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# A GLMER-based pedotransfer function expressing the relationship between total organic carbon and bulk density in forest soils

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**Abstract:** Owing to its role in mitigating $CO_2$ in the atmosphere, the total organic carbon (TOC) stock of soil, a key component of the terrestrial carbon cycle, is of significant interest as regards climate change. To determine TOC stock, it is first necessary to determine the soil's bulk density (*BD*), determined through intact soil sampling; however, in forest soils, it can be difficult to determine *BD* in soils with high levels of stoniness and/or tree root coverage. Furthermore, the method is time-consuming and labour-intensive, making it impractical for studies over large areas. In such cases, *BD* can be determined using a pedotransfer function (PTF) expressing the relationship between forest soil TOC and *BD*. The aim of this study was to determine a forest soil PTF using actual data obtained from 777 soil pits dug as part of the Czech Republic's National Forest Inventory (NFI). Within the NFI, *BD* is assessed from undisturbed core samples, while TOC is assessed from mixed samples from the same soil genetic horizons. Both generalised linear (GLM) and generalised linear mixed-effects (GLMER) models were used, with the final GLMER model best expressing the relationship for individual natural forest areas within the NFI dataset. The GLMER-based PTF described in this study can be widely applied to accurately estimate soil *BD* via TOC concentration at temperate forest sites where stoniness and/or root cover previously made it technically impossible to take undisturbed samples using standard methods.

**Keywords:** carbon stock; climate change; Czech National Forest Inventory; Czech natural forest areas; soil properties; soil stoniness

The total organic carbon (TOC) stock stored in soil is a key component in the global carbon cycle. In terrestrial ecosystems, soil has the largest proportion of stored carbon (Davidson, Janssens 2006; Lorenz, Lal 2010; FAO 2020), with approximately 299 504 million tonnes present in soils around the world (FAO 2020). Overall, forests tend to be of more importance than agrarian systems

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in terms of both quality and quantity of carbon stock (Ferreiro-Domínguez et al. 2022; Valjavec et al. 2022; Teixeira et al. 2024), though both carbon quality and quantity can vary greatly in forests according to climate zone, vegetation type, land use and management regime (Waqas et al. 2020; Andreetta et al. 2023; Buczko et al. 2023; Mäkipää et al. 2023; Roth et al. 2023; Sahu et al. 2023; Wani et al. 2023).

Knowledge of soil TOC stocks and TOC fractions (Koorneef et al. 2023; Krahl et al. 2023; Wu et al. 2024), and how they change over time, is of increasing importance in the light of ongoing climate change as soil organic carbon capture plays an important role in mitigating increasing $CO_2$ concentration in the atmosphere (Scharlemann et al. 2014; Minasny et al. 2017). For example, increasing atmospheric $CO_2$ has been shown to increase the primary production of plant biomass, leading to an increase in soil TOC stock (Lloyd 1999; Schimel et al. 2015; Cheng et al. 2023; Ziegler et al. 2023). Alongside increasing $CO_2$ concentrations, however, there has also been a gradual increase in temperatures, which is of fundamental importance for TOC as higher temperatures increase the rate of organic material decomposition, potentially decreasing soil TOC stocks (Wiesmeier et al. 2013; Tashi et al. 2016; Kupka et al. 2023).

To obtain a general expression of soil TOC (as well as other elements, nutrient stock, water holding capacity or content of toxic substances), soil scientists apply equations based on the mass of nutrient per unit mass of soil, the thickness of the soil layer, the volume fraction of coarse stone fragments and the soil's bulk density (*BD*), defined as weight per unit volume (Huntington et al. 1989). *BD* is determined by measuring the weight of a dry soil sample of known volume sampled in such a way that the natural structure of the sample is undisturbed. This is most often accomplished using a 100 cm$^3$ steel cylinder, though other methods include the use of hammer probes (Walter et al. 2016) or reflectometry measurements (Bittelli et al. 2021). While the steel cylinder method is accurate, it is both time-consuming and laborious, making it unsuitable for studies requiring *BD* assessments over large areas. Furthermore, as the soil sample is obtained through 'spot sampling', the method is highly dependent on soil spatial diversity, meaning that many repetitions may be required to obtain representative values. Finally, *BD* assessment is often complicated by issues such as the presence of stones or rock fragments and extensive tree root systems (Throop et al. 2012), factors that can make it effectively impossible to obtain intact soil samples in forest soils. For example, while determining TOC stocks in forest soils for the second Czech National Forest Inventory (NFI) between 2011 and 2015 (FMI 2024), 5 659 organo-mineral and mineral soil horizons were sampled for chemical analysis (note: organic horizon bulk density was not determined in the NFI); however, it was only possible to obtain intact soil samples for *BD* from 1 945 of those horizons, or just 34.4%. Subsequently, samplers formulated an empirical rule that suggested if the soil horizon comprised > 25% stone fragments of 4 mm or larger, it would be practically impossible to obtain an intact sample as the stones, together with forest vegetation roots, created an impassable mechanical obstacle. As a consequence, TOC stock values for Czech forest soils were distorted by the reduced number of samples obtained.

A potential solution to this problem would be the use of a pedotransfer function (PTF) that allows the determination of soil properties (e.g. *BD*) from other soil properties or parameters, usually obtained more cheaply and/or less laboriously than classical methods (Van Looy et al. 2017; Szatmári et al. 2023). PTFs are predictive statistical models that use known relationships between different soil properties to express unknown or unobtainable properties. In our study, we use the relationship between *BD* and TOC concentration to establish estimated *BD* values for soils where core samples cannot be obtained. PTFs may also be complemented with other available covariates (e.g. random effects, as used in linear mixed models) to underline regional specificities in environmental conditions (de Souza et al. 2016; Al-Shammary et al. 2018). For example, in our area of interest, natural forest areas, which differentiate the territory of the Czech Republic based on specific regional differences in soil-forming rocks, terrain geomorphology, climate and altitude class, could be used to differentiate natural conditions.

The aim of this study, therefore, is to use a series of linear models to establish a generalisable PTF equation expressing the mathematical relationship between soil TOC concentration and *BD*, based on the wide range of organo-mineral and mineral

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bedrock/soil types represented in the third Czech NFI forest soil sample database (FMI 2024). To ensure accuracy, the PTF equations will be validated against known data from the area of interest (Nanko et al. 2014; Palladino et al. 2022). We hypothesise that (*i*) the much reduced mass ratio of soil organic matter to mineral matter in typical forest soils results in a negative relationship between TOC and *BD*, and (*ii*) the inclusion of natural forest areas (NFAs) as spatial identifiers in the models will provide a significantly better match to known TOC/*BD* data for the sites.

