quotient is one of the currently applied climate indices with the potential of assessing possibly suitable climate conditions for the occurrence of European beech in forest communities. In the CZ, beech is utilized as an indicator in a vertical zonation of forests. Although attempts were made to apply this concept in forestry-typological mapping, their previous results are only informative.

This study presents intervals of the *EQ* values for vertical vegetation frames of the Czech (forest) vegetation which were calculated using objective data of the National Forest Inventory and which represented relatively intact forest communities with *Fagus sylvatica*. For the verification process of the analysis, we selected plots from the 'zonal sites' category, for which macroclimate is a significant gradient of tree vegetation growth and occurrence. The statistical comparisons showed not only disagreements in the FVZs' values but also differences in how the *EQ* climate index behaved within Hercynicum and Carpaticum.

Comparing the calculated *EQ* intervals with the results of the NFI field survey also pointed to the inconsistency between the sites' climatic potential and the FVZs' definitions. The results show that in the case of Carpaticum, the *EQ* values better correspond to the results of the NFI field survey. For Hercynicum, however, the results highlight the need for a more profound revision. The Ellenberg quotient seems to be a significant factor able to crucially contribute to the optimisation of the vertical vegetation zonality of the Czech Republic and similar spatial-functional patterns elsewhere. Aside from the possibility of revising the concept of vertical vegetation zonation, the *EQ* can also be an appropriate indicator for verifying prediction models of potential vegetation migration affected by climate change.

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