## MATERIAL AND METHODS

**Sampling methodology.** Data used to establish the TOC/*BD* relationship were obtained from the third NFI cycle, which took place between 2016 and 2020 (FMI 2024). The dataset, which was based on the NFI network covering all forests in the Czech Republic, contained *BD* and TOC as continuous variables with a spatial identifier as a categorical variable. Natural forest areas (NFAs; Figure 1) were chosen as the spatial identifier as they differentiate the territory of the Czech Republic based on regional differences in soil-forming rocks, terrain geomorphology and climate at a regional level (Plíva, Žlábek 1986). The NFAs were then further divided into altitude classes describing their geographic character based on relative elevation [Demek et al. 2006; Table S1 in the Electronic Supplementary Material (ESM)].

During the third NFI cycle, a complete soil survey was undertaken at each inventory plot, including excavation and description of a deep soil pit and sampling of organo-mineral and mineral pedogenic horizons greater than 2 cm in thickness and with a stone content of < 25% for analysis of chemical and physical soil properties. *BD* was determined at each site by drying undisturbed soil samples, collected with a 100 cm$^3$ steel cylinder at 105 °C for 24 h, after which reduced volumetric weight was calculated according to Equation (1):

$$BD = \frac{m}{V} \tag{1}$$

where:
*BD* – bulk density (g·cm$^{-3}$);
*m* – weight of the dried sample;
*V* – sample volume (100 cm$^3$).

The percentage content of soil TOC was determined by burning a soil sample in a stream of oxygen at 1 100 °C in a PRIMACSSLC single-purpose TOC analyser (PT Unitama Analitika Perkasa,

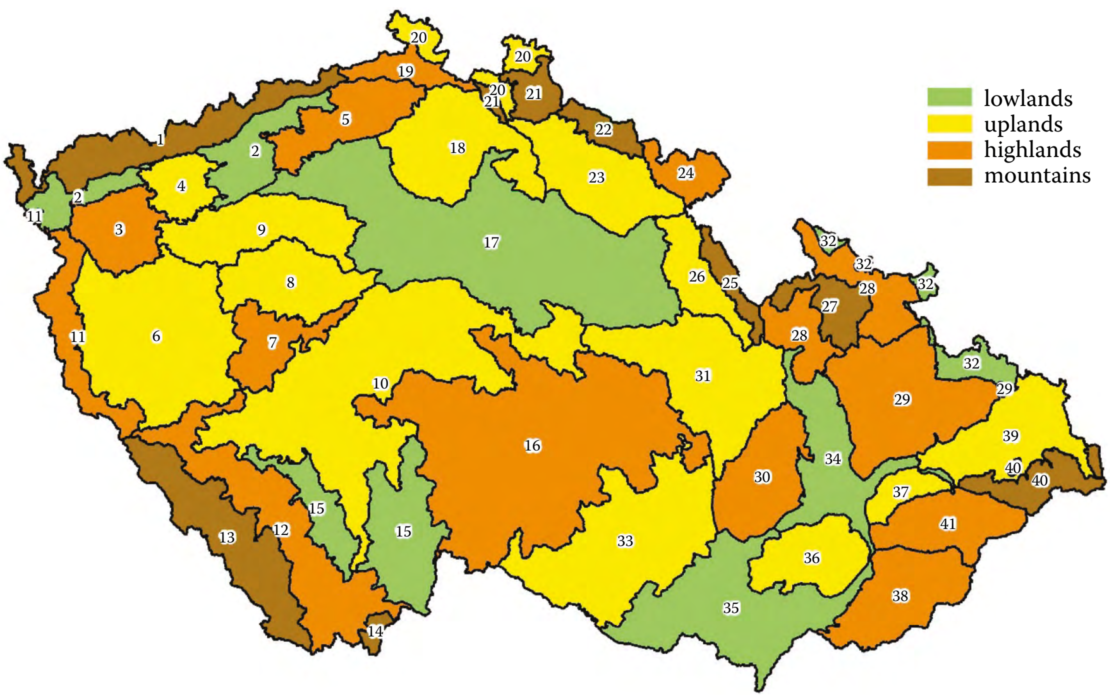


Figure 1. Natural forest areas (NFAs) used as spatial identifiers differentiating the territory of the Czech Republic

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Indonesia). TOC is thereby oxidised to $CO_2$, the concentration of which is measured using non-dispersive infrared detection (NDIR).

In total, data were obtained for 1 945 soil samples collected from 777 soil pits in 40 NFAs, the actual number of samples taken from each pit varying depending on the number of horizons, their thickness and the presence of stones. Unfortunately, no samples could be taken from NFA 4 (Doupov Mountains) as its relatively small area (69 711 ha) falls almost completely within a military training area. For obvious safety reasons (e.g. the presence of unexploded munitions), digging of soil pits and soil samples was prohibited in this area.

**Data analysis.** All *BD* data (both that directly assessed in the laboratory and that expressed by different models) were tested for normality using the Shapiro-Wilk test and, where data normality was not confirmed, the non-parametric Wilcoxon two-tailed test was used. The relationship between TOC and *BD* was then expressed using regression analysis (Meloun et al. 2005).

To find the most accurate expression of *BD* by TOC, we modelled *BD* using three different methods. As natural conditions, including edatopes, are specific to each NFA, the relationship between TOC and *BD* was first quantified using a generalised linear mixed-effect (GLMER) model including NFA as random effect. Next, we used the same GLMER excluding the random effect, i.e. using the global model only, and finally, we used the simplified generalised linear model (GLM). For the GLMER, statistical significance was assessed using the 'lme4' (Bates et al. 2023) and 'performance' (Lüdecke et al. 2024) packages within the R software environment (Version 4.3.1, 2023; R Core Team 2000).

Equation (2) below represents the general model equation:

$$y \sim \mathrm{TOC} + \frac{1 + \mathrm{TOC}}{\text{grouping 1}} \tag{2}$$

where:

$y$ – bulk density (*BD*);

TOC – total organic carbon – fixed effect;

grouping 1 – grouping variable of random effect [in this case, natural forest area (NFA)].

As the measured data were not normally distributed, and negative values are not allowed for transformed data, all data were transformed by Gamma transformation with inverse link function prior to analysis. Coefficients of determination were expressed as marginal $R^2$ ($R^2_{\mathrm{marg}}$), expressing the variability of the fixed effect only, and as conditional $R^2$ ($R^2_{\mathrm{cond}}$), expressing the variability of fixed and random effects. As, in many cases, NFA turned out to be a redundant component, the model was simplified to a global GLMER by removing the random effect.

To assess the significance of the random effect (NFA), the GLM was constructed as *BD* ~ TOC, using equal data transformation (gamma distribution with inverse link), with Akaike's information criterion (*AIC*; Akaike 1974) and coefficient of determination ($R^2$) used to assess model quality, the latter expressing how much of the total variance was explained by the model. In this case, the best model would have the lowest *AIC* value and highest $R^2$.

Graphic outputs were prepared using the 'ggplot2' package in the R statistical environment (Wickham et al. 2020), with box plots showing the 1st and 3rd quartiles and the median value and the whiskers 1.5 times the 1st and 3rd quartiles. All statistical tests were performed at a significance level of $\alpha = 0.05$.

## RESULTS

TOC values in the dataset had a strong left-sided distribution, with more than 1 200 of the 1 945 total samples (i.e. 62%) having a TOC value of < 2% (Figure 2A). In comparison, *BD* data for reduced soil samples displayed a slightly right-skewed distribution (Figure 2B).

For individual NFAs, most areas had > 75% of all TOC values at < 5%, with just four NFAs (NFAs 13, 14, 22, and 27) having noticeably higher TOC concentrations (Figure 3A). Interestingly, the distribution of *BD* in individual NFAs indicated that the four NFAs with the highest TOC content had the lowest *BD* values (Figures 3A, B).

Overall, the GLMER expressed approximately 65% of total variability when both fixed and random effects were included, and approximately 61% of variability when only fixed effect was included (Table S2 in the ESM). While the GLM accounted for approximately 55% of variability, the GLMER *AIC* value was markedly lower than that for GLM (–682.99 *vs.* –850.4; Table S2 in the ESM).

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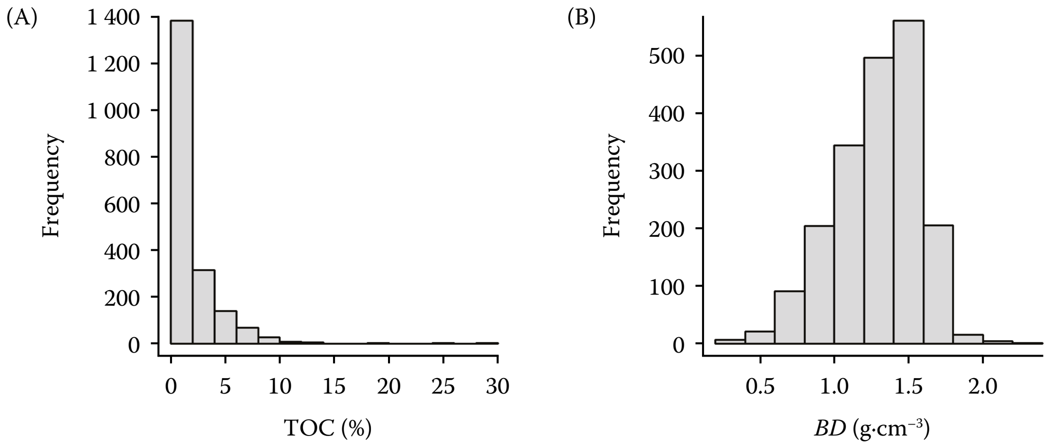


Figure 2. Distribution of soil (A) total organic carbon (TOC) values and (B) bulk density (*BD*) in the third National Forest Inventory (NFI) dataset

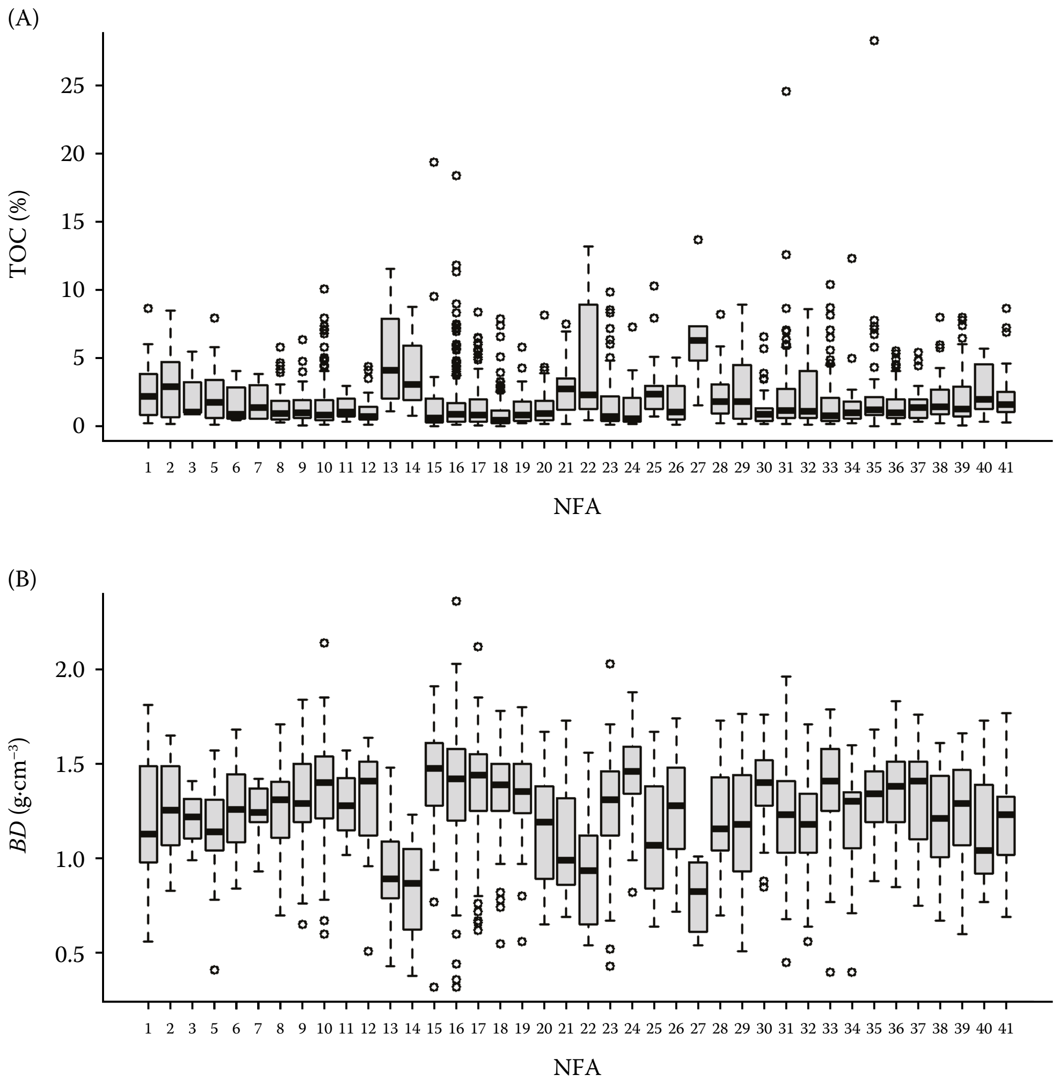


Figure 3. Box plots showing the distribution of (A) soil total organic carbon values (TOC) and (B) bulk density (*BD*) for individual natural forest areas (NFAs)

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The resulting equations for *BD* and TOC after fitting the global model parameters are presented below as Equations (3) and (4):

$$BD = (b + a \times \text{TOC})^{-1} \quad (3)$$

$$\text{TOC} = \frac{1}{a \times BD} \times \frac{b}{a} \quad (4)$$

where:

$a$ – slope (0.088349);

$b$ – intercept (0.668562).

When NFA was included as random effect, the equation then became Equation (5):

$$BD = [(b + b_{\text{NFA}}) + (a + a_{\text{NFA}}) \times \text{TOC}]^{-1} \quad (5)$$

where:

$a_{\text{NFA}}$ – slope of the random effect;

$b_{\text{NFA}}$ – intercept of the random effect.

A comparison of the TOC/*BD* regressions produced by the GLM and global GLMER provided very similar results (Figure 4), with the GLM intercept being only slightly higher than that for GLMER with a systematic shift of ca. + 0.2 g·cm$^{-3}$ on the *y* axis.

At the NFA level, the regressions were even closer, with GLM and GLMER regressions for almost all NFAs (except NFA 14 Novohradské Mountains) overlapping (Figure 5). In almost all cases, both models showed a high degree of determination, as indicated by the very narrow 95% confidence intervals.

Individual NFAs differed significantly in both the number of locations sampled and the range of both TOC and *BD* values ($P < 0.05$ for both slope and intercept in all cases; Figure 5), with the lowest maximum TOC value (approx. 3%) recorded at NFA 11 (Bohemian Forest) and highest (approx. 19%) at NFA 15 (South Bohemia Basins). Though values this high occurred only rarely, NFA 13 (Šumava Mountains) displayed consistently higher TOC concentrations than all other sites.

When comparing the GLMER and laboratory-measured results for *BD*, values for most NFAs were

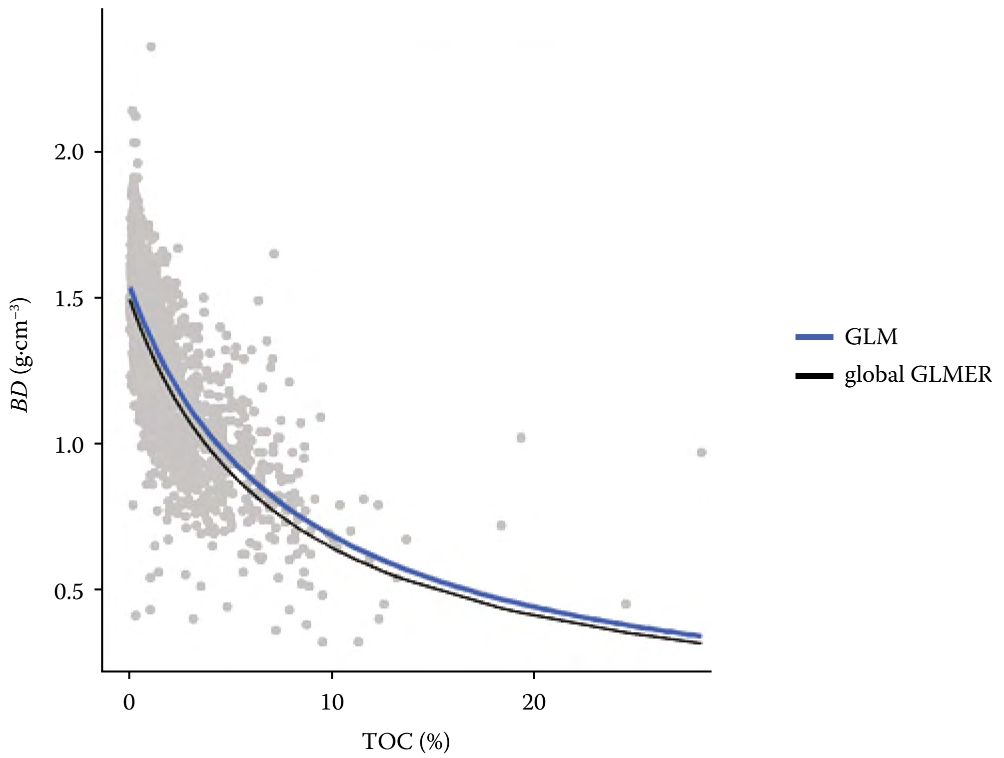


Figure 4. Comparison of results for the global generalised linear mixed-effects model (global GLMER) and generalised linear model (GLM)

*BD* – bulk density; TOC – total organic carbon

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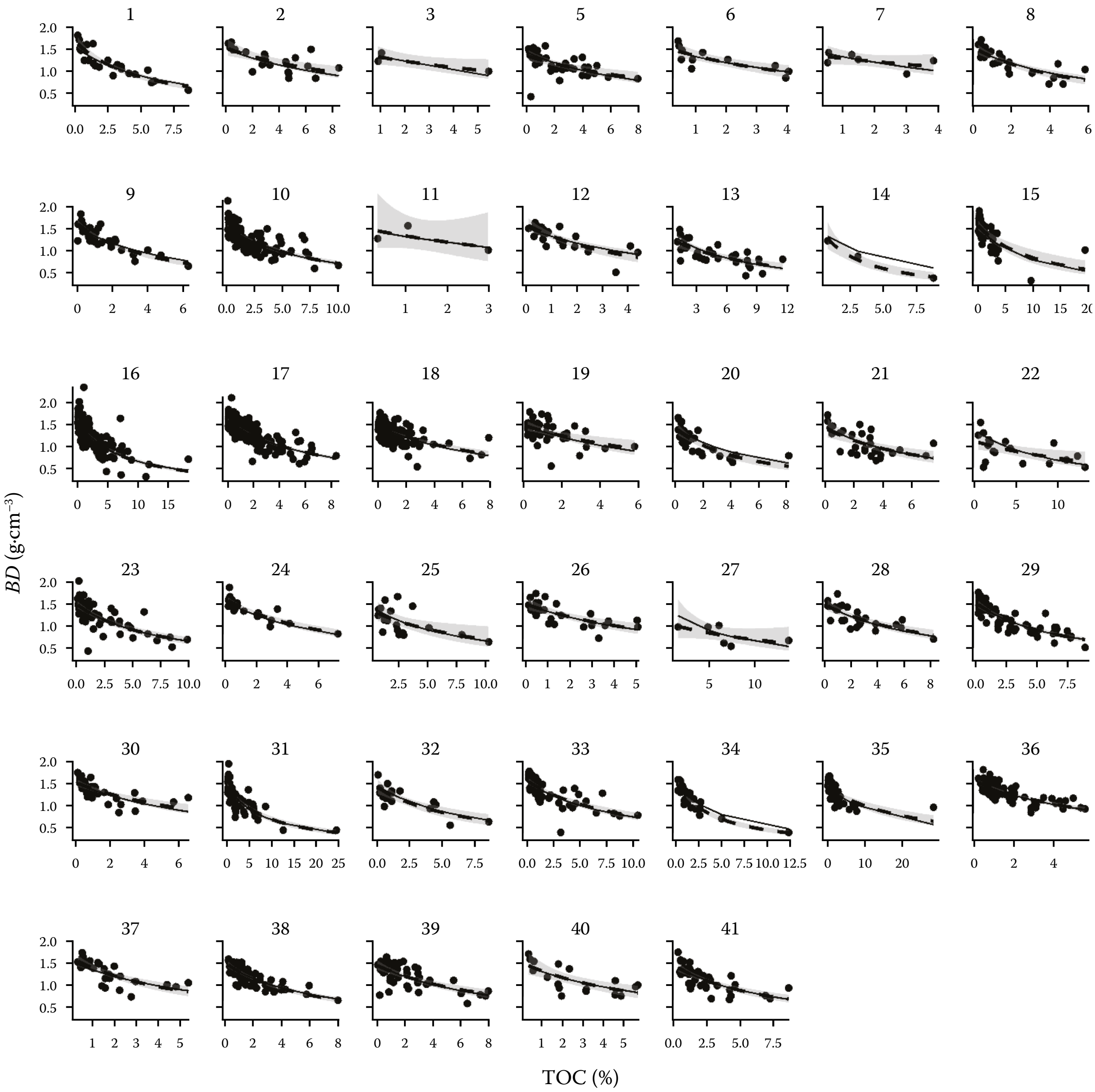


Figure 5. Comparison of generalised linear mixed-effects model (GLMER, solid line) and generalised linear model (GLM, dashed lines with confidence intervals) runs for each natural forest area (note strong overlap)

Grey shaded area – 95% confidence levels; points – measured laboratory values; *BD* – bulk density; TOC – total organic carbon

very close, with median residual values close to zero and delta only exceeding ± 0.5 g·cm$^{-3}$ exceptionally (eight values < –0.5 and ten values > 0.5; Figure 6). When expressed as percentage difference, however, these numbers were reduced, with seven NFAs displaying values more than 100% higher than laboratory values, and just two (NFAs 5 and 23) more than 200% higher. An exceptional case was the values for NFA 14 (Novohradské Mountains), where a large difference between laboratory and model values was probably due to the low number of values measured ($n$ = 3), one of which was very low ($BD$ = 0.38 g·cm$^{-3}$).

A summary comparison of GLMER and GLM residuals as absolute and percentage values for all NFAs combined confirmed the GLMER model as more accurately describing the *BD*/TOC relationship (Figures 7A–D). While all medians were close to zero, as with the GLMER model, percentage residual values for the global GLMER and GLM

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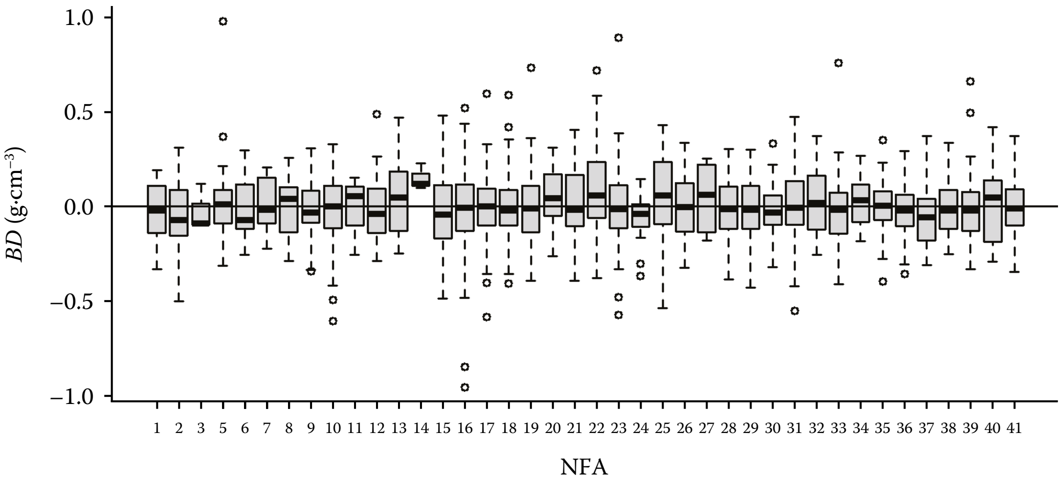


Figure 6. Box plots showing differences between modelled and laboratory-measured bulk density values for each natural forest area (NFA), calculated using the generalised linear mixed-effects model (GLMER)

*BD* – bulk density

models were skewed, with 16 values exceeding 67% difference (maximum percentage among negative residual values; Figure 7B). However, GLM residuals displayed a wider range of positive and negative values, with values exceeding 250% (Figures 7C, D). As these outliers did not originate from less-represented NFAs with a low number of values (e.g. NFA 14), they clearly represent increased variability in edaphic conditions.

Regressions expressing the relationship between laboratory-measured *BD* and GLMER-modelled *BD* for individual NFAs indicated that, for almost all NFAs, the model provided an excellent fit to the pre-measured data, though both the model and measured data fell slightly below the ideal curve (Figure 8). Exceptions included NFA 22 (Krkonoše Mountains) and NFA 27 (Hrubý Jeseník Mountains), which displayed a higher intercept and lower slope, while NFA 14 (low number samples) had a lower intercept but an almost ideal slope. In all these cases, however, the ideal curve still lay within the 95% confidence intervals. Overall, the results suggest that while model quality is not necessarily dependent on the

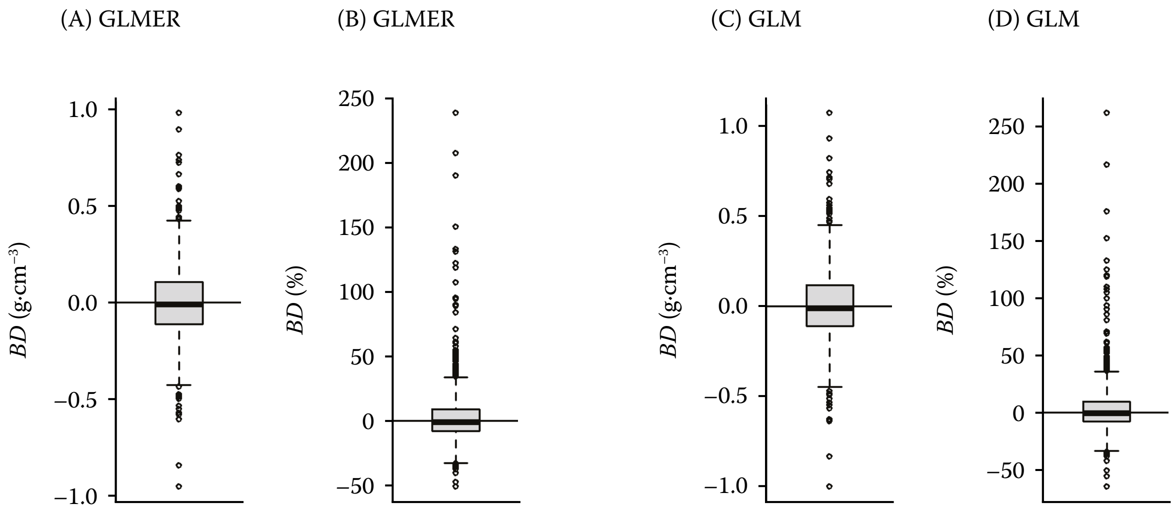


Figure 7. Box plots showing residuals for the generalised linear mixed-effects model (GLMER) as (A) absolute values and (B) percentage, and generalised linear model (GLM) as (C) absolute values and (D) percentage

*BD* – bulk density

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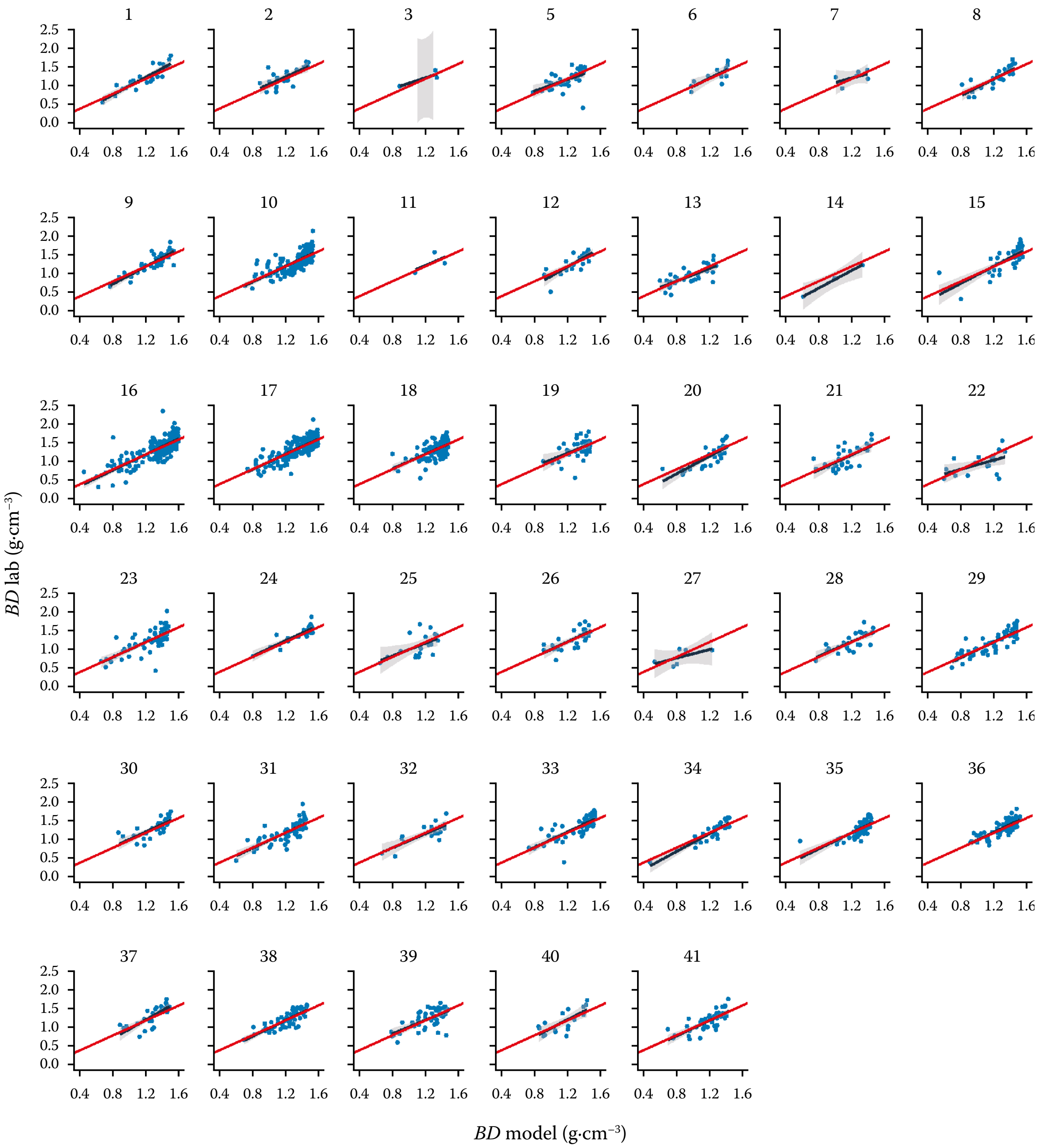


Figure 8. Regressions for laboratory-measured bulk density (*BD* lab) and GLMER-based *BD* model, for individual natural forest areas

The red line represents the ideal match between measured and theoretical values; thus, if the points in the graph lie exactly on the straight line, the measured and model values are the same

number of samples, its range of applicability may be low for NFAs with few values, e.g. NFA 3 (Karlovy Vary Highlands).

In almost all cases, there was no significant difference between data sets of different origins grouped by NFA ($P > 0.05$; Figure 9). Note, however, that significant differences were recorded between GLMER and GLM ($P < 0.05$) and between laboratory values and GLMER ($P < 0.05$) for NFAs 16 and 17 (Figure 9).

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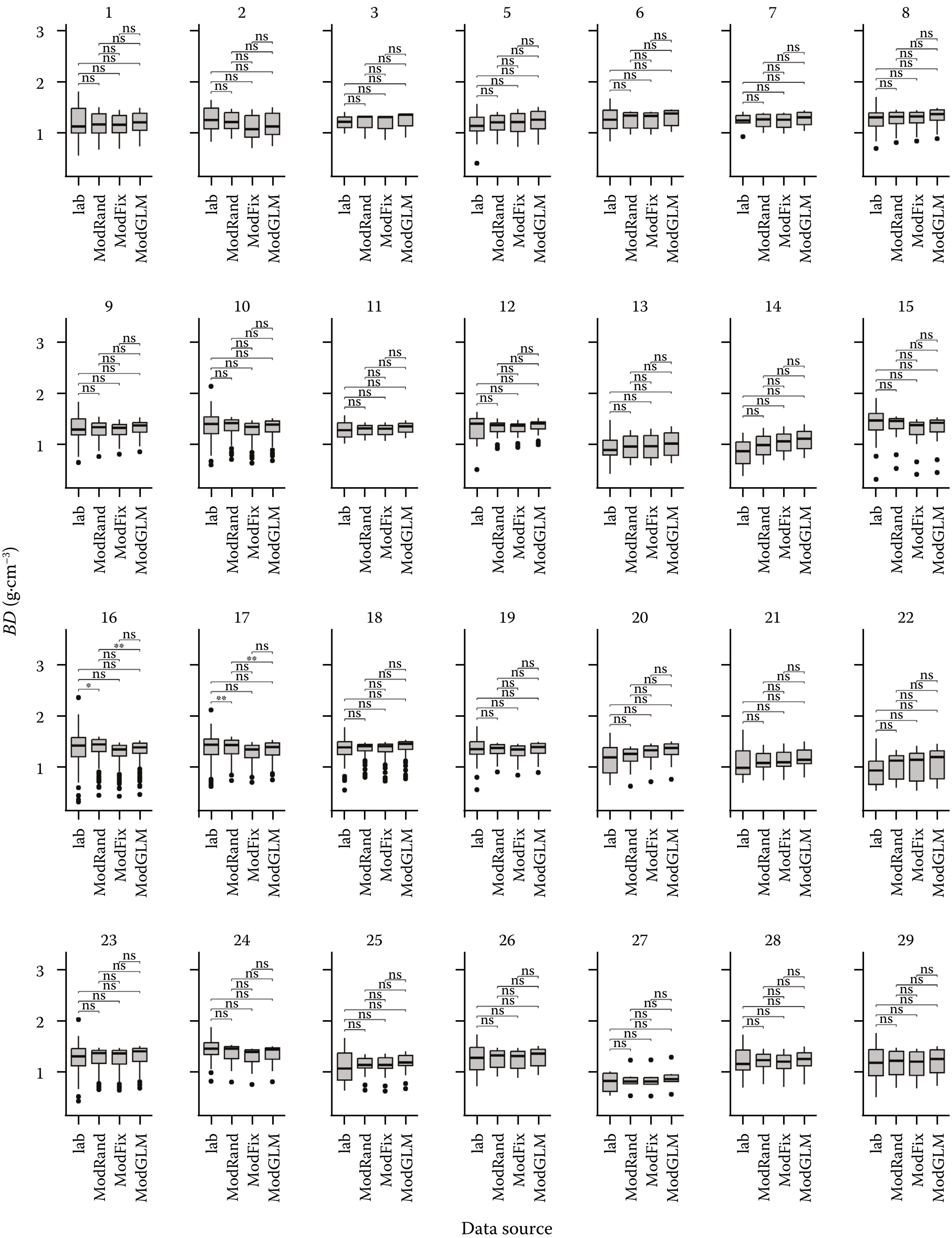


Figure 9. Wilcoxon two-tailed tests for data sets of different origins grouped by individual natural forest areas; box plots show bulk density (*BD*) calculated using (*i*) laboratory-measured values (lab), (*ii*) the generalised linear model with random effects (GLMER; ModRand), (*iii*) the global GLMER including fixed effects only (ModFix), and (*iv*) the simple generalised linear model (ModGLM)

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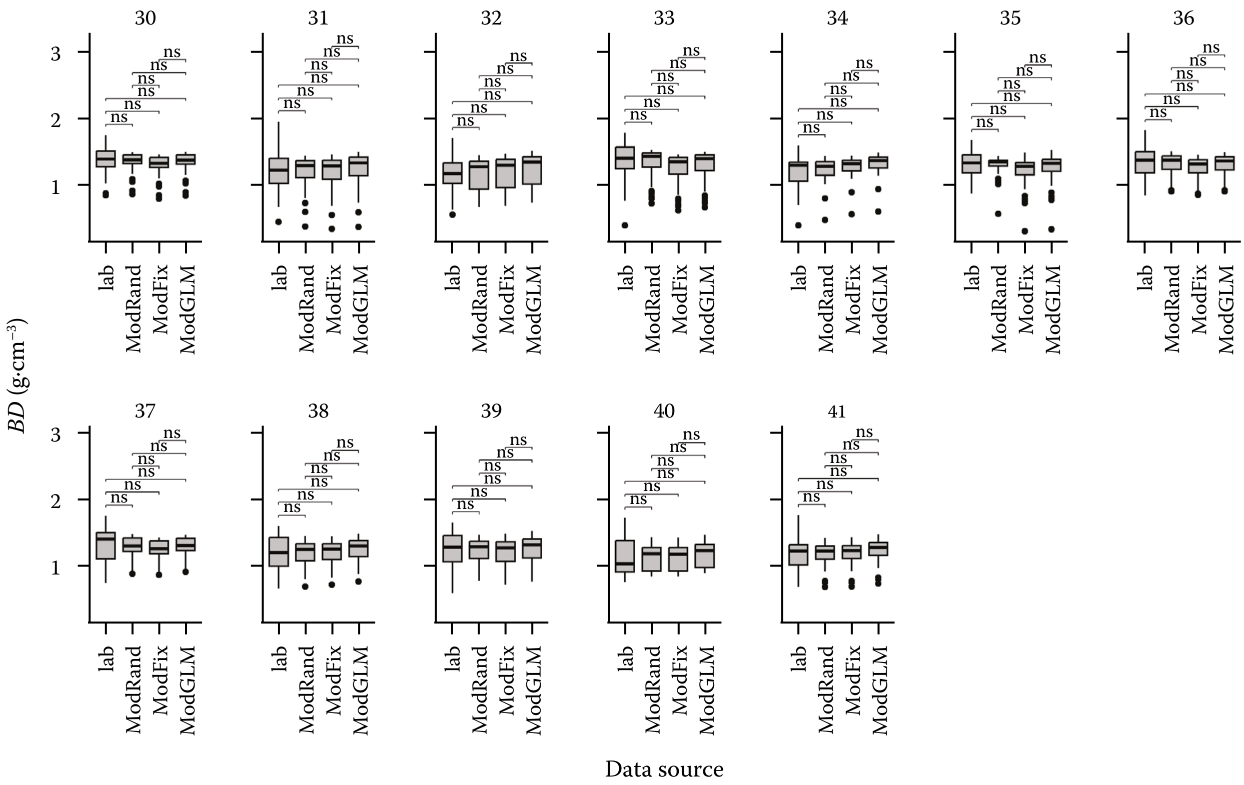


Figure 9. To be continued

*$P$ = 0.01–0.05; **$P$ = 0.001–0.01; ns – not significant

## DISCUSSION

TOC values at NFAs 13 (Šumava Mountains), 14 (Novohradské Mountains), 22 (Krkonoše Mountains) and 27 (Hrubý Jeseník Mountains) were all markedly higher than those at other sites, while those at NFA 1 (Ore Mountains), NFA 21 (Jizerské Mountains), NFA 25 (Orlické Mountains), NFA 29 (Nízký Jeseník Mountains) and NFA 40 (Moravskoslezské Beskydy Mountains) all being slightly higher. Notably, all of these NFAs are sited in mountainous areas. These results align with those of Sarkodie et al. (2023), who also recorded higher TOC concentrations in mountainous areas and concluded that altitude was the most important parameter for predicting TOC stocks in Czech forest soils. A similar relationship between altitude and increased soil TOC has also been observed in other parts of the world (e.g. Tashi et al. 2016; Chen et al. 2023). In our case, however, altitude may be considered a surrogate parameter as the actual amount of TOC in soil will have been heavily influenced by climatic factors, such as temperature and/or humidity (Bu et al. 2012; Wiesmeier et al. 2013; Kupka et al. 2023), which are strongly correlated with altitude (Drewnik 2006). On the other hand, we also recorded high TOC values at NFA 2 (Podkrušnohorské Basins), a low-altitude area. In this case, the high TOC values could be attributed to the forest stands being located on areas reclaimed from surface mining of brown coal. More than half of the samples taken at NFA 2 came from Technosols, some of which had TOC values far above average levels for natural forest soils, presumably caused by the mine waste and materials brought in for site reclamation.

As hypothesised, we observed a clear negative mutual dependence between *BD* and TOC in Czech forest soils (Figures 3A, B), with the lowest *BD* values (NFA 13, 14, 22, and 27) found in areas with highest TOC values and, conversely, areas with lower TOC values having higher *BD* values. This same negative correlation between *BD* and TOC was also confirmed by Stavi et al. (2008), Patton et al. (2019), Harbo et al. (2022), and Xiao et al. (2024).

A range of different methods have been used in the past to express this negative relationship between *BD* and TOC, including non-linear ex-

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ponential models (Harbo et al. 2022), multiple linear regressions (Palladino et al. 2022) and GLMs (Stavi et al. 2008). There have also been a number of studies comparing several different models for expressing the *BD*/TOC relationship on the same dataset, e.g. Crnobrna et al. (2022), who tested nine different models and found the 'ideal mixing model' to be best, and Sevastas et al. (2018), who compared 56 models and found the 'regression tree-based model' to be most accurate. In our own study, we compared GLMER and GLM models on a standard dataset and found that, overall, GLMER provided the best fit to the dataset due to the positive influence of using NFAs as a random effect in the model. In this case, the model considers the influence of regional and local differences in natural conditions, e.g. geological substrate and soil, in each NFA, rather than using averaged conditions for the whole Czech Republic. Nevertheless, we found close agreement between mean *BD* values expressed by the GLMER and GLM models (Figure 9), the only exceptions being NFA 16 (Bohemian-Moravian Highlands) and NFA 17 (the Polabí region), both of which had a high number of repetitions (NFA 16 = 218, NFA 17 = 206). At NFA 16 in particular, both TOC concentration and *BD* fell within the higher range of values, presumably due to the more diverse natural conditions found at this site. While differences in the mean values differed by ± 0.015 $g \cdot cm^{-3}$, differences at the other NFAs were even more pronounced, suggesting that the ecological significance of differences in mean values were comparable with those for median values. As such, the values may be considered marginal in comparison to overall variability in the inventory data in relation to forest stand edatope ecological characteristics. Similar conclusions were also reported by Tellen and Yerima (2018), who found that the marginality of variability was up to one order of magnitude higher in a study testing soil properties in relation to different types of land use.

## CONCLUSION

In this study, we compared three linear models (GLM, GLMER with and without random effects) to establish a PTF equation expressing the relationship between soil TOC concentration and *BD*, based on the organo-mineral and mineral bedrock/soil types presented in the third Czech NFI forest database (FMI 2024), calibrating and validating the model outputs against known data to ensure accuracy.

The PTF based on a GLMER with NFAs as mixed (random) effect provided best overall results (explaining 65% of variability). While differences in output between GLMERs with and without random effects were not great, the inclusion of Czech natural forest area (NFA) data as a random effect to differentiate regional differences provided noticeably better results, thereby confirming our hypothesis. It should be noted, however, that while our *BD* test samples were obtained from undisturbed core samples, as in previous studies (Huntington et al. 1989; Périé, Ouimet 2008; Sakin 2012), TOC content was assessed from a mixed (disturbed) sample, though both were obtained from the same genetic horizon. As such, the model parameters may not have the same predictive power as one where *BD* and TOC values originate from the same sample, though further tests will be needed to confirm this (Kučera et al. 2024).

Overall, therefore, the validated PTF put forward in this paper can be used with confidence to provide accurate assessments of *BD* from TOC, or *vice versa*, from a variety of organo-mineral and mineral temperate forest soils, particularly in those areas where stony soils or extensive root systems have previously prevented collection of standard intact soil samples, and allow more accurate determination of conservation and climate change factors, such as whether forest soil TOC differs between lowland, hilly and mountainous areas or over time.

